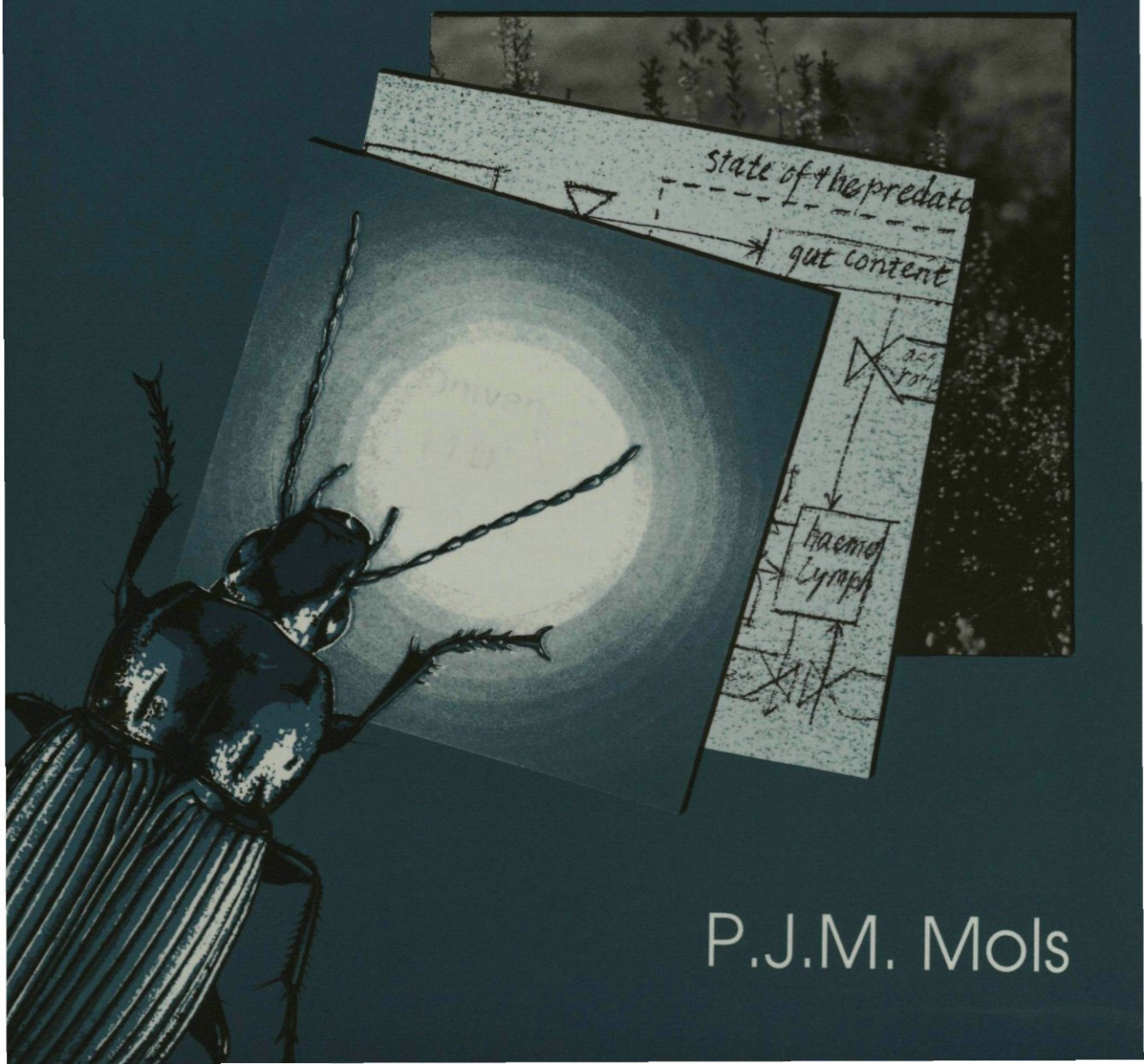
WALKING TO SURVIVE

Searching, feeding and egg production
of the carabid beetle *Pterostichus coerulescens* L.
(= *Poecilus versicolor* Sturm)



P.J.M. Mols

WALKING TO SURVIVE

Searching, feeding and egg production of the carabid beetle *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm).

P.J.M. Mols

PROEFSCHRIFT

ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
Dr. C. M. Karssen,
in het openbaar te verdedigen
op vrijdag 22 oktober 1993
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen

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STELLINGEN

1. De loopaktiviteit van de loopkever *Pterostichus coerulescens* L. wordt in de reproduktieve fase voornamelijk bepaald door temperatuur en hongerniveau.
   Dit proefschrift.

2. Bij *Pterostichus coerulescens* L. alleen de darminhoud gebruiken als maat voor de motivatie tijdens zoekgedrag is niet voldoende. (Ook de reserves en de in het lichaam aanwezige eieren moeten er bij betrokken worden.)
   Dit proefschrift.

3. Het aantal loopkevers dat in een bodemval wordt gevangen is afhankelijk van: type val, populatiedichtheid, klimatologische condities, lokale struktuur van bodem en vegetatie en hongerniveau van de kevers.
   Dit proefschrift.

4. De vorm van de functionele responsecurve wordt vaak sterk bepaald door de experimentele omstandigheden en is dan onbruikbaar voor het weergeven van de predator-prooiinteraktie.
   Dit proefschrift.

5. Polyfage predatoren spelen een grote rol bij de bestrijding van plagen.
   Wratten, S.D. (1988). In:"Ecology and effectiveness of aphidophaga", (Niemczyk,E. & Dixon A.F.G. eds), 161-173.
   Mueller,T.F., L.H.M. Blommers & P.J.M.Mols (1988). Entomol. exp. appl.47: 145-152.
   Walde,S.J., J.P.Nijrop and J.M.Hardman (1992). Exp. & Appl. Acarol., 14, 261-291.

6. Hardlopers zijn geen doodlopers.
   Dit proefschrift.

7. Bij een lineaire relatie tussen intrinsieke ontwikkelingssnelheid van een populatie (r_m) en de temperatuur, verdient het aanbeveling r_m uit te drukken als relatieve groei per daggraad boven een ontwikkelingsdrempel.

8. Doordat roofmijten kunnen overleven en zich kunnen voortplanten op pollen zijn ze zo succesvol bij de bestrijding van fruitspint.
   Schausberger,P. (1992). J. Appl. Ent., 113, 476-486.
   Duso,C., Camporese,P. (1991). Exp. & Appl. Acarol.,13,117-128.

9. Het inbouwen van toxinegenen van *Bacillus thuringiensis* in planten vergroot sterk de kans op het verloren gaan van een waardevol selektief insekticide.
McGaughey,W.H. and M.E. Whalon (1992). Science, 258, 1451-1455.

10. Zonder selektieve insekticiden is geen geintegreerde bestrijding mogelijk.

11. Het publiceren van ieder voorlopig resultaat, maakt het voor collega's steeds moeilijker om overzicht te houden, vergroot de papierberg en is daarom mens- en milieuonvriendelijk.

12. De in de politiek dikwijls gebruikte term "no nonsense" duidt vaak meer op no sense.

13. Boeken zijn de kleren van de intellektueel.

Stellingen behorende bij het proefschrift "Walking to survive. Searching feeding and egg production of the carabid beetle *Pterostichus coerulescens* L. (=*Poecilus versicolor* Sturm)", door P.J.M. Mols.

Wageningen, 22 oktober 1993.

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VOORWOORD

Het in dit proefschrift beschreven onderzoek was een samenwerking tussen de vakgroepen Theoretische produktie-ecologie en de toenmalige sektie dierecologie van het Biologisch Station Wijster. Het praktische gedeelte is voor het merendeel op het Biologisch Station uitgevoerd, het theoretische gedeelte heeft vooral later zijn beslag gekregen op de vakgroepen TPE en Entomologie. In het begin zou prof. dr. C.T. de Wit mijn promotor zijn maar later heeft prof. dr.ir R. Rabbinge deze rol met verve overgenomen. Dr P.J. den Boer heeft als co-promotor een grote rol gespeeld bij de initiering en begeleiding van het onderzoek. Hiervoor dank ik hen van harte, omdat zij mij geleerd hebben het kaf van het koren te scheiden en de resultaten van het onderzoek en gedachtengang daarbij ook voor anderen inzichtelijk te maken. Rudy, je persoonlijke belangstelling voor mij, mijn gezin en het onderzoek, de stimulans die er van je uitging om de zaken af te ronden en het daarbij gestelde vertrouwen in de goede afloop heeft zeer veel bijgedragen aan dit uiteindelijke resultaat en ik ben je daar zeer dankbaar voor. Piet je hebt mij ingeweid in de geheimen van de risicospreiding, je was altijd bereid een discussie aan te gaan, hoewel ik daar achteraf gezien te weinig gebruik van heb gemaakt. Je kommentaar op de aangeleverde teksten was veelal grondig en uitgebreid, waarmee je mij op het goede spoor hebt gehouden. Ook Wil den Boer dank ik hierbij voor de hartelijke ontvangst thuis als ik met Piet de zaak kwam doorpraten.

Van de collega's op het Biologisch Station was het vooral Theo van Dijk die mij met veel enthousiasme en met raad en daad heeft begeleid bij de praktische uitvoering van de experimenten. Dankbaar heb ik van zijn ervaring gebruik gemaakt waardoor ik nu meer inzicht heb in het carabiden gebeuren. Ide Jongema verzamelde en kweekte de beesten die door mij weer geofferd werden aan de wetenschap. Theo en Ide zeer hartelijk bedankt daarvoor. De tijd die ik op het Biologisch Station heb doorgebracht was een van de leukste periodes van het onderzoek, mede ook door de hartelijke sfeer die er heerste, daarvoor dank ik ook alle andere medewerkers die er vertoefden. Natuurlijk droegen ook de toenmalige studenten daar hun steentje aan bij zoals: Froukje Balk, Richard Daamen, Mark den Does, Marianne Inkelaar en Richard Stouthamer. Zij allen brachten leven in de brouwerij, verdiepten met hun discussies mijn inzicht in de materie en leverden een gedeelte van de onderzoeksresultaten af die in dit proefschrift verwerkt zijn. Ik ben hen daarvoor zeer dankbaar.

Mous Sabelis bedank ik ook hier speciaal, omdat hij mij geholpen heeft met de eerste opzet van het loopprogramma, wat later, mede door Richard Stouthamer, is uitgegroeid tot het uiteindelijke simulatie programma van het loopgedrag.

De vakgroep Entomologie en met name Joop van Lenteren wil ik bedanken voor het bieden van de gelegenheid om het proefschrift af te ronden. Piet Kostense ontwierp de prachtige omslag van dit proefschrift, ook daarvoor dank ik hem.

Rita, Jorn, Arvid en Floortje mijn zeer speciale dank omdat zij het meeste te lijden hebben gehad van de groei van dit proefschrift. De zwangerschap van Rita gaf de inspiratie tot het concept 'Potje vol' wat later als het motivatiemodel de wereld is ingegaan.

Mijn ouders bedank ik voor hun steun en voordurende aanmoediging.

Peter Mols
Augustus 1993

ALGEMENE INLEIDING

Voor ieder organisme is voedselopname een levensvoorwaarde om te kunnen groeien en zich voort te planten. Dieren die aktief op zoek gaan naar voedsel, voor zichzelf of voor hun nageslacht, maken daarbij verschillende keuzen betreffende de lokatie van zoeken, de tijd waarop en de soort voedsel die gezocht moet worden. Die keuzen bepalen de overlevingskans van het individu en zijn mogelijkheid om tot reproduktie te komen. Het is een voortdurende afweging tussen de kosten van het zoeken en de baten van het vinden en consumeren van voedsel. Daarbij wordt uitgegaan van de hypothese dat natuurlijke selektie de sturende kracht is die bij dieren die zoekmechanismen laat voortbestaan die leiden tot maximalisatie van het verschil tussen de baten en de kosten (Bell, 1990; Krebs & Davies, 1978), binnen genetisch haalbare grenzen. Bij dat zoekgedrag spelen een aantal faktoren een grote rol:

a) endogene soortspecifieke faktoren, die te maken hebben met de wijze van voortbewegen, de perceptie van prooi en prooihabitat en met de interne motivatie;
b) exogene biotische en abiotische faktoren, die de beschikbaarheid van de prooi bepalen, zoals de habitat waarin de predator en zijn prooi leven, met de vegetatiecompositie en de struktuur ervan en de daarin heersende (micro-) klimatologische condities die van grote invloed zijn op de snelheid waarmee allerlei levensprocessen zich afspelen.

In de natuur zijn vele organismen meestal niet homogeen of random verdeeld maar juist geaggregeerd (Southwood, 1966), als gevolg van plaatselijke verschillen in microklimaat, voedsel of als gevolg van voortplanting (bijv. bladluiskolonies). Vele soorten predatoren en parasitoiden lijken aan deze geaggregeerde verdeling van prooien en/of gastheren op de een of andere manier aangepast. Zij vertonen een specifiek gedrag wat het hen mogelijk maakt de geaggregeerd voorkomende prooien effektief te exploiteren (Carter et al., 1982; Curio, 1976; Nakamuta, 1985). Een van de aanleidingen voor deze studie was dan ook dat door Varley et al.(1973) gevonden was dat de mortaliteit van wintervlinderpoppen, die in de zomer en herfst in de grond te vinden zijn, voor een groot deel toegeschreven kon worden aan de vraataktiviteit van loopkevers en kortschildkevers. Wintervlinderpoppen komen zeer geaggregeerd voor onder hun waardplant en de predatoren zouden daarop effektief gereageerd hebben. De vraag kwam toen op : Hoe doen deze predatoren dat? Welke gedragseigenschappen spelen daarbij een rol en wat is dan de uiteindelijke predatie, meestal uitgedrukt als een relatie tussen prooidichtheid en predatie (functionele respons)? Deze vragen zijn voor andere predatoren en voor parasitoiden gesteld en ook al gedeel-

telijk beantwoord (Holling, 1966; v. Lenteren et al., 1976, Hassell, 1978, Arditi, 1983). Daarbij kan een algemene tendens m.b.t. het zoekgedrag naar prooien worden gedestilleerd. In het algemeen kan het zoekgedrag in een aantal fasen worden onderscheiden:

a) zoekgedrag naar prooihabitat
b) zoekgedrag in habitat naar prooi of prooiaggregaties
c) zoekgedrag in prooiklusters
d) zoekgedrag na prooiontmoeting/en of prooiconsumptie.

Het lokaliseren van de prooihabitat kan plaats vinden door random zoekgedrag maar ook door zich te orienteren op speciale eigenschappen van die habitat, zoals geur, kleur en vorm, temperatuur en vochtigheid van de habitat. Sommige natuurlijke vijanden gebruiken geen stimulus van de habitat maar zijn geheel gericht op de stimuli die rechtstreeks van de prooi uitgaan of van de prooi in combinatie met diens waardplant (Vet & Dicke, 1992). Eenmaal aangekomen in de prooihabitat wordt vaak het zoekgedrag aangepast van gericht naar een meer random zoekpatroon of een specifieke geur van prooi, of prooi-waardplant wordt gebruikt ter orientatie. In prooiclusters wordt vaak een sterk geconcentreerd looppatroon gevonden dat bij lage snelheid wordt uitgevoerd hetgeen tot een langer verblijf in de prooicluster en tot een hogere ontmoetingskans met prooien leidt.

Na een ontmoeting met een prooi volgt dan de prooibeoordeling leidend tot acceptatie of verwerping. Bij de zoek en beoordelings processen speelt de mate waarop de predator op de prooi gericht is (van mono naar polyfagie) een grote rol (Vet et al.1990). Deze gerichtheid bepaald ook gedeeltelijk op welke stimuli de predator of parasitoid normaliter reageert en ook of de hele sequentie van zoekgedrag (a-d) en acceptatie gevolgd zal worden. Over het algemeen wordt in de meeste experimentele studies slechts over relatief korte waarnemingsperioden (1 uur-1 dag) naar dit gedrag gekeken en de resultaten daarvan worden in een functionele of numerieke responscurve weergegeven. Deze curven worden dan gebruikt om het predatie-of parasiteringsgedrag over langere perioden te voorspellen. Met strukturele veranderingen in de motivatie (door groei of door uitputting van de eivoorraad), die juist gedurende langere perioden kunnen optreden, wordt meestal onvoldoende rekening gehouden waardoor overschatting van predatie/eiproduktie kan optreden. Dat is ook een van de redenen dat in deze studie er naar gestreefd is meer inzicht te krijgen in de processen die het individuele zoekgedrag sturen, waardoor het beter mogelijk wordt de rol van deze processen te evalueren en ook voorspellingen betreffende predatie onder een uiteenlopende reeks van externe omstandigheden (temperatuur, prooidichtheden en verdelingen) te kunnen maken. Het onderzoek aan het zoek- en predatiegedrag van de polyfage loopkever *Pterostichus coerulescens* L (= *Poecilus versicolor* Sturm.) volgt deze procesbenadering. Het richt zich op het prooizoekgedrag in de habitat, in de prooiclusters en op de prooiacceptatie in relatie tot de motivatie van de loopkever. Het volgt eerst de weg van de analyse, van motivatie en zoek- en acceptatie gedrag en poogt, na quantificering van de belangrijkste relaties met een simulatie-model uitspraken te doen over de predatie en eileg

gedurende een reproduktie periode, onder verschillende externe omstandigheden. De rol die de verschillende gedragingen daarbij spelen wordt daarbij geëvalueerd.

Deze benadering kan tot betere prognoses leiden betreffende de rol die een specifieke predator zou kunnen spelen bij de bestrijding van een plaaginsekt. Daarnaast wordt inzicht verkregen in randvoorwaarden voor overleving van lokale populaties en in de processen die ten grondslag liggen aan de ruimtelijke verspreiding van natuurlijk voorkomende predatoren hetgeen kan leiden tot een beter beheer van hun populaties in het veld.

ALGEMENE SAMENVATTING

Deze studie houdt zich bezig met het prooizoek- en vraatgedrag van een polyfage predator de loopkever *Pterostichus coerulescens* L (=*Poecilus versicolor* Sturm) een algemene soort van zandgronden. Deze loopkever vliegt zeer zelden, daarom speelt het prooi-zoekgedrag zich lopend af. De kever is dagaktief. Als onderzoeksobjekt leent dit soort predatoren zich prima omdat ze goed te hanteren zijn, hun gedrag is zonder veel hulpmiddelen waar te nemen (rechtstreeks en d.m.v. video) en ze zijn ruimschoots voorhanden. Over de biologie (van Dijk, 1979a, 1979b, 1982, 1986), populatiedynamica (Baars & van Dijk, 1984,a,b; den Boer, 1977) en de verspreiding van deze loopkever in het veld (Baars, 1979; den Boer, 1971) was al eerder onderzoek gedaan. Daarnaast is de rol van loopkevers als belangrijke natuurlijke vijand van een aantal akkerbouwplagen een punt van onderzoek waaraan deze studie ook wil bijdragen.

Het uiteindelijke doel van deze studie is dan ook: Het bestuderen van de rol van prooi dichtheid en -distributie op het zoekgedrag en de daaruit resulterende predatie en eiproduktie van de loopkever *P.coerulescens*.

De wijze waarop deze studie is aangepakt is m.b.v. systeemanalyse en simulatie. Allereerst werd het gedrag in een aantal hoofdcomponenten ontleed (zoekgedrag, acceptatiegedrag, vraatgedrag). Daarna werd gezocht naar sturende factoren ('de motivatie') voor deze gedragingen. Het onderzoek naar de motivatie, voedselopname en eiproduktie wordt in deel I van dit proefschrift besproken. De relaties van motivatie met zoekgedrag en prooiacceptatie vormen het onderwerp van deel II. Door middel van experimenten zijn de relaties tussen 'de motivatie' en de diverse gedragingen zoveel mogelijk gekwantificeerd en daarna geintegreerd in een simulatie model. Met behulp van simulaties is uitgezocht in hoeverre bij verschillende prooiverdelingen en prooidichtheden de diverse componenten van het gedrag bijdragen aan de functionele en numerieke respons door het simuleren van prooiontmoetings-, prooivangst- en eilegsnelheid.

Gedrag wordt beinvloed door externe en interne faktoren. De interne faktoren zijn afkomstig van de fysiologische conditie of toestand van de kever en zij vormen de 'motivatie' voor gedrag. Deze motivatie is het resultaat van de toestand van verschillende organen, maar is vooral sterk verbonden met voedselopname en vertering, die kwantitatief worden bepaald door lichaamsgrootte, maximale darmomvang, leegheid van de darm, het wel of niet reproduktief zijn enz. Deze interne toestanden worden beinvloed door externe faktoren waarvan de temperatuur en de daglengte de belangrijktste zijn. De leegheid van de darm is als maat genomen voor het hongerniveau van de kever, waarbij aangenomen is dat honger de belangrijkste motiverende faktor is in het predatieproces. De darmleegheid bleek door een complex van faktoren bepaald te worden die met elkaar

in nauwe relatie staan zoals: snelheid van voedselopname, vertering en defaecatie. De verteringssnelheid is afhankelijk van het wel of niet reproduktief zijn. De maaltijdgrootte is afhankelijk van de prooigrootte maar ook van de darmcapaciteit. De darmcapaciteit is op zijn beurt afhankelijk van de de maximale darmcapaciteit en van de ruimte die in het abdomen van de kever beschikbaar is. Deze beschikbare ruimte wordt bepaald door de omvang die andere organen in het abdomen innemen. De omvang van die andere organen zoals ovarien, het aantal rijpende eieren in het ovidukt, het vetlichaam voor de opslag van reserves wordt bepaald door de fysiologische toestand van de kever: in diapauze of in reproduktieve fase en natuurlijk ook door de hoeveelheid voedsel die in de loop van de tijd al is opgenomen. Om invloed van dit complexe geheel op het hongerniveau te kunnen begrijpen en te kunnen schatten is een simulatie programma ontwikkeld waarin deze faktoren zijn geintegreerd. Experimenten zijn uitgevoerd voor de bepaling van de verteringssnelheden bij verschillende temperaturen, de opname efficientie van voedsel, de repiratie snelheid bij verschillende temperaturen en de verblijfstijd van eieren in het ovidukt. De darmcapaciteit is bepaald in relatie tot de vulling van het abdomen door vetlichaam en door ovarien en rijpende eieren in het ovidukt. Met dit model is het mogelijk de motivatie van de kever te schatten bij een uiteenlopende reeks van toestandsvariabelen, terwijl de eiproduktie berekend kan worden in afhankelijkheid van de hoeveelheid voedsel die opgenomen wordt bij de fluktuerende temperaturen die in het veld voorkomen. Het hongerniveau uitgedrukt in RSATL (Relatieve verzadigingsniveau) kon op deze manier verbonden worden met de diverse gedragscomponenten die bij het predatieproces van de kever een rol spelen. Het hongerniveau heeft een sterke invloed op het aktiviteitsniveau van dè kever. Hongerige kevers (< 5% darmvulling) kunnen wel meer dan 5 uur per dag aktief zijn op zoek naar voedsel. Verzadigde kevers (> 80% darmvulling) daarentegen zijn maximaal een uur per dag aktief. Ook het loopgedrag blijkt sterk afhankelijk te zijn van het hongerniveau. De loopsnelheid van hongerige kevers is bij 20 °C ongeveer 2 maal zo hoog als bij kevers die meer dan 5% darmvulling hebben. Net als bij veel andere predatoren vertoont deze kever een intensief zeer draaierig zoekgedrag na consumptie van een prooi. De duur van dit intensieve zoekgedrag is afhankelijk van de darmvulling, hongerige kevers zoeken ongeveer 12 minuten intensief, terwijl boven 80% darmvulling dit intensieve zoekgedrag zich niet meer voordoet. De draaierigheid van het looppatroon hangt sterk samen met de loopsnelheid, naarmate de kever harder loopt neemt de draaierigheid af. De succes ratio (het aantal succesvolle ontmoetingen gedeeld door het totaal aantal ontmoetingen met een prooi) is afhankelijk van de prooisoort en van de darmvulling van de kever.

Allereerst is van het individuele zoekgedrag een simulatiemodel gemaakt, waarmee het gecombineerde effect van loopsnelheid (hard lopen bij honger, intermediair loopgedrag als er meer dan 5% darmvulling is en intensief zoeken met lage loopsnelheid na prooiconsumptie) en de draaierigheid op prooiontmoeting kon worden onderzocht. De voordelen van het intensieve zoekgedrag na consumptie van een prooi, van het hongerige hardloopgedrag en van het

intermediaire loopgedrag komt goed tot zijn recht bij geclusterde prooidichtheden. In een random prooiverdeling is het intensieve zoekgedrag van de kever na prooiconsumptie nadelig. Na koppeling van het motivatiemodel aan het zoek- en predatiemodel, waarin zowel het loopgedrag als de loopaktiviteit en succesratio zijn opgenomen, kan de functionele en de numerieke respons van de kever op prooidichtheidsverandering geschat worden voor diverse aggregaties van de prooi, zowel voor korte als voor lange tijdsperioden. De kever blijkt uitermate flexibel te reageren op veranderingen van prooidichtheid of mate van prooiclustering. Met dit volledige model blijkt dat het intensieve zoekgedrag slechts voordelig is bij lage geclusterde prooidichtheden (minder dan 1 prooi/m^2). Boven deze lage prooidichtheden werken de verschillende gedragingen compenserend op elkaar, zodat het uiteindelijke resultaat is dat het verdelingstype van de prooi m.b.t. predatie en eiproduktie slechts weinig invloed heeft. Vooral de duur van de loopaktiviteit compenseert gedeeltelijk het negatieve effect van intensief zoeken in random prooiverdelingen.

Bij deze simulaties komt het praktische nut van deze modellen naar voren. Door het stochastische karakter van de processen is het zeer moeilijk tot bijna onmogelijk dergelijke proeven in het laboratorium, laat staan in het veld, uit te voeren doordat er vele herhalingen vereist zijn voordat een betrouwbaar gemiddelde verkregen is. Terwijl experimenten met diverse prooiverdelingen, die zich over tijdsperiodes van een reproduktieseizoen uitstrekken, helemaal onuitvoerbaar zijn. Door terugkoppeling tussen de toestandsvariablelen van de kever treden juist over langere periodes effekten op waarvan de waarde moeilijk is in te schatten. Met behulp van deze modelbenadering is daar meer zicht op verkregen. Ook kan de betrekkelijke waarde van laboratorium experimenten m.b.t. functionele en numerieke responsen beter worden ingeschat.

Met behulp van de modellen kan een schatting gemaakt worden van de verspreidingssnelheid van de kever bij bepaalde voedseldichtheden en -verdelingen hetgeen van belang kan zijn om de uitwisseling tussen locale populaties te kunnen schatten. Dit laatste kan vooral bij natuurbeheer van groot belang zijn omdat bij onvoldoende uitwisseling maatregelen kunnen worden geformuleerd, die kunnen voorkomen dat locale populaties uitsterven.

GENERAL INTRODUCTION

For every organism, food consumption is a prerequisite for growth and reproduction. Animals that actively search for food, for themselves or for their offspring, make different choices concerning the location where to search, when to search and the kind of food to search for. These choices determine the individual's chances of survival and reproduction. The costs of searching are constantly being balanced against the benefits of finding and consuming food. This follows from the hypothesis that in animals natural selection is the driving force that leads to the survival of those searching mechanisms which maximize the difference between costs and benefits (Bell, 1990; Krebs& Davies, 1978), of course within attainable genetic boundaries. In such searching behaviour several factors play a role:

a) Endogenic factors specific to that species, concerning the way of moving, the perception and recognition of prey and prey habitat and the internal motivation;
b) Exogenic biotic and abiotic factors, that determine the availability of the prey, such as the composition and structure of the vegetation of the habitat in which the predator and its prey live, and the prevailing micro-climatological conditions that greatly influence the rate of all kind of biological processes.

In nature, because of local differences in micro-climate, food supply or as a result of reproduction (e.g. aphid colonies), many organisms are not homogeneously distributed but aggregated (Southwood, 1966). Many predator and parasitoid species seem to be adapted to this aggregated ditribution of prey or hosts in one way or another. They show a specific behaviour that makes it possible for them to exploid aggregated prey that effectively (Carter et al., 1982; Curio, 1976; Nakamuta, 1985). One of the reasons for the present study was the observation by Varley et al. (1973) that the mortality of the pupae of the winter moth, that are found in the soil during summer and autumn, could for a large part be attributed to the feeding activity of ground beetles and rover beetles. Pupae of the winter moth aggregate under their host tree and the predators seem to react to that very effectively. The question was raised of how these predators do this. What behavioural characteristics play a role and what is the ultimate predation, usually expressed as the relationship between prey density and predation i.e. the functional response? These questions have been asked for other predators and parasitoids and are already partly answered (Holling, 1966; v. Lenteren et al., 1976; Hassell, 1978; Arditi, 1983). From these answers some generalities can be made concerning the searching behaviour to prey. In general, different phases can be distinguished in searching behaviour:

a) location of the prey habitat
b) location of prey or prey aggregations in the prey habitat
c) searching in prey clusters
d) searching behaviour after encountering a prey or consuming one.

Location of a prey habitat can be achieved by random search or by orientation (directed search) to specific properties of the habitat such as odour, colour, form, temperature and humidity. Some natural enemies do not use stimuli associated with the habitat but are instead completely guided by stimuli that come from the prey itself, or from the prey in combination with its host plant (Vet & Dicke, 1992). Once they arrive in the prey habitat, their searching behaviour often changes from a directed to a more random searching pattern, or they use a specific scent of the prey or prey-host combination for orientation. In prey clusters, a strong area restricted search is often observed, carried out at low speed. This means a longer stay in the prey cluster which increases the chance of encountering prey. Prey encounter is followed by the determination of prey suitability leading to its acceptance or rejection. In the process concerning searching for and judging the prey, the degree of dependence on the type prey (from monophagous to polyphagous) plays a large role (Vet, 1990); to a certain extent, its diet also determines which stimuli the predator or parasitoid will react to and also whether the whole sequence of searching behaviour (a-d) and acceptance will be followed. In most of the experimental studies, the observations generally only last for short periods, (from one hour to one day) and the results are expressed as functional and numerical responses. These curves are used to predict predation or parasitization behaviour over longer periods. Hence, structural changes that affect motivation, by for example, increase or depletion of egg load, that may occur over longer periods, are largely not accounted fore, leading to overestimation of predation or egg production. This is also one of the reasons that in this study we have tried to obtain more insight into the processes that govern the individual searching behaviour, to make it easier to evaluate these processes and to predict predation under a range of external conditions (including temperature, prey density and prey distribution). Our research on the searching and predation behaviour of the polyphagous groundbeetle *Pterostichus coerulencens* L. (= *Poecilus versicolor* Sturm.) follows this process approach. It is directed at the prey searching behaviour in the habitat, in the prey clusters and at prey acceptance in relation to the motivation of the ground beetle. Firstly, we analysed the motivation for searching and acceptation behaviour and subsequently, after quantification of the major relationships, we tried, with a simulation model, to estimate predation and egg production over the reproduction period under different external conditions. The part behavioural components play during this period is evaluated. This approach can lead to better prognoses concerning the role played by a predator in the control of a pest insect. In addition, better insight is obtained into the conditions for the survival of local populations by the processes underlying the conditions of dispersal of natural occurring predators. This can lead to better conservation of their populations in the field.

SUMMARY

This study concerns the prey-searching and feeding behaviour of the polyphagous groundbeetle *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm), a common species on sandy soils. This ground beetle rarely flies, thus prey-searching behaviour involves walking. The beetle is diurnal. As object of research, predators of this kind are very suitable because they can be handled easily, their behaviour can be observed directly or filmed with a video camera. Furthermore they are abundantly available. Much research has been done on its biology (van Dijk, 1979a, 1979 b, 1982, 1986), population dynamics (Baars & van Dijk, 1984,a,b; den Boer, 1977) and dispersal in the field (Baars, 1979; den Boer, 1971). This study aims to contribute to the role of groundbeetles as important natural enemies of some agricultural pests. The ultimate aim of this study is to investigate the role of the density and distribution of the prey on the searching behaviour of the groundbeetle *P. coerulescens* and the resulting predation and egg production.

This study is tackled with the help of system analysis and simulation. Firstly, behaviour was divided in its major components of searching, acceptation and feeding. Subsequently the factors governing these components, the motivation, were for looked for. The investigation of the motivation, food ingestion and egg production will be discussed in part I of this thesis. The relationship between motivation and searching behaviour and prey acceptation are the subject of part II. The relationships between motivation and behavioural components were quantified experimentally as far as possible and subsequently integrated in a simulation model. How the different behavioural components take part in the functional and numerical response was sorted out with help of simulations concerning prey discovery, prey capture and egg production for a range of prey densities and different prey distributions.

Behaviour is influenced by external and internal factors. The internal factors are determined by the physiological condition or state of the beetle and they form the motivation for behaviour. This motivation results from the state of different organs and is strongly connected with food consumption and digestion, which are quantitatively determined by body size, maximum gut capacity, emptiness of the gut, whether reproductive or not etc. These internal states are influenced by external factors of which temperature and daylength are the most important. Assuming that hunger is the most important motivating factor in the predation process, the emptyness of the gut is taken as a measure of the hunger level of the beetle. It was found that the emptyness of the gut is determined by a complex of closely connected factors including the rates of food intake, digestion and defaecation. Digestion rate depends on the reproductive

state of the beetle. The size of a meal depends on prey size and on gut capacity. In turn gut capacity depends on maximum gut capacity and on the room in the abdomen of the beetle. How much room is available depends on the size of the other organs in the abdomen. The size of these other organs, for example the ovaries, number of maturing eggs in the oviduct, the fat body, for the storage of reserves, is determined by the physiological phase of the beetle, whether in diapause or in the reproductive phase, and of course by the quantity of food ingested in the course of time. To be able to understand and estimate the influence of this complex system at hunger level, a simulation programme was developed in which these external and internal factors are integrated. Experiments were carried out to estimate gut emptying rates at different temperatures, the assimilation efficiency, the respiration rate at different temperatures and how long the maturing eggs stay in the oviduct. Gut capacity was assessed in relationship to the filling of the abdomen by fatbody, ovaries and maturing eggs. With this model it is possible to estimate the motivation of the beetle under a range of state variables, while the egg production can be calculated in relation to the quantity of food ingested at fluctuating field temperatures. Hunger level expressed as relative satiation level (RSATL) could be related to the different components of behaviour that play a role in the foraging process of the beetle. Hunger level has a strong influence on the locomotory activity of the beetle. Hungry beetles (gut filled $<5\%$) can be actively in search for food for more than 5 hours per day. Satiated beetles (gut filled $>80\%$) are active for not more one hour per day. Also walking behaviour is strongly influenced by the hunger level. At 20 °C, the walking speed of hungry beetles is twice that of beetles with more than 5% of the gut filled. Just as many other predators this beetle shows an intensive, tortuous walking behaviour after consumption of a prey. The duration of this intensive searching behaviour depends on fullness of the gut, hungry beetles search for about twelve minutes intensively while this intensive search behaviour is absent when the gut is more than 80% full. How winding the walking pattern is depends on the walking speed, the faster the beetle walks the straighter its pattern. The success ratio (number of successful encounters divided by the total number of encounters with prey) depends on the prey species and on the relative satiation level of the beetle.

Firstly, a simulation model was constructed of the individual searching behaviour. With this model the effect of walking speed (fast in a hungry state, intermediate when the relative satiation level is more than 5% and tortuous after prey consumption) on the discovery of prey could be investigated. The advantages of the different walking types are best seen in aggregated prey distributions. In random prey distributions, intensive search after prey consumption is disadvantageous. By coupling of the motivational model to the searching and predation model, in which both walking behaviour, locomotory activity and success ratio are integrated, the functional and numerical response of the beetle to changes in prey density and prey distribution, both for short and for long periods, can be estimated. In this combined model the beetle seems to react very flexibly to changes in prey density or in prey aggregation. This model shows

that intensive search is an advantage at generally low prey densities (less than 1 prey/m^2) only when prey is aggregated. Higher than this low prey density, compensation for one behaviour by another occurs in such a way that prey distribution has hardly any effect on prey capture and egg production. Longer walking behaviour compensates partly for the negative effect of intensive search in random prey distributions.

During simulation, the practical use of these models is apparent. Because of the stochastic character of the processes, it is very difficult if not impossible, to carry out those experiments in the laboratory not mention those in the field, because they require many repetitions before we can have confidence in the means obtained. Besides, experiments with a range of prey densities and prey distributions, carried out over a season, are completely unpracticable. Over longer periods, feedback mechanisms between state variables of the beetle produce effects that are difficult to estimate. With the help of this modelling approach more insight into them is obtained. The value of laboratory experiments for estimating functional and numerical responses can be better assessed.

With the help of these models the area of the dispersal of beetles at specific food densities and distributions can be estimated, which may be important for assessing the exchange of individuals between local populations. Such data can be especially important in nature conservation because when not enough exchange takes place, measures can be taken to prevent local populations from becoming extinct.

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PART I

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

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CONTENTS

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

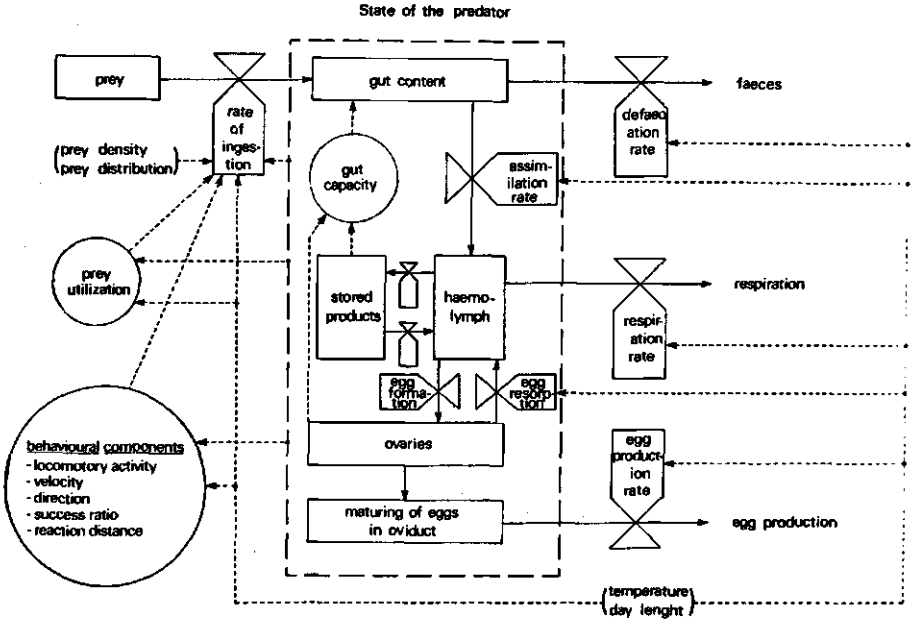


FIG. 1. Relational diagram of the 'motivational' state of the carabid beetle *P. coerulescens*. The rectangles indicate states, valves correspond with rates of change, ccircles with auxiliary variables, solid arrows with the flow of material, broken arrows with flow of information, and forcing variables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

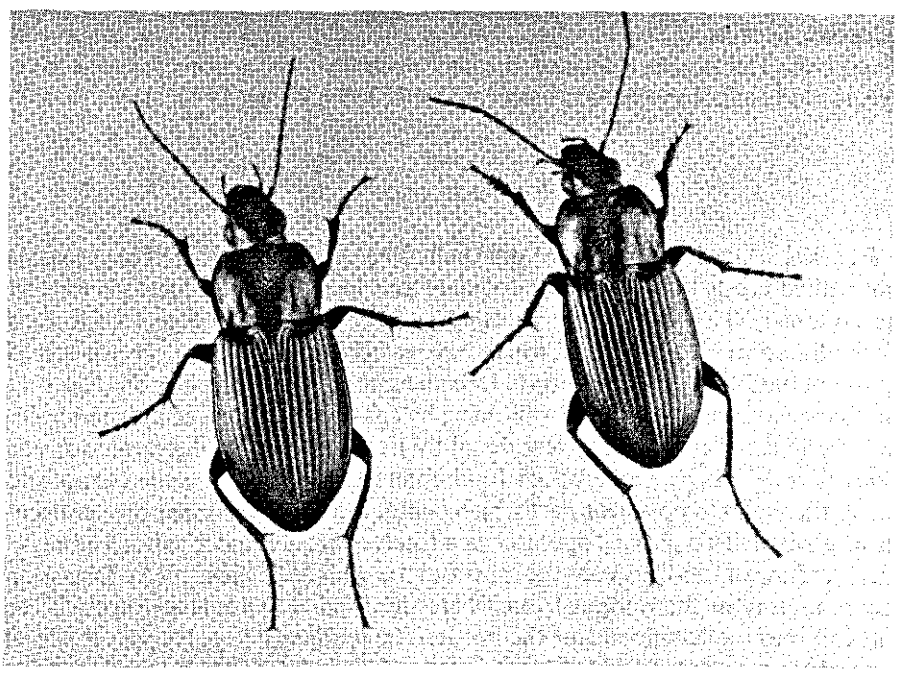


FIG. 2.1. The ground beetle *P.coerulescens* (left female, right male).

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.coerulescens* 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-

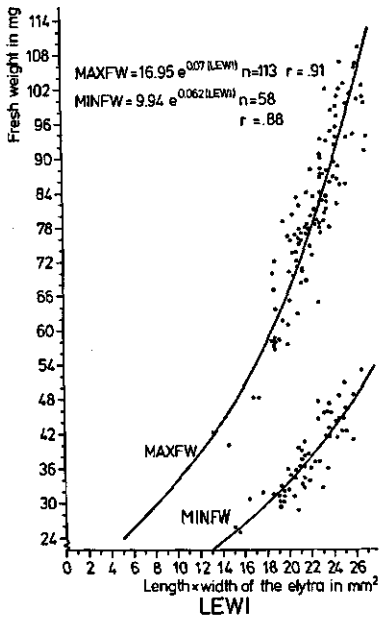


FIG. 3.1. The relationship between length times width of the elytra (LEWI) in mm^2 and maximum (MAXFW) and minimum (MINFW) fresh weight of *P.coerulescens* expressed in mg.

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.

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

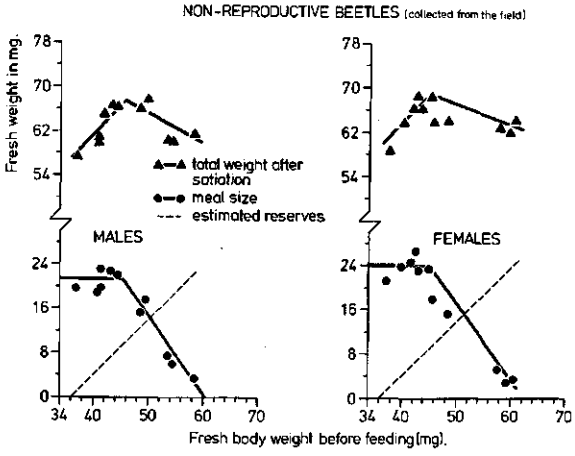


FIG. 3.2a. The relationship between initial net body weight (NBODYW) and the meal size of beetles captured in the field. LEWI is between 19 and 21 mm^2.

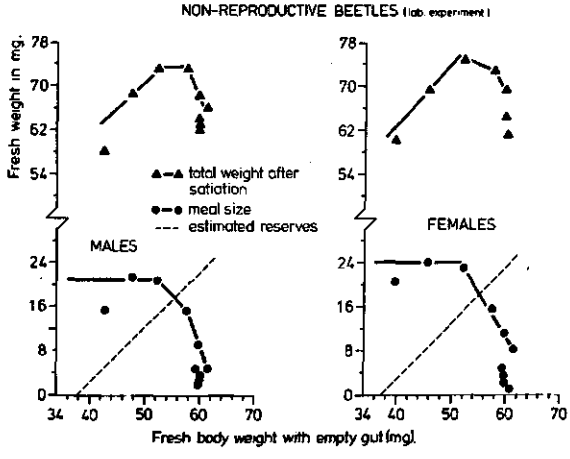


FIG. 3.2b. The same relationship, but now from beetles reared in the laboratory. LEWI is between 22 and 24 mm^2.

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

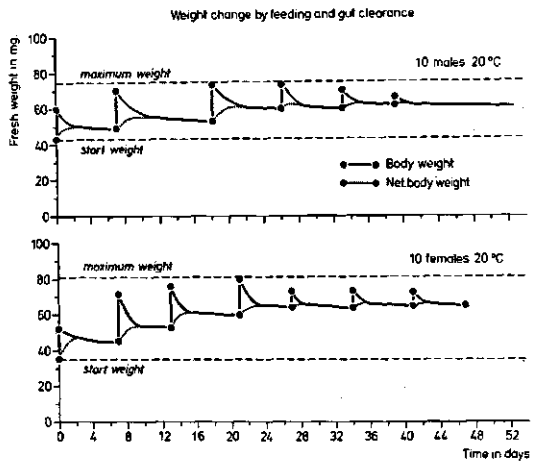


FIG. 3.3. Change in weight by feeding and gut emptying. The solid line corresponds with total fresh body weight, the dotted line with body weight without gut content. In the latter, increase of reserves by assimilation of the ingested food can be observed.

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

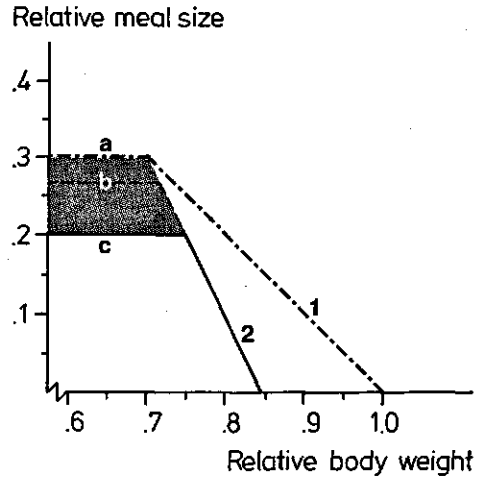


FIG. 3.4. Relationship between net body weight (NBODYW) and meal size (MEALW) both relative to the maximum fresh weight (MAXFW): (a) Relative maximum gut capacity. (b) Relative average meal size to satiate non-reproductive beetles. (c) Relative average meal size to satiate reproductive beetles. (1) Relative 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 ± 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 ± 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.

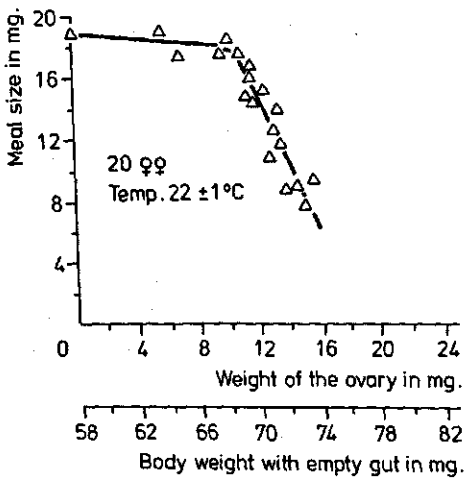


FIG. 3.5. Relationship between initial body weight of reproductive beetles (including eggs) and meal size. LEWI is 23.4 mm^2.

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_1 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:

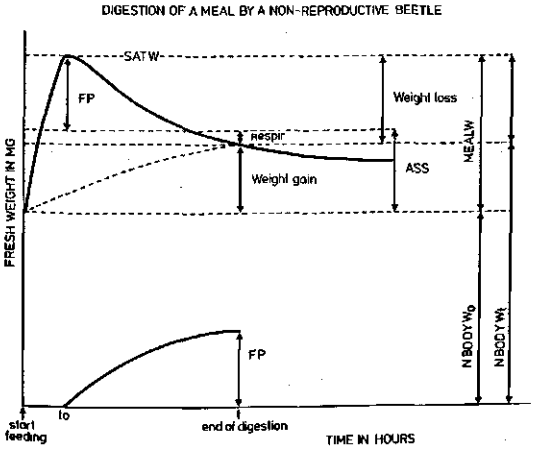


FIG. 3.6. A schematic representation of the changes in weight of the beetle and of faeces produced during and after ingestion of a prey caused by digestion and egestion.

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

$NBODYW_o$ = 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,

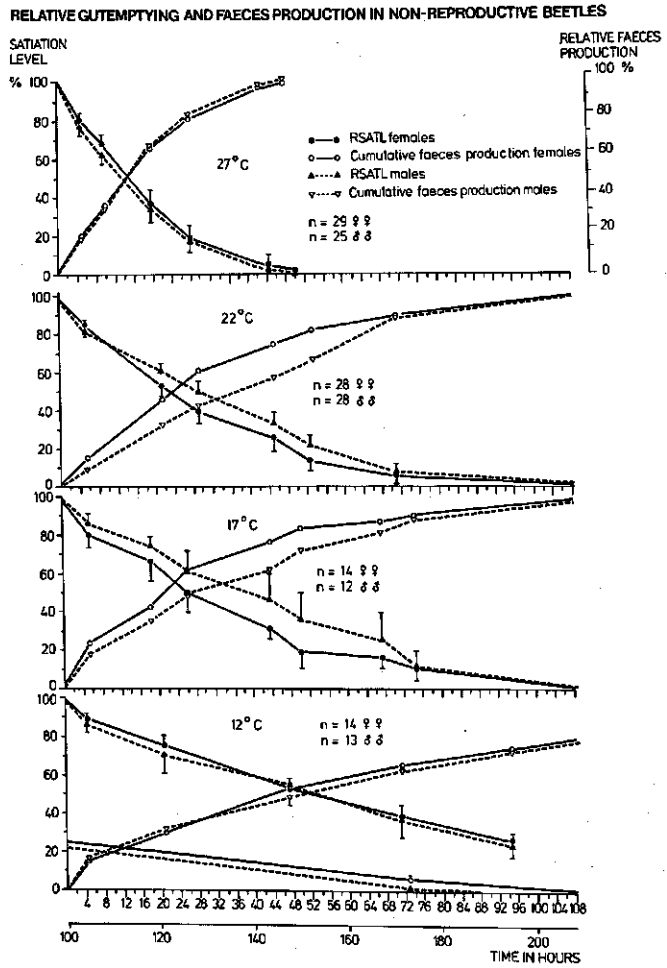


FIG. 3.7. The change of the relative gut content and the relative production curve of faeces after satiation for 12, 17, 22 and 27°C in non reproductive beetles. For 12°C the curve of the relative gut content continues after 96 hrs at the left side of the figure.

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,

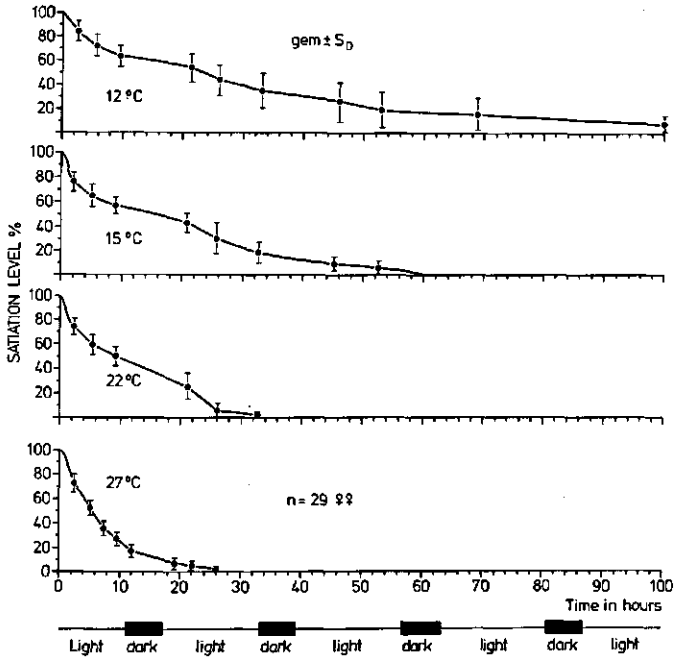


FIG. 3.8. The change of the relative gut content after satiation in reproductive beetles.

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

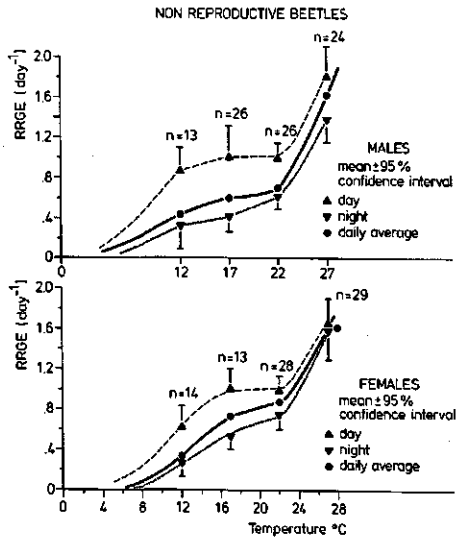


FIG. 3.9. The relative gut emptying rate for both non- reproductive males and females. The average RRGE for the whole day, the night time and the day time is given.

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-

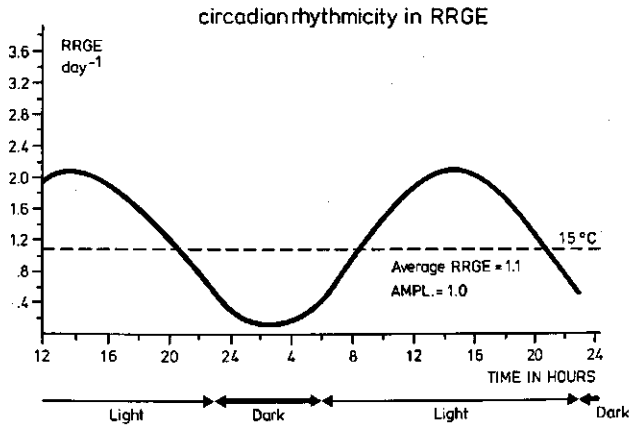


FIG. 3.10. The relative gut emptying rate (RRGE) shows a circadian rhithmicity which can be mimicked by a sinusoid function with an average of:
$(RRGE_{max} + RRGE_{min})/2$ and an amplitudo of $(RRGE_{max} - RRGE_{min})/2$
The time of the minumum is set at 2.00 o'clock, the maximum at 14.00 o'clock.

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

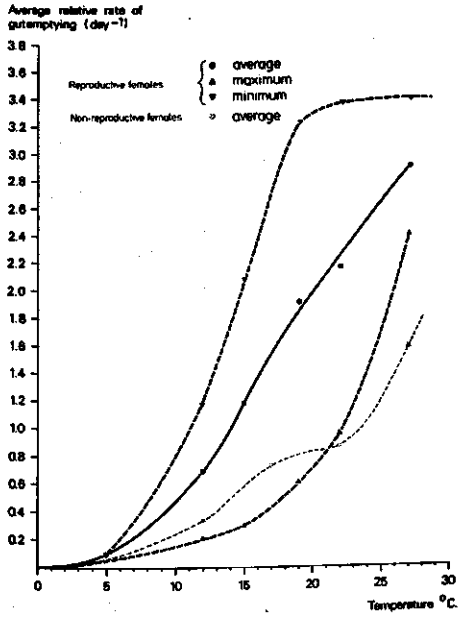


FIG. 3.11. The average relative gut emptying rates (RRGE) both for reproducing and non-reproducing female beetles.

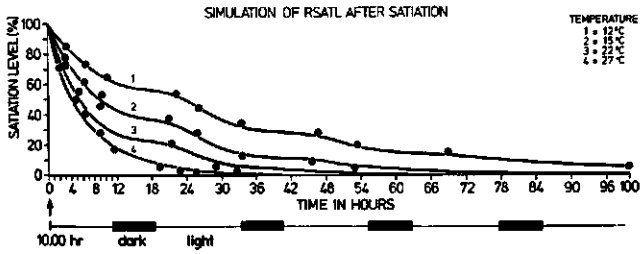


FIG. 3.12. The change of the relative satiation level (RSATL) using the sinusoid function for the circadian rhythmicity of the relative gut emptying rate (RRGE) for 12, 15, 22 and 27 °C in reproducing females. (The black dots are the observed values.)

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

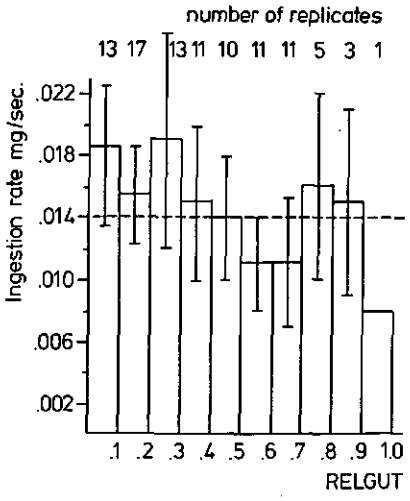


FIG. 3.13. Relationship between relative gut content and ingestion rate in *P.coerulescens*, with maggots as food.

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

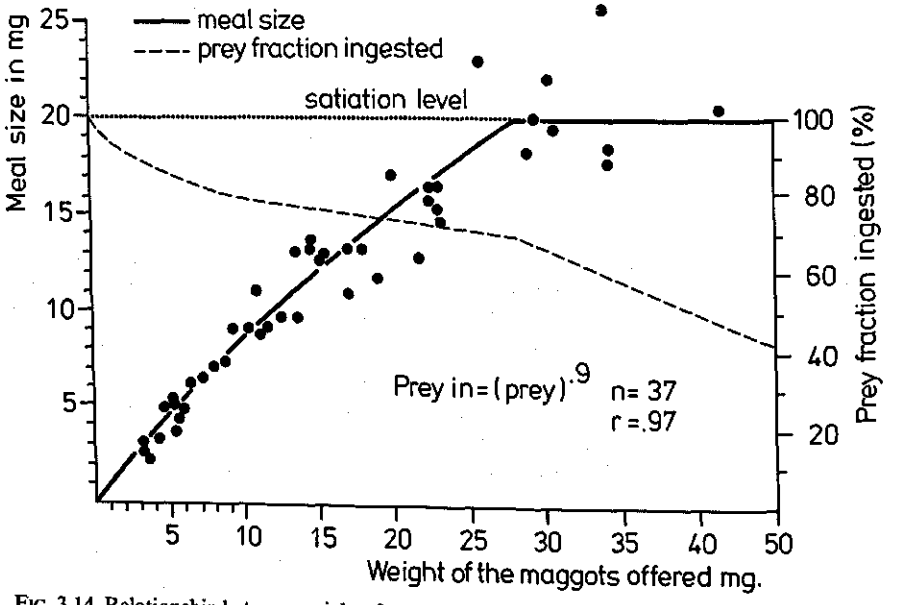


FIG. 3.14. Relationship between weight of maggots offerd and the final quantity of food (PREYIN) ingested. The solid line and black dots represent the weight of the prey ingested. The broken line represents the fraction of the prey ingested.

into the soil. In this experiment the meal size required to satiate these beetles was 20.6 $\pm$ 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

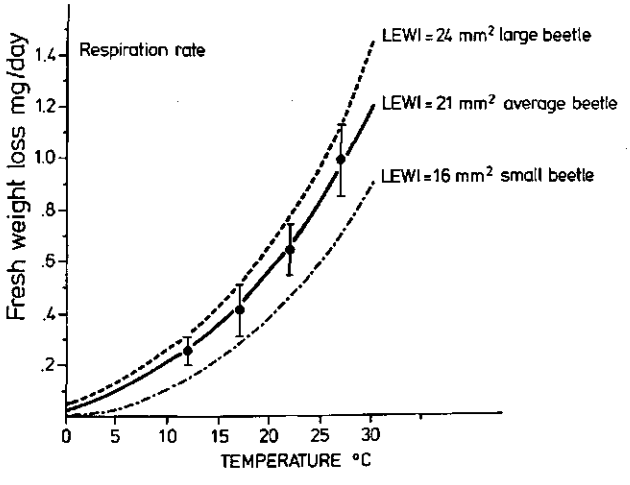


FIG. 3.15. The experimentally established relationship between temperature and the rate of fresh weight loss (RFWL) in mg/day in starved beetles (mean ± SD). The relationship is exponential according to: $RFWL = 0.0935e^{(0.0087 * TEMP)}$
RFWL

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:

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

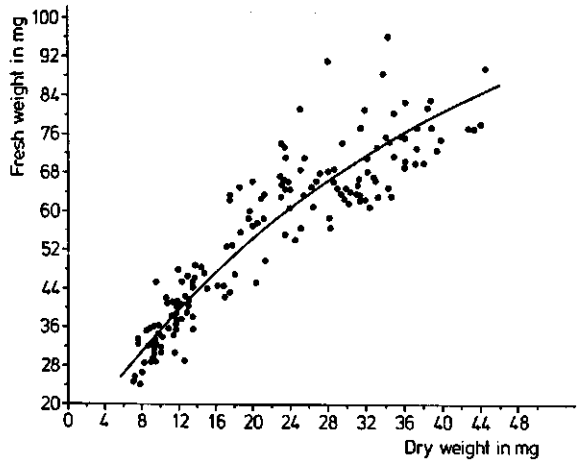


FIG. 3.16. The relationship between dry and fresh weights of beetles varying from starved and exhausted to reproducing and full of eggs.
$DW = (0.1 * FW)^{1.7763}$

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:

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

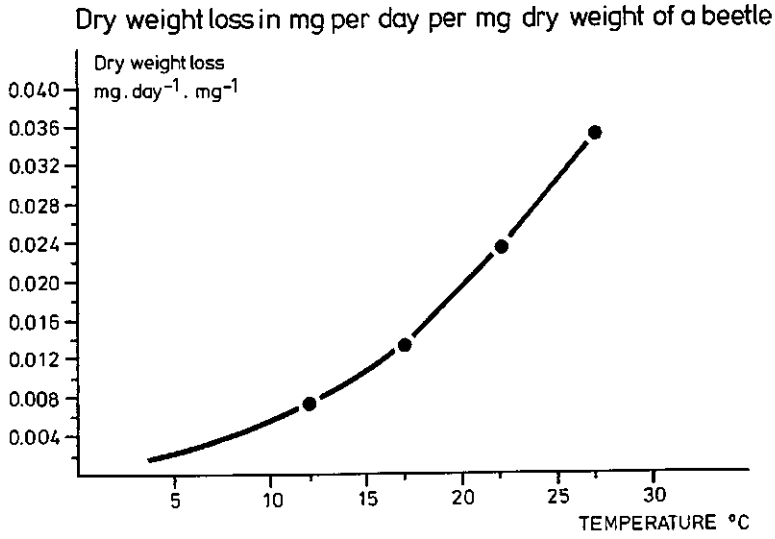


FIG. 3.17. The relationship between dry weight loss expressed in mg per day per mg dry beetle weight and the temperature.

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

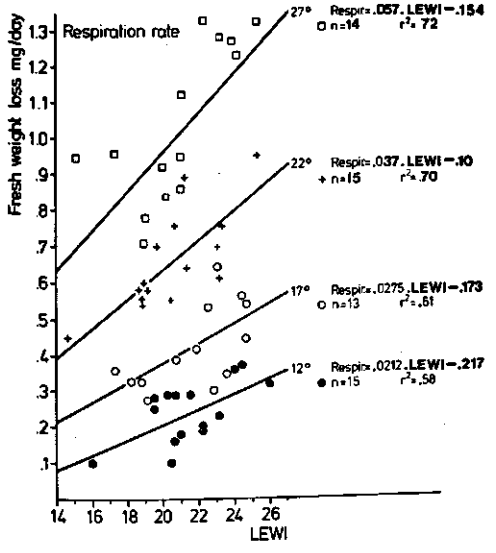


FIG. 3.18. The relationship between the size of the beetle and the fresh weight loss in starved beetles at different temperatures.

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

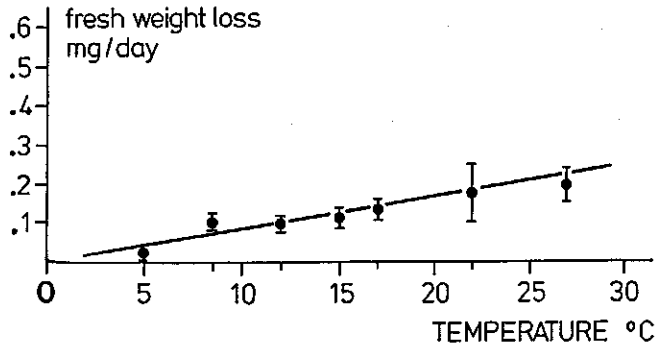


FIG. 3.19. The relationship between fresh weight loss and temperature in starved beetles in the post-reproductive and diapause stage.

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

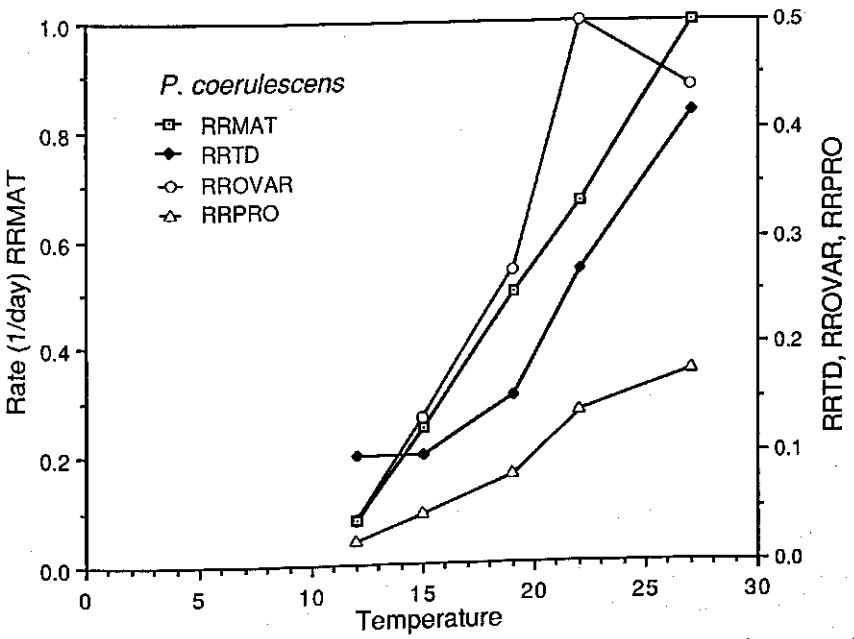


FIG. 3.20. The relationship between the temperature and: RRTD (the relative reaction rate to change in daylength), RROVAR (the relative growth rate of the eggs in the ovaries), RRMAT (the relative maturation rate of eggs in the oviduct), RRPRO (the relative pre-oviposition rate).

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

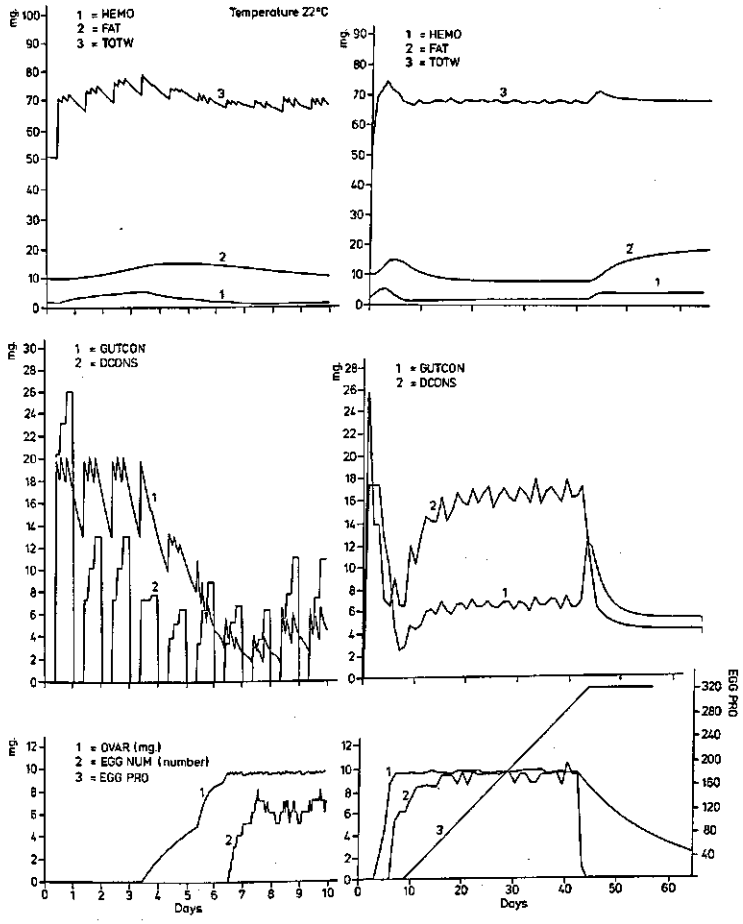


FIG. 4.1a,b. The change of weights at a constant temperature of 22 °C of: the total beetle (TOTW), haemo-lymph (HEMO), stored products (FAT), gut content (GUTCON), daily consumption (DCONS), ovaries (OVAR) and the change of the number of eggs in the oviduct (EGGNUM) and the number of eggs produced. Fig (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 ± 2.3 n = 16, males LEWI = 17.3 ± 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

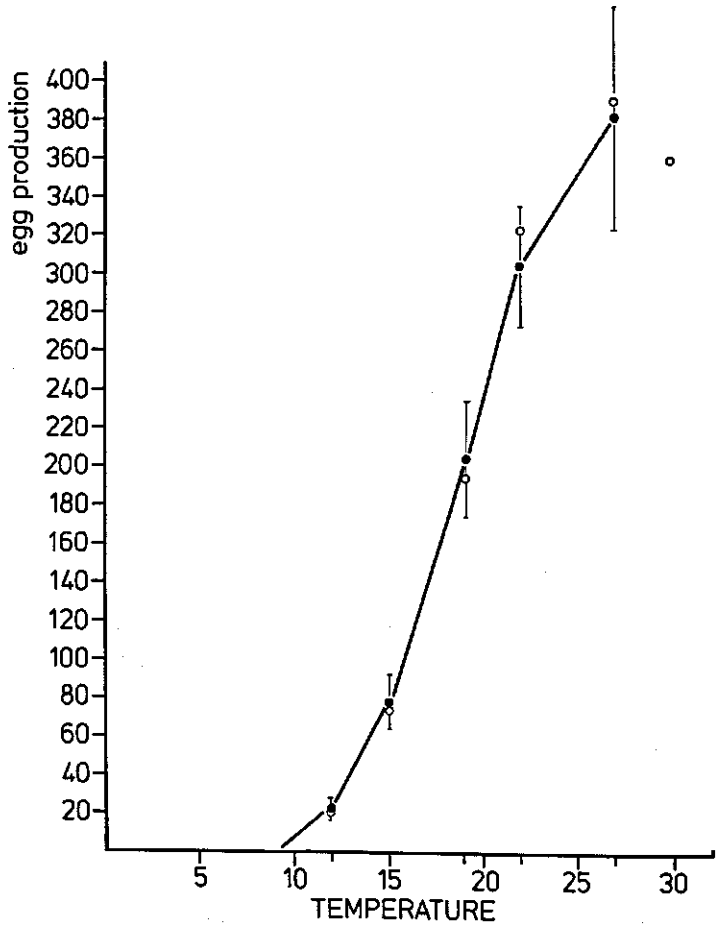


FIG. 4.2. Experimental (black dots) (mean ± SE) and simulated (open dots) results of egg production at different constant temperatures, when food is available in excess.

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.

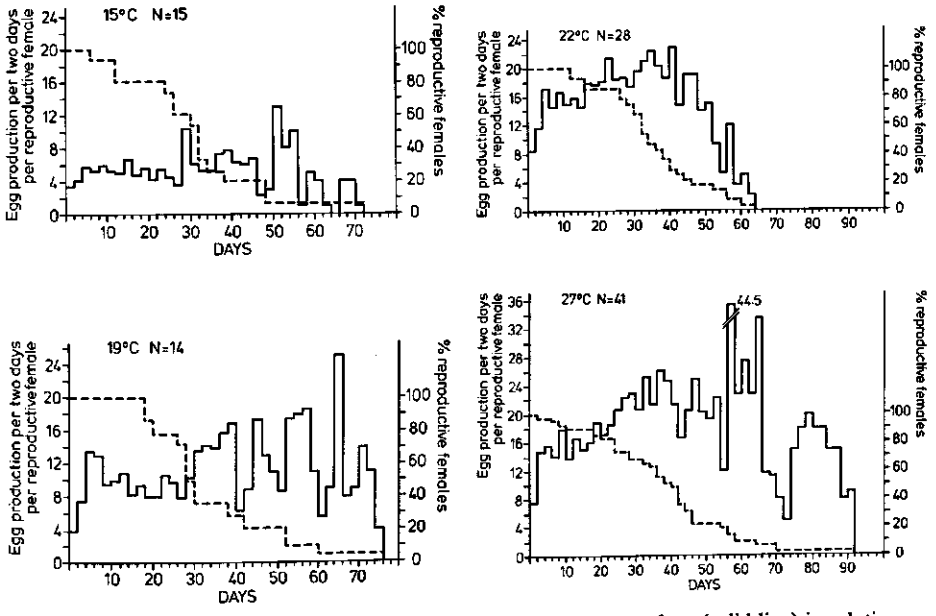


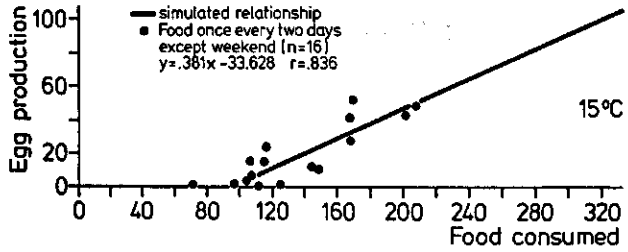
FIG. 4.3. The average egg production per reproducing female per two days (solid line) in relation to reproductive age, and the % females reproducing (broken line) at different temperatures. The start of oviposition of each individual female is taken as day one.

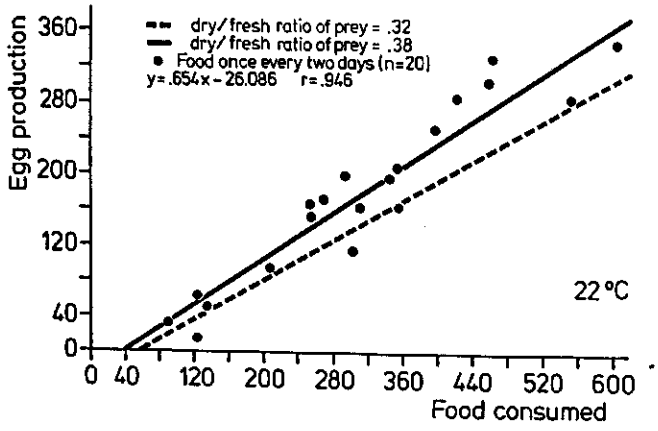
b) Egg production at limited food conditions.

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





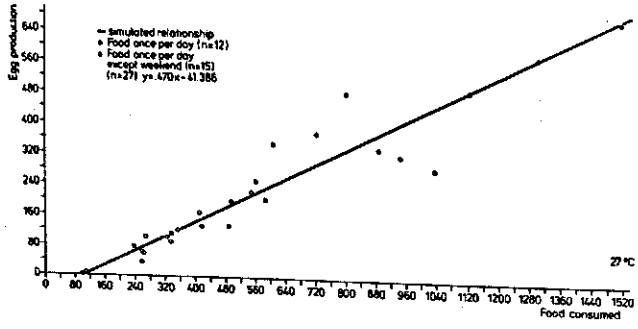


FIG. 4.4. The relationship between total food consumption (from the start of the experiment until the end of the reproduction period) and the total amount of eggs produced per individual beetle at constant temperature. The lines represent the results of simulation with the same conditions.

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

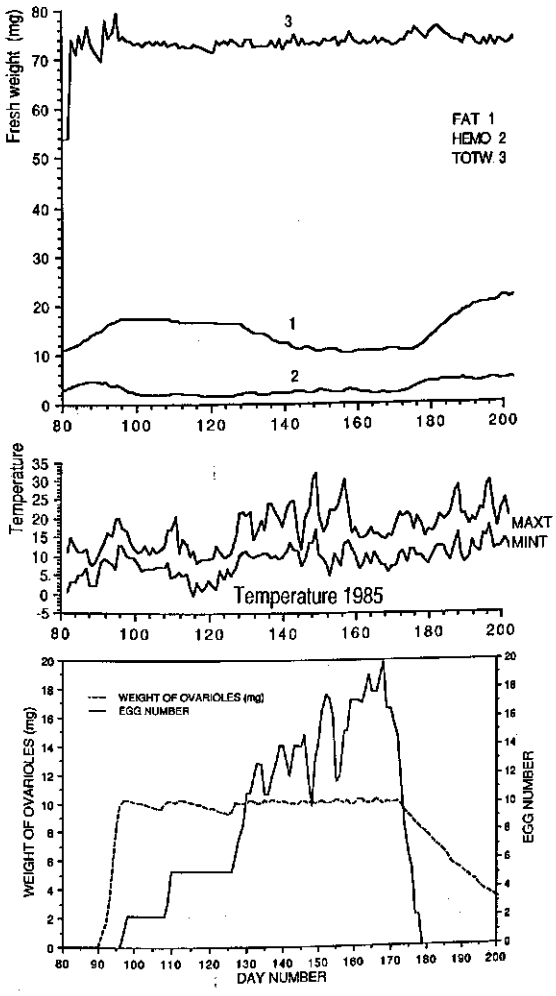


FIG. 4.5a. The simulated change of weights at field temperatures (1985) of the total beetle (TOTW), materials in the haemolymph (HEMO), stored products (FAT),b) the ovaries (OVAR) and the number of eggs in the oviduct (EGGNUM). Food is available in excess.

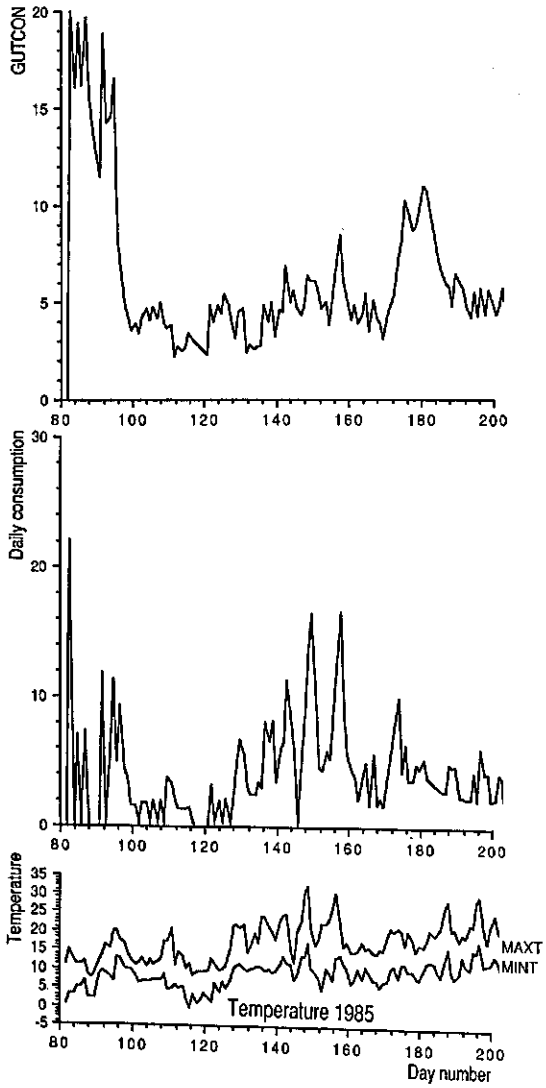


FIG. 4.6a. The change of weight of the gut content (GUTCON). b) The daily consumption (DCONS). during the reproduction period in 1985.

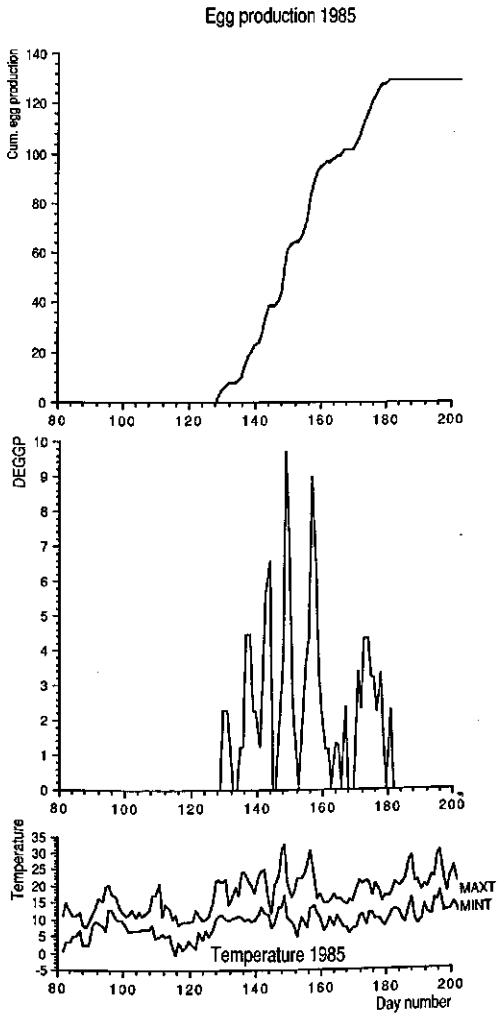


FIG. 4.7. The daily and total egg production at field temperatures for the year 1985. Food is available in excess.

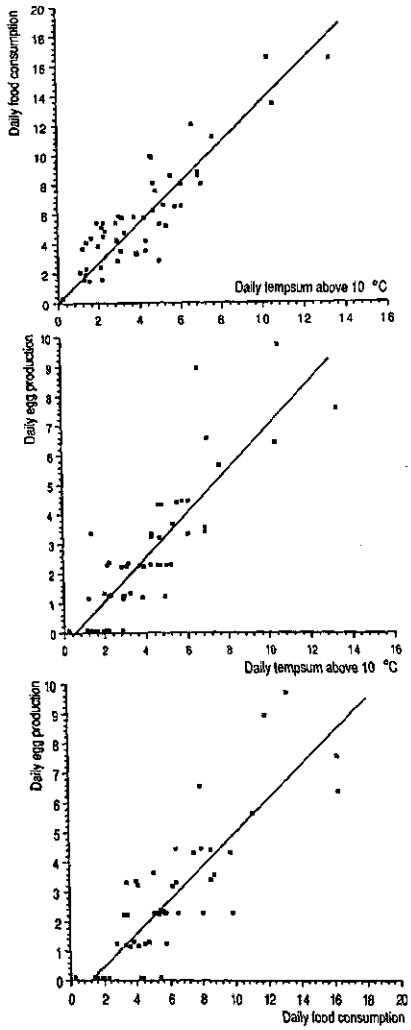


FIG. 4.8. The relationship between:

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 Variables and parameters	MF	C 210 SC	EP 20 SEP	C 257 SC	EP 71 SEP	C 466 SC	EP 193 SEP	C 692 SC	EP 326 SEP	C 912 SC	EP 387 SEP	C 978 SC	EP 345 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.

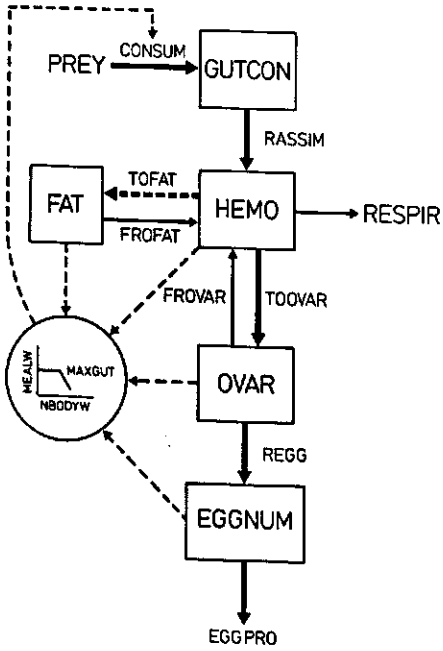


FIG. 5.1. The relationships between the various state variables. The feedback loops between FAT and HEMO and between OVAR and HEMO buffer the fluctuations of HEMO. The ingestion of food is regulated by the combined quantity of FAT, HEMO, OVAR and EGGNUM via the relationship between net body weight and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

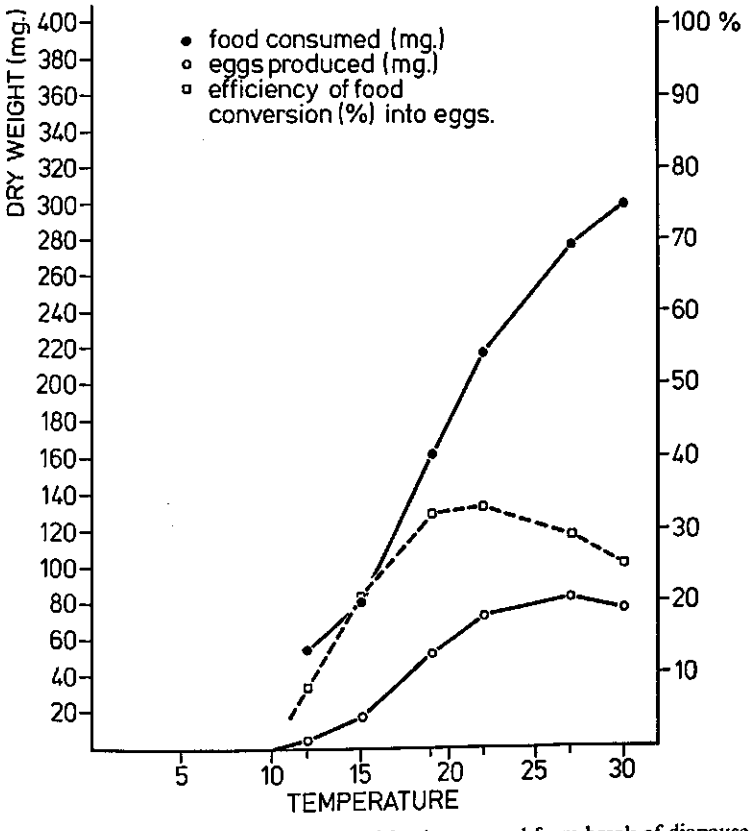


FIG. 5.2. The simulated total quantity of food consumed from break of diapause until the end of the oviposition period, the quantity of eggs produced (both expressed in mg dry weight), and the efficiency of conversion of food into eggs at constant temperatures.

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

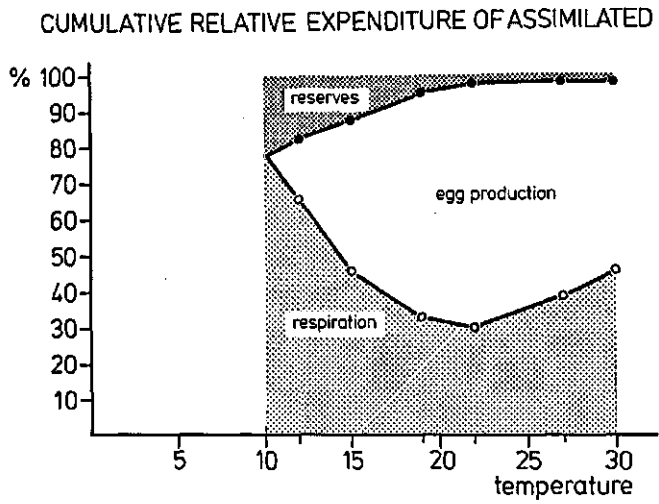


FIG. 5.3. The simulated cumulative expenditure of food assimilated throughout the gut wall used for reserves, respiration and egg production, during the oviposition period at constant temperature.

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.	0.01		0.005		0.004		0.0033	
Year	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

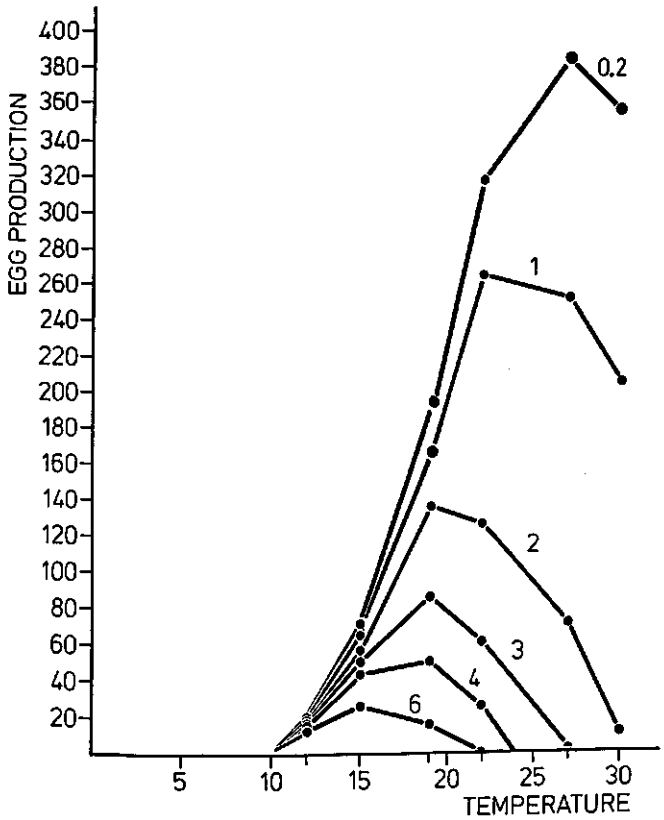


FIG. 5.4. Simulated egg production at constant temperatures but with different intervals of starvation. Feeding varied from 5 times a day (0.2), once per day (1), once per two days (2), once per three days (3), once per four days (4), to once every 6 days (6).

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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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.

FORAGING BEHAVIOUR OF THE CARABID BEETLE *PTEROSTICHUS COERULESCENS* L. (= *Poecilus versicolor* Sturm) AT DIFFERENT DENSITIES AND DISTRIBUTIONS OF THE PREY.

(PART II)

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CONTENTS

ABSTRACT

By means of systems analysis and simulation, predation and egg production of the carabid beetle *Pterostichus coerulescens* L (= *Poecilus versicolor* Sturm) is studied in relationship to prey density and prey distribution. Foraging behaviour is divided into its most dominant components: searching, acceptance of prey and feeding which are in turn related to the most important internal and external factors. Hunger or its opposite, the relative satiation level (RSATL), is the internal factor that determines the 'motivation' for a large part of the behaviour and it results from the physiological state of the beetle. RSATL is estimated by means of a simulation model (Mols, 1988) and correlated to the behavioural components that play a role in searching and predation. The hunger level has a strong influence on the locomotory activity, walking speed, duration of area-restricted search and prey acceptance. Three types of searching behaviour were distinguished: 1. Straight high-speed walking when RSATL is below 5%, 2. Intermediate walking when RSATL exceeds 5% and 3. Intensive tortuous walking behaviour (area-restricted search) after consumption of a prey.

The searching model developed shows the advantage of the tortuous walk (TW) when prey is aggregated and its disadvantage in random prey distributions. When the searching model is coupled to the motivation model the advantage of TW is restricted to aggregated prey at overall low prey densities (< 1 prey/m^2 generally). Walking speed, time spent walking and success ratio (prey captured/prey discovered), which in turn all depend on the relative satiation level, in combination with prey density and prey aggregation determine the predation rate and the egg production.

1.0 INTRODUCTION

Obtaining food is a basic requirement for every organism. Animals that actively search for food, for themselves or for their offspring make different choices concerning the locality to search for, the period during which to search, the kind of food to search for and ultimately the quantity of food to ingest. In that searching behaviour a number of factors play an important role which can be divided in: a) species specific properties, like the way of locomotion, the perception of habitat and prey and the internal motivation to come into action and b) environmental properties which determine the availability and attainability of the prey like vegetational composition and habitat structure, and the prevailing microclimatological conditions that affect the rates at which several vital processes of both prey and predator take place.

The ultimate aim of this study is to gain insight into the impact of spatial distribution and density of prey on predatory behaviour and on the resulting egg production of the carabid beetle *Pterostichus coerulescens*. This may lead to better insight and understanding of the survival strategy of this carabid beetle, reflected in its ability to cope with specific prey distributions varying from random to aggregated.

The carabid beetle, *Pterostichus coerulescens* L.(= *Poecilus versicolor* Sturm), is a predator of small arthropods such as aphids, spiders, caterpillars and maggots (Hengeveld, 1980), and lives in heathland and grassland poor in nutrients. In most cases prey distribution is aggregated, which is a general phenomenon (Southwood, 1966). Flight has only rarely been observed in *P. coerulescens*. Therefore, all vital behavioural functions such as searching for food, finding a mate, escaping from predation by birds, toads and rodents (Larochelle, 1974 a,b) occur by walking. The pattern of movement in relation to the density and distribution of the prey affects the rate of feeding and as a consequence the rate of reproduction and thus the spatial and temporal dynamics of the population in the field.

To understand the dynamics of the processes governing searching and predatory behaviour, information is required on the motivational drives for predatory behaviour. In many species behaviour is governed by some internal 'motivational drive'. For several predators this motivational drive is found to be equivalent to the satiation level of the gut (Holling, 1966; Nakamura, 1972; Fransz, 1974; Rabbinge, 1976; Sabelis, 1981; Kareiva et al., 1987). For *P. coerulescens* the satiation level of the gut, defined as the actual gut content divided by the apparent gut capacity (which is the weight of a meal to satiate a beetle that starts eating with an empty gut), is used as a measure for the 'motivation' of the beetle (Mols, 1988). The apparent gut capacity cannot exceed a physical maximum

(the maximal gut size) and it depends on the size of other organs and tissues needed for egg formation and storage of reserves as well. The actual gut content changes by ingestion, excretion and resorption. The rates of changes are predominantly affected by ambient temperature and daylength, the latter determining the onset of vitellogenesis. Thus the physiological drive for behaviour, i.e. the satiation level or its complement hunger, results from a complex of internally related states which in their turn are affected by the rate of prey ingestion under various climatic conditions.

The internal factors which determine the 'motivational state' of the beetle (here used as an equivalent for the term relative satiation level: RSATL) were integrated in a simulation model (Mols, 1988). The output of that model was compared with the results of experiments and showed that it was possible to estimate continuously the 'motivational state' of the beetle. This 'motivational state' of the beetle is used as the most important state variable that dictates walking and predatory behaviour.

1.1 Components of behaviour

In general the predation rate is determined both by the encounter rate (Er) with prey, and by the fraction of encountered prey killed by the predator :the succes ratio (Sr) (Fransz, 1974; Sabelis, 1981).

The encounter rate is a function of the following variables:

(A) Locomotory activity: The fraction of the time that both predators and prey are locomotory active. If the prey is mainly sessile and the predatory beetle hides away in the soil or litter when resting, only the locomotory activity of the predator has to be considered.

(V) Velocity: The walking speed of the beetle (cm/sec) of both predator and prey. In *P. coerulescens* the majority of prey items are small caterpillars, aphids and maggots (Hengeveld, 1980), which show a very low walking speed in comparison to the beetle. In those cases the speed and the turning rate of the prey can be neglected. If mobile spiders and ants are important prey items, then walking speed has to be included in the resulting velocity, but if only immobile or slowly walking speciments are important prey items their velocity may be neglected also.

(E_{ff}) Effectiveness of searching per unit of walking distance depends on the windingness of the walking pattern. The latter can be expressed by the turning rate (expressed as degrees/time unit) or by the turning angle per unit of distance. When the pattern is very windy the effectiveness of searching per unit of walking distance decreases because recrossing of previous visited spots will occur more often.

(R) Reaction distance: The distance at which a predator reacts to a prey. It determines the searching path width of the predator and therefore it plays an important role in the area of discovery of the beetle.

(D) Density of the prey. In case of prey aggregation its density will differ from

place to place. To avoid confusion in terminology the following terms will be used:

1. 'Overall density' is the total number of prey items (prey total in an area) divided by the surface of the total area.
2. 'Within cluster density' is the number of prey items in a cluster divided by the surface of a prey cluster.

From this follows that the area of discovery will be dependent both on the walking speed, the effectiveness of searching (determined by the windingness of the walking track) and on the reaction distance. For clumped prey distributions increased winding may result in a longer stay of the predator in the prey cluster and in a more intensive search over the area, which ultimately may result in a higher encounter rate with prey.

If it is assumed that the predator searches at random and that the walking directions of both predator and prey are mutually independent, the predation rate can be calculated from the encounter rate multiplied with the succes ratio (Sabelis, 1981; Mols 1986)

$$P = Er.Sr \quad (1)$$

$$Er = 2.R.V.D.A.E_{ff} \quad (2)$$

However, searching is not at random when a predator is able to orient itself towards prey individuals or to prey cues, or when both the walking speed and direction of walking are changed after contact with prey. In such cases these formulae cannot be used, or have to be restricted to those parts of time in which searching is still at random. Then it is necessary to quantify the walking behaviour itself and to relate its features (speed and turning rate) to the internal and external stimuli. In that case the distribution of the prey becomes very important, because it will interact with the degree of windingness of the searching behaviour and thus with the efficiency of searching. The searching efficiency then depends on the type of walking behaviour (speed and turning rate) and has to be included as a separate function in the predation function.

In the predation process not every encounter with a prey is followed by an attack and not every attack is successful. Among others this depends on the motivational state of the predator (Fransz, 1974; Rabbinge, 1976; Sabelis, 1981, Mols, 1987). A hungry predator will be more eager to attack a prey and will continue an attack longer resulting in a higher success ratio. Prey exhibiting a defensive reaction, for example some caterpillars, may have a greater chance to escape. This implicates that the succes ratio depends on the relative satiation level of the beetle. Thus the predation rate is a function of:

$$P = f(R,V,E_{ff},D,A,Sr) \quad (3)$$

The behavioural components mentioned above may be both determined by the relative satiation level of the beetle and by external stimuli such as tempera-

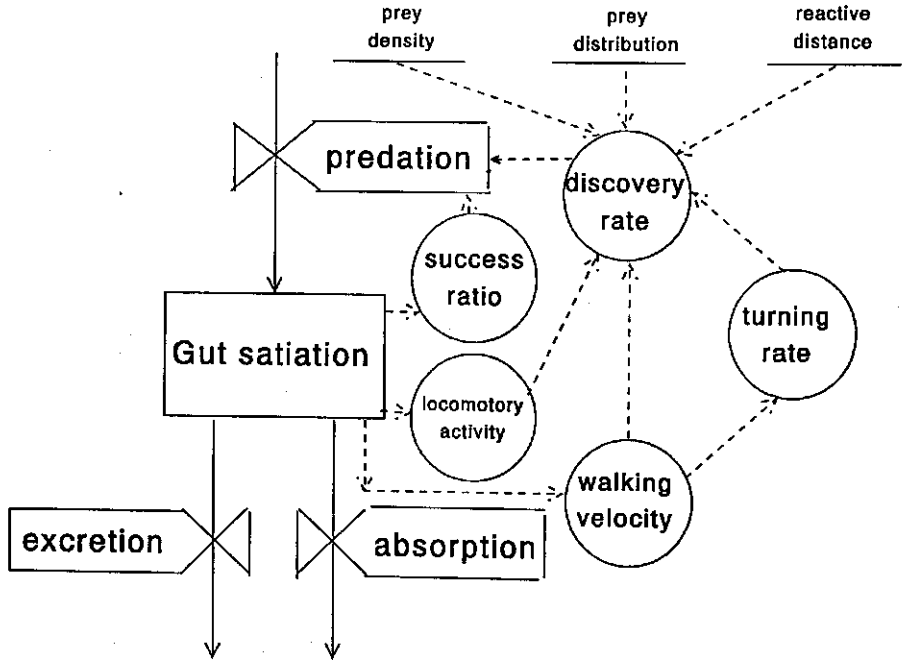

FIG. 1.1 Relational diagram of the relationship between behavioural components involved in searching and predation.(Rectangles are state variables, valves are rate variables, circles are auxiliarly variables, underlined statements are parameters. Solid lines represent streams of matter, broken lines represent streams of information).

ture and diurnal rhythmicity (fig. 1.1). These factors change both throughout the day, and after consumption of prey as has been observed in many predators (e.g. Coccinellids, Dixon 1958; Anthocorids, Evans, 1976).

1.2 APPROACH

Therefore, the relationships between the relative satiation level and locomotory activity, walking behaviour and succes ratio had to be quantified experimentally and integrated into a model that simulates predation and that is coupled to the motivational model (Mols, 1988). With this model it is possible to simulate walking behaviour and egg production under different sets of environmental conditions, prey densities and prey distributions.

The value of specific behavioural components in the total predation process can be estimated for these different conditions thus giving insight when specific behaviour shows full advantage for the predator. The results obtained may offer basic background information for the interpretation of the functional and numerical response of the beetle to different prey densities which are important features of the population dynamics of this species in time and space.

2.0 QUANTIFICATION OF THE COMPONENTS OF BEHAVIOUR IN RELATION TO HUNGER

The set up of the experiments in general is such that they are done in relatively simple environments (Petri-dishes, arena's with light vegetation etc.) under relatively constant conditions of temperature, humidy, light intensity and prey type to quantify the relationships between the components of searching behaviour and the motivational state. The field situation may be much more complex, but the basic processes are assumed to be the same and therefore this appraoch may lead to the unraveling of this complex system.

2.1 LOCOMOTORY ACTIVITY

2.1.1. Methods

Measurements of locomotory activity in relation to the satiation level were restricted to the reproductive period, because the beetles are most active then. Before the experiments the beetles were weighed and their apparent gut capacity was estimated. Ten pairs of male and female beetles were each placed in large Petri-dishes (20 cm diam.). The substrate on the bottom of the dish consisted of loamy sand and some peat-mull. On the substrate small pieces of bark were placed under which the beetle could hide. The females were marked by a small dot of yellow paint on one of the elytra so that during observation they could be easily distinguished from the males. The observations were carried out at 20 ± 1 °C and at 12 ± 1 °C during a period of 16 hours (from 5 am to 9 pm, this was also the duration of the photoperiod). Two days before the start of the observations the beetles were placed in the dishes without food, to standardize them and to accustom them to the situation. The first day of the observation for two hours from 6-8 am the beetles were given abundant food to satiate them. The food consisted of dead blowfly maggots. After this feeding period the prey remains were removed. Next the beetles were starved for four days. This sequence of feeding and starvation was repeated three times. The last starvation period took five days. The fifth day of the last starvation period the beetles were offered food at 11 am.. That day the activity was followed untill 4 pm.

Every hour the beetles were observed for a period of 15 min (the observation period) and their activity was recorded. The satiation level was estimated with the help of the motivational model (Mols, 1988).

After the period of hourly observations the beetles were held in the same Petri dishes and fed abundant maggots every third day. Each day at 9 am and at 2 pm the activity was recorded for a quarter of an hour. The egg production was measured by washing the substrate each week following the method of Mols

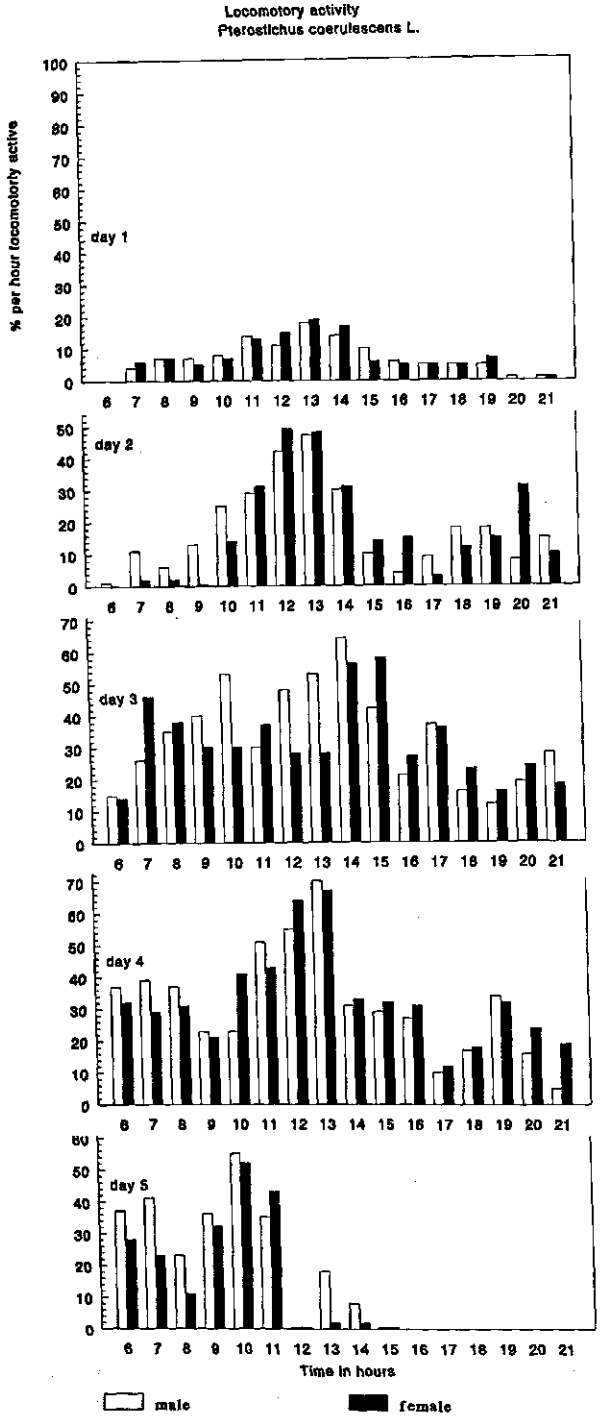

FIG. 2.1 Hourly distribution of locomotory activity of *P.coerulescens* at 20 °C for starved beetles on 5 successive days. The 5th day food was offered at 12.00. Light period from 5.00 to 21.00.

et al. (1981). The observations were finished at the end of the reproduction period of each beetle. From these observations a relationship between locomotory activity and egg production could be established and information on the persistence of the individual locomotory activity in the course of time both during the intensive and the extensive observation period could be collected.

2.1.2 Results

Frequency distribution of the locomotory activity during daytime.

The distribution of the percentages of hourly locomotory activities over the day for each of the five days in sequence is shown in fig 2.1. In general locomotory activity increases until noon, next it decreases. The level of activity increases up to the third day. At the fourth and fifth day activity is already high at the start of the photoperiod. At the end of the day also a weak increase in locomotory activity can be observed. When food is offered at the noon of the fifth day the activity drops drastically especially in the females. This clearly shows the influence of satiation on the level of locomotory activity. The effect of the satiation level on the daily distribution pattern of locomotory activity is eliminated by dividing the duration of activity calculated for each hour by the corresponding daily duration of activity. This gives an average pattern of locomotory activity over the day that is independent of the relative satiation level. Thus a distinct diurnal rhythm of locomotory activity was found (fig. 2.2), with a maximum at noon and a minimum during the night.

In the experiment carried out at 12 °C the beetles showed hardly any activity during the observational period. Only very short moments of activity could be recorded. The activity at this temperature was about 10% of the activity at 20 °C.

Duration of daily locomotory activity.

It is assumed that during a quarter of an hour sufficient information is obtained to be able to estimate the hourly locomotory activity of the beetles. Therefore, the duration of locomotory activity per hour was estimated by multiplying by four the duration of locomotory activity measured during a quarter of an hour. By summing up the hourly estimates over the whole daily observation period the duration of daily locomotory activity was estimated. The daily sum of locomotory activities during the successive days following feeding is shown in fig 2.3. The duration of locomotory activity increases from the day of satiation until a level (MAXACT) of 5.3 hours/day is reached at the third day. This level remains approximately constant at least until the fifth day. No significant difference in the duration of daily locomotory activity could be observed between the sexes.

The locomotory activity in relation to the relative satiation level.

At 20 °C it takes two days to empty the gut (Mols, 1988) while in the experiments it took 2 days to reach the maximum level of locomotory activity. To express the relationship between locomotory activity and the relative satiation

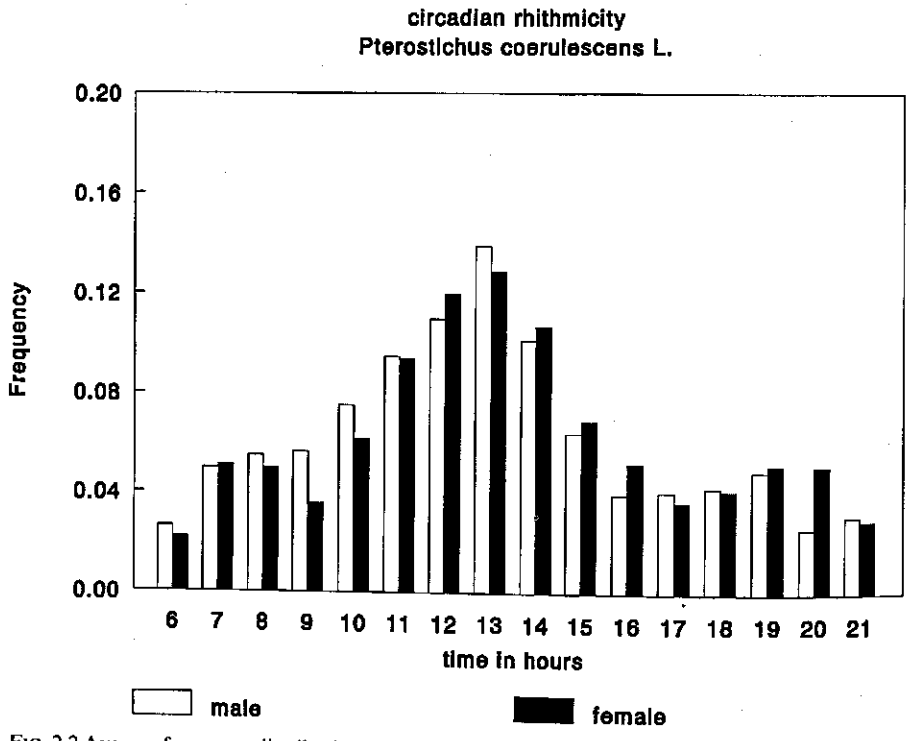

FIG. 2.2 Average frequency distribution of locomotory activity during the lightperiod at 20 °C.

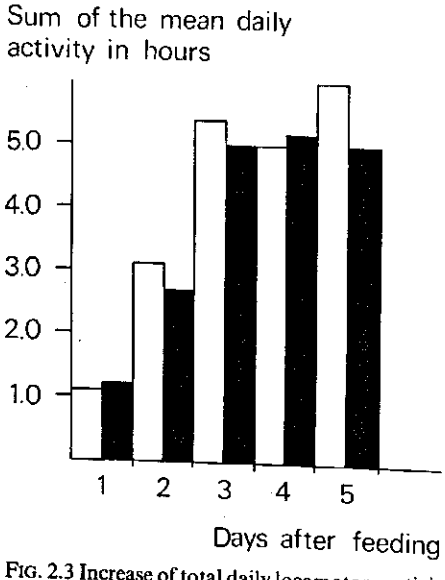

FIG. 2.3 Increase of total daily locomotory activity after complete satiation on the first day.

level, the effect of the time of the day on locomotory activity (diurnal rhythmicity of locomotory activity) has to be corrected for. Therefore, the locomotory activities during the hourly observation periods on the first and second day were calculated as a fraction of the average maximum activity found for the corresponding hour of the third, fourth and fifth day. The relative satiation level of the beetle in each observation period was computed by the motivation model (Mols, 1988). In this way it was possible to obtain an estimate for the relative locomotory activity at a range of satiation levels. The relation is shown in fig.2.4. The relative locomotory activity, here called the relative activity coefficient (AC), has a correlation with the relative satiation level (RSATL). This relationship can be fitted by the hyperbolic equation :

$$AC = 1/(5.7*RSATL+1) \qquad r^2 = 0.80$$

The locomotory activities of the males and the females were combined in this figure, because between the sexes no significant difference in locomotory activity could be observed

Locomotory activity and reproduction.

The average locomotory activity measured at 9 am and 2 pm during daytime

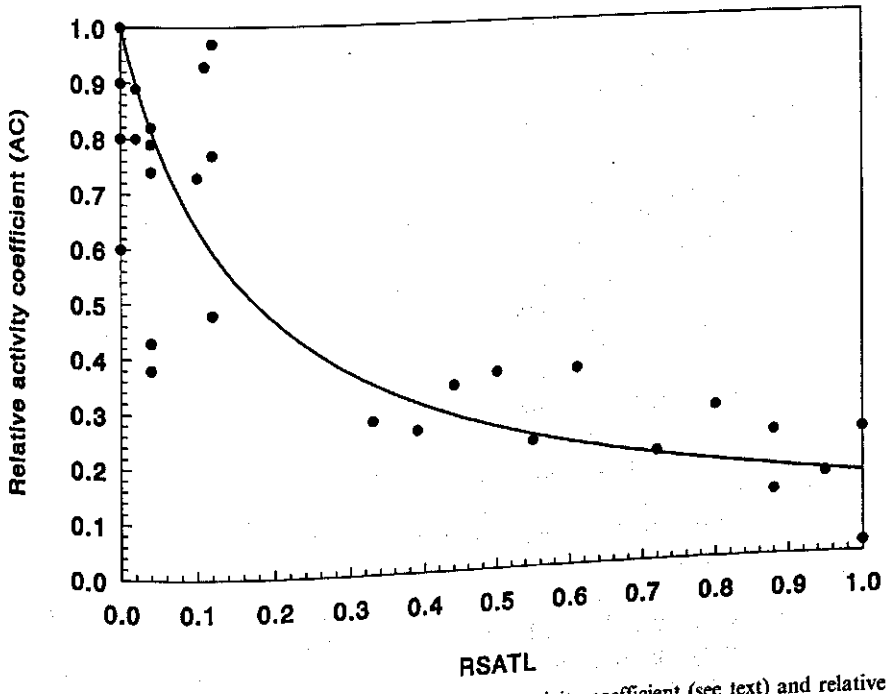

FIG. 2.4 Relationship between the relative locomotory activity coefficient (see text) and relative satiation level.

was used as an index for the overall locomotory activity of each beetle. These data are given in table 2.1 together with the individual total reproduction and the average of the locomotory activity at the same hours during the intensive observation periods.

To compare activity levels of the beetles in the pre-reproductive period and in the reproductive period the activities are expressed as a percentage of the total activity of all beetles in the experiment.

TABLE 2.1 The relationship between the locomotory activity (LA) in the pre-oviposition and in the oviposition period and the egg production of a beetle. (Spearmans r :ab r=.87, P=0.009; bc r=.81,P=0.015; ac r=.56, P=0.093)

beetle no	1	2	3	4	5	6	7	8	9	10
egg production	376	73	320	32	113	134	141	211	198	465
a) eggs% of total	21.0	4.8	17.9	1.8	6.3	7.5	7.9	11.8	11.1	26.0
b) LA in repro%	25.4	4.7	9.8	1.4	5.4	2.6	11.1	7.4	24.4	32.9
c) LA.in pre-repro%	27.1	9.0	11.8	10.5	16.7	10.1	23.1	7.9	23.9	42.2

The table shows that if the activity and the egg production are ranked in increasing order beetles with a high level of activity have also a high egg production. The ranks of locomotory activities in the pre-reproductive period and in the reproductive period resemble each other quite well, though not yet significantly so. The table also shows the great differences in the general level of activity between the beetles, for instance beetles 2 and 4 are 'low activity' beetles and 1 and 10 are 'high activity' beetles.

2.1.3 Discussion

Under the highly simplified experimental conditions the course of locomotory activity through the day at constant temperature apparently follows a rhythmic periodicity with a peak at daytime and a dip at night, although the latter was not measured in the experiments. This rhythmicity is similar to observations in other carabids (Greenslade, 1963; Luff, 1978). For example the nocturnal groundbeetle *Pterostichus oblongopunctatus* L. at constant temperatures shows a clear peak during the night and non or a low activity during daytime (Brunsting, 1983). But in this species the activity increases with increasing temperature and extends partly to the daytime. In *P. coerulescens* at field temperatures nocturnal activity amounts to approximatly 10% of total activity (Greenslade, 1963) and the level of this nocturnal activity probably depends on night temperature. Although it was not measured in the experiments the high activity, at the start of the photoperiod after two days of starvation, may be an indication that nocturnal activity was raised also. In the field the difference between diurnal and nocturnal activity will be more extreme, because of the difference between daytime temperatures and those occurring during the night.

Satiation level influences the level of daily locomotory activity. The increase

from a low activity level after satiation till the maximum level after two days corresponds closely to the time needed for a beetle to digest the food at 20 °C (Mols, 1988). The effect of satiation, or the inverse, hunger on the level of locomotory activity of insects was first found by Edney (1937) who provided quantitative data that starvation for a few hours caused a marked increase in the 'spontaneous activity' of the locust *Locusta migratoria migratorioides*. Further evidence is given in later papers by Ellis(1951) and Chapman(1954). Barton-Browne and Evans (1960) studied the effect of feeding and starvation on locomotory activity in the fly *Phormia regina* (Meigen). It was found that flies fed glucose, fructose or mannose were much less active than were flies that had been starved for 24 hours. Immediately after feeding flies were less active than any other time, but activity increased progressively thereafter. Evidence was given that locomotory activity is some function of crop volume and, hence of the rate of crop emptying. This last hypothesis corresponds closely with the observations in *P. coerulescens*. Also Sirota (1978) found that the larvae of *Culex pipiens molestus* moved more intensively at low food levels than at higher ones. Williams (1959) was able to increase the activity during day of the nocturnal carabid *Pterostichus madidus* by feeding the beetles during daytime only. Grüm (1966, 1971) found that starving beetles showed a higher overall locomotory activity and more activity by daytime.

The locomotory activity at 12 °C (10% of that at 20 °C) was extremely low. One may wonder whether this is caused solely by the slow decrease of the relative satiation level after satiation or by a combination of temperature and relative satiation level. The relative satiation level can be estimated with relative gut emptying rate at 12 °C (Mols, 1988). The food was offered every third day thus, after 54-68 hours RSATL did decrease to about 20%. The relative activity coefficient at 20 °C for this hunger level is about 0.45 (see fig. 2.4). If is assumed that maximum daily activity (= 5.3 hours) is the same for each temperature, the total daily activity at the third day should be approximately 2½ hours. Thus in the observation period of a quarter of an hour at noon (according frequency distribution of total activity in fig 2.2) the beetles should be 0.13*150/4 = 4.9 minutes active (or 32.5% of the observation period), but only 10% activity was observed. This is an indication that total daily activity is also directly temperature-dependent and not only governed via the satiation level and that it decreases with decreasing temperature. This is also known from field observations (Luff, 1978, Kegel, 1990) The latter states that in diurnal species daytime activity is positively correlated with soil temperature.

It may be hypothesized that for insects starvation is a direct stimulus for locomotion but that its level also depends directly on temperature. The metabolic rate of poikilothermic animals increases with increasing temperature. This was also found in *P.coerulescens* (Mols, 1988). This increases the need for food. Therefore the duration of locomotory activity and/or the speed of walking have to be extended with increasing temperature to be able to cover a larger area in search for food. In *P.coerulescens* we know now that both speed (Mossakowsky, 1985) and locomotory activity are increased.

In the experiments the individual difference in locomotory activity was very high. This individual variation in locomotory activity was strongly correlated with egg production. As the latter results from a high intake of food and a rapid and efficient food conversion it may be hypothesized that the relative rate of gut emptying (RRGE) and the efficiency of food conversion (EFF) (See Mols, 1988) are the most important variables at this level.

Luff(1978), Desender et al.(1984) and Kegel (1990) did not found differences in daily activity patterns of males and females, which is confirmed by the present study.

2.2 Analysis of walking patterns

2.2.1 Method

Set up for observations in the laboratory.

The beetles were studied in an artificial arena of 85-100 cm. The substrate consisted of loamy sand with some litter and a few heather plants. Video-equipment was used to registrate the walking pattern of the beetle (fig. 2.5).

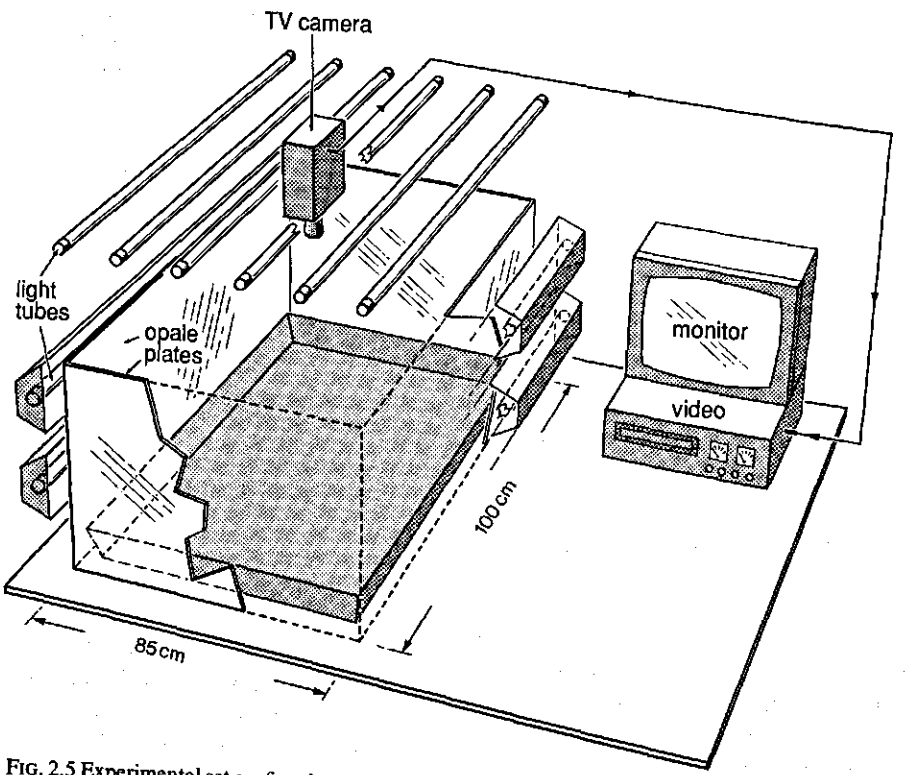

Fig. 2.5 Experimental set-up for observing of walking patterns in the laboratory.

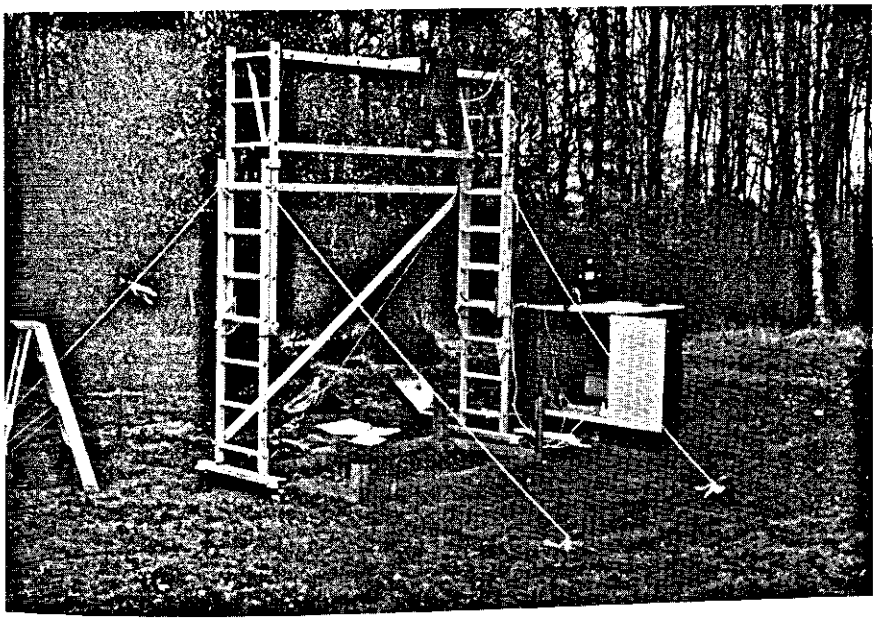

FIG. 2.6 Experimental set-up for observing of walking patterns in the field.

To prevent possible orientation of the beetle to an unequal light distribution or to a horizon silhouet, the experimental arena was enclosed by four opal Perspex plates, which spread the light of the light tubes behind them. A row of 6 fluorescent light-tubes hung above the arena. The light intensity was about 1800 lux. The temperature during the observations was 20 ± 1 °C.

Set up for field observations.

To registrate the walking patterns in the field an arena was constructed of 100*200 cm. The temperature in the arena was registrated by thermo-couples. Here also video-equipment was used to registrate the walking behaviour (fig 2.6). The intention here was to see how far the walking behaviour was comparable with that found in the laboratory. The observation equipment only allowed observations during dry weather. The vegetation in the arena was more dense than in the laboratory set up.

Beetles were marked individually with small dots of yellow paint on the elytra.

Experiments.

The walking patterns of beetles with different motivational states were observed. The beetles used in the observations were weighed before and had a known quantity of food in their gut. The hunger levels ranged from: starved for three days at 20 °C (RSATL = 0) to completely satiated (RSATL = 1). The different relative satiation levels were obtained by feeding beetles up to satiation and then starve them for different time periods before recording the walking

behaviour. Before the observations the beetles were brought into the arena where they were allowed to adapt to the situation for approximately half an hour.

The observations made were:

a) the walking pattern of the beetle without extra feeding. This pattern represents the behaviour belonging to a specific relative satiation level. As time passed on during these observations the appropriate RSATL was calculated for each walking pattern recorded.

b) the walking pattern after consumption of a small prey. A weighed maggot of 1-2 mg was carefully offered at the point of a long pincet just before the mandibles of the beetle. In most cases the beetle accepted the maggot and started feeding immediately. The appropriate RSATL of the beetle was calculated.

c) The walking pattern in an arena with prey clusters. Small prey clusters consisted of 7 maggots of 2 mg. at 10 cm from each other: One in the centre and the others at the corners of a hexagon at a distance of 10 cm from the central one.

Analysis.

The recorded walking patterns were traced on a plastic sheet taped on a monitor. The walking pattern was recorded in units of two-second steps. The positions of the two-second points was read into a computer by means of a magnetic tablet. The walking patterns along the borders of the arena were excluded for analysis to prevent edge effects. The walking of the beetles was frequently interrupted by short or long stops. Stops lasting less then one second were included into the walking time. The duration of a walking pattern (a path or a track) varied from a few minutes to a quarter of an hour depending on the activity of the beetle).

A path (or a track) can be represented by a sequence of points (X_o,Y_o), (X_1,Y_1)..., (X_N,Y_N) such that for any i (INTEGER,$1 \leq i \leq N$), the ith step is a vector $Pi=(X_i-X_{i-1},Y_i-Y_{i-1})$ with length Pi. Because these points are measured at constant time intervals Pi also represents the velocity of the beetle during that period.

The value of the change of direction between vectors Pi and P_{i+1} is measured algebraically by the turning angle $_i$ ($1 \leq i \leq N-1$). The distribution of changes of direction is characterized by a mean vector M (Batschelet, 1981). Its orientation, $M = \text{arctg}(\Sigma\sin\alpha_i/\Sigma\cos\alpha_i)$, defines the angular mean of the distribution. To take into account the forward tendency of locomotion of most animals, the distribution of changes of direction is taken to be symmetrical and have an angular mean $M=0$. The mean vector length r is defined as $r=(\Sigma 2\cos\alpha_i+\Sigma 2\sin\alpha_i)^{1/2}/(N-1)$. It ranges between 0 and 1 and expresses the concentration of the distribution around M and it offers a measure of correlations between the directions of successive steps. When this correlation is zero one obtains the random walk model, when the correlation is one a straight line movement is obtained.

Thus to characterize the tracks the following variables were estimated from the experiments:

1. The turning rate in degrees per time unit and turning angle per length unit respectively.
2. The mean, standard deviation and kurtosis of the frequency distribution of the turning rates according to the TUKEY distribution (Montford & Otten, 1976). This is a theoretical distribution which can be fitted to a range of experimentally observed frequency distributions, from uniform to contagious. It is a symmetrical distribution and it is characterized by three parameters: The mean (M), the standard deviation (σ), and a kurtosis related parameter (K). In its cummulative form the distribution can be described by:

$$Xp = M + \sigma * Yp \qquad (4)$$
$$Yp = (p^K - (1-p)^K)/K \quad \text{if } K \neq 0$$
$$Yp = \ln(p/(1-p)) \quad \text{if } K = 0$$

p = cumulative frequency of the turning rates $\{p = P(\Phi < x)\}$

Calculation of the parameters is done according to Sabelis (1981). The standard deviation of the frequency distribution offers information on the windingness of the track. The higher the standard deviation the more winding the track. The kurtosis tells us more about the form of the distribution curve, whether it is relatively 'flat' or 'sharply peaked' at its mode. According the value of k the following distributions can be obtained:

k = -0.85 :Cauchy
k = 0 :logistic
k = 0.14 :normal
k = 1 or 2 :uniform

3. The velocity, expressed in cm/sec. To obtain information more rapidly a part of the tracks were divided in 10 second parts and analysed by hand for the walking velocity only.
4. The concentration around M according to the length of vector r.

All these variables were analysed for the whole range of RSATL to examine possible relationships.

2.2.2 *Results.*

General observations.

Visual observations on the walking tracks of beetles in different motivational states soon revealed that there were three distinct types of walking. Hungry beetles walked more straight and at a higher speed. Beetles with some food in their stomach up to satiated walked more winding and also slower, while beetles that had consumed a prey showed a very winding walking pattern at a speed that gradually increased. When no other prey were found these walking patterns have been given the indications of straight (also sometimes called high speed

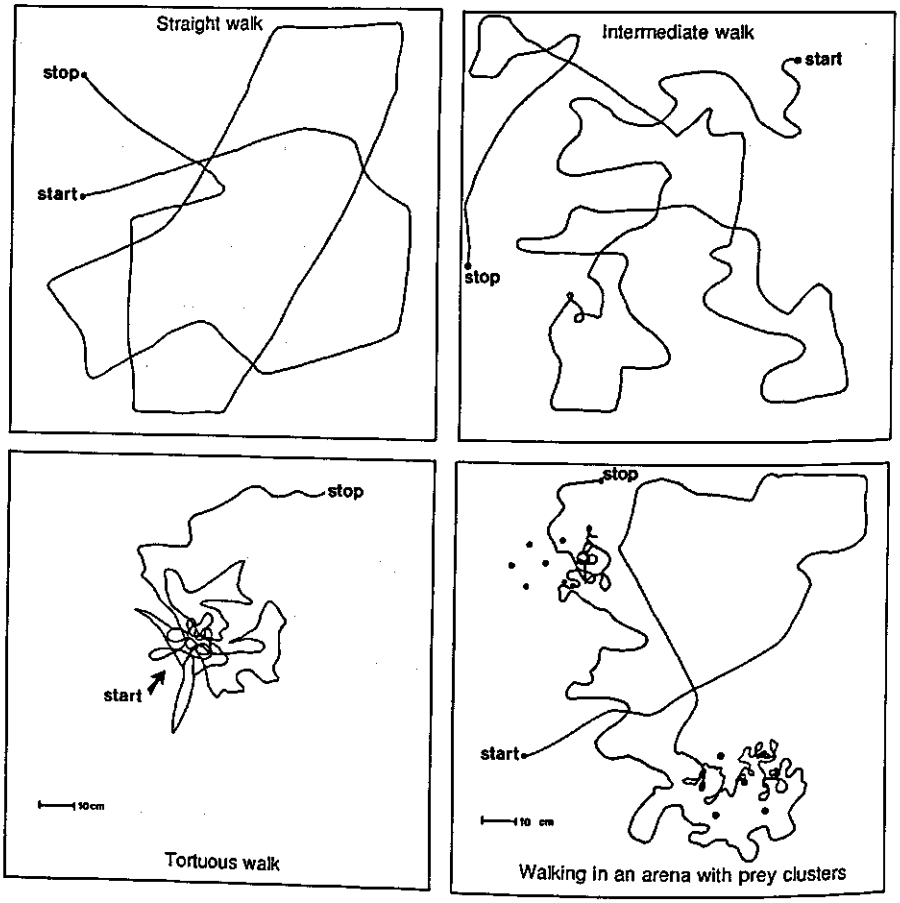

FIG. 2.7 Types of walking patterns observed in *P.coerulescens*.

walking), intermediate and tortuous (TW) walk, respectively. These patterns are shown in fig 2.7. The characterisation of these patterns in turning rate and speed is given in table 2.2. When more prey items are found in a prey cluster tortuous walk continues and remains very winding at a low walking speed.

Turning rates.

The average turning rate expressed in degrees/second and the turning angle in degrees per cm. of the different tracks increase with the windingness of the track. Although hungry beetles which perform straight walk showed a smaller average turning rate than those having a RSATL > 5% this difference was not significant. However, the average turning angle per cm is significantly smaller for straight walking beetles than for intermediate walking ones.

The average turning rate of tortuous walk is larger than that of an intermediate walking pattern. If the beetle walks in a prey cluster after each consumption

TABLE 2.2 Speed (cm/sec), turning rate (degr/sec), turning angle (degr/cm) and concentration grouped according to walking pattern and motivation level (RSATL < 5% and RSATL > 5%) and for tortuous walk in and outside a prey cluster (n = number of beetles, SE is the standard error of the mean)

		Speed		Turning rate		Turning angle		Concentration	
	n	cm/sec	SE	degr/sec	SE	degr/cm	SE	mean	SD
Straight (RSATL < 5%)	20	4.66	0.71	16.00	4.7	3.51	0.97	0.76	0.1
Intermediate (RSATL > 5%)	20	2.2	0.33	19.64	2.91	9.34	1.32	0.68	0.07
Tortuous walk	23	1.04	0.22	23.5	2.77	23.33	2.65	0.59	0.08
TW in prey cluster	4	1.03	0.34	30.2	3.16	30.1	3.08	0.43	0.08

the tortuous pattern starts over again, this results in an even larger average turning rate and turning angle.

The turning rates per 2 seconds of all the tracks grouped for the three walking types were summarized in frequency distributions, which appear to be symmetrical around zero and extend from –180 degrees to +180 degrees (fig. 2.8). The

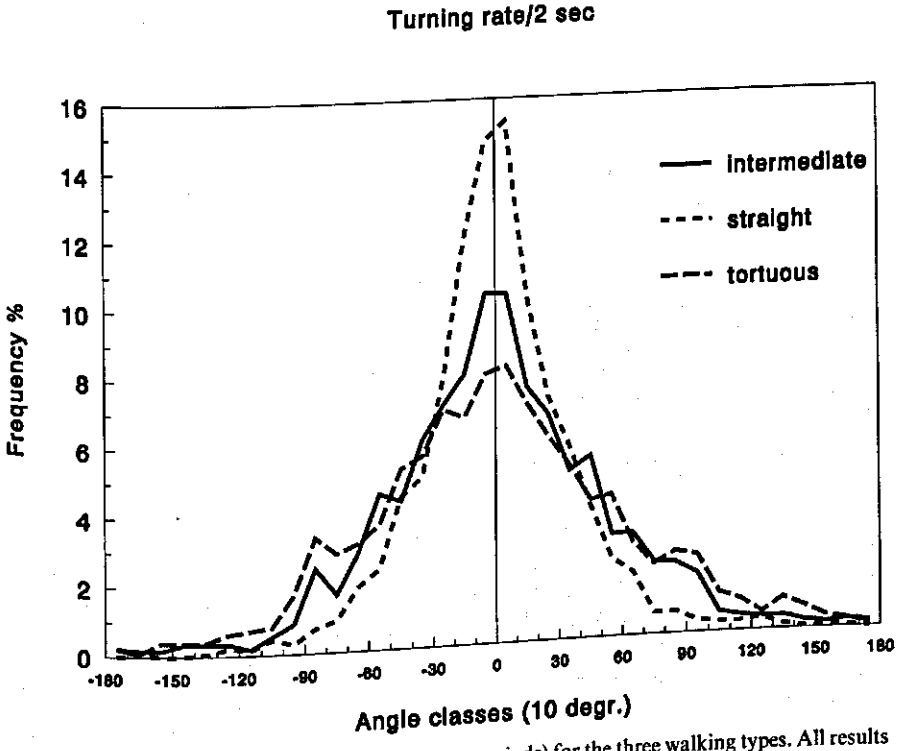

FIG. 2.8 Fequency distribution of turning rate (2 sec.periods) for the three walking types. All results of observations combined.

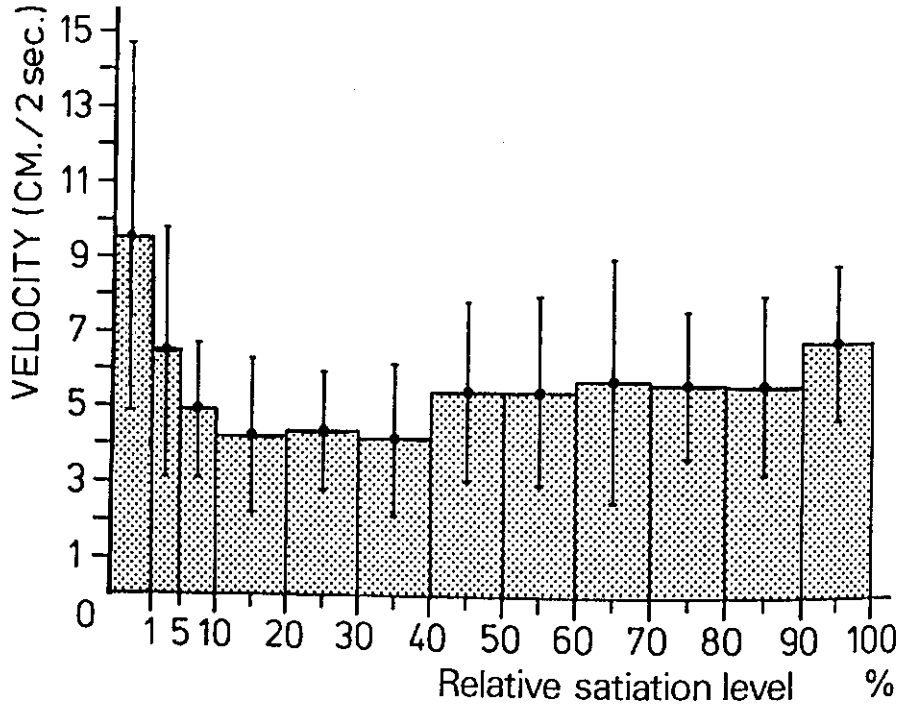

FIG. 2.9 Walking velocity at different relative satiation levels at 20 °C

more winding the walking type the larger the standard deviation of the distribution.

Velocity

The relationship between walking speed and relative satiation level, with exclusion of tortuous walk, is shown in fig. 2.9. In this figure both the results of completely analysed tracks and those of tracks which were only analysed for speed are combined. The figure shows a breakpoint around a satiation level of 5%. Above 5% satiation the average velocity is almost constant having a tendency to increase a little at the higher satiation levels. But in general the velocity is approximately 2.5 cm/sec, which is a little bit higher than the speed found in the completely analysed tracks. Below a relative satiation level of 5% walking velocity increases rapidly to approximately 5 cm/sec. Thus using velocity as a criterium 2 types of walking patterns could be distinguished. After prey consumption the beetle resumed walking at a very low speed. Gradually the speed increased until it reached a velocity of approximately 2-3 cm/sec. The average walking velocity after consumption of a prey was approximately 1 cm/sec.

When the speeds of all the time steps of all the tracks of these different walking patterns were grouped according to the three walking types this gives fig. 2.10. The frequency of these distributions of velocities per 2 sec. time steps shows

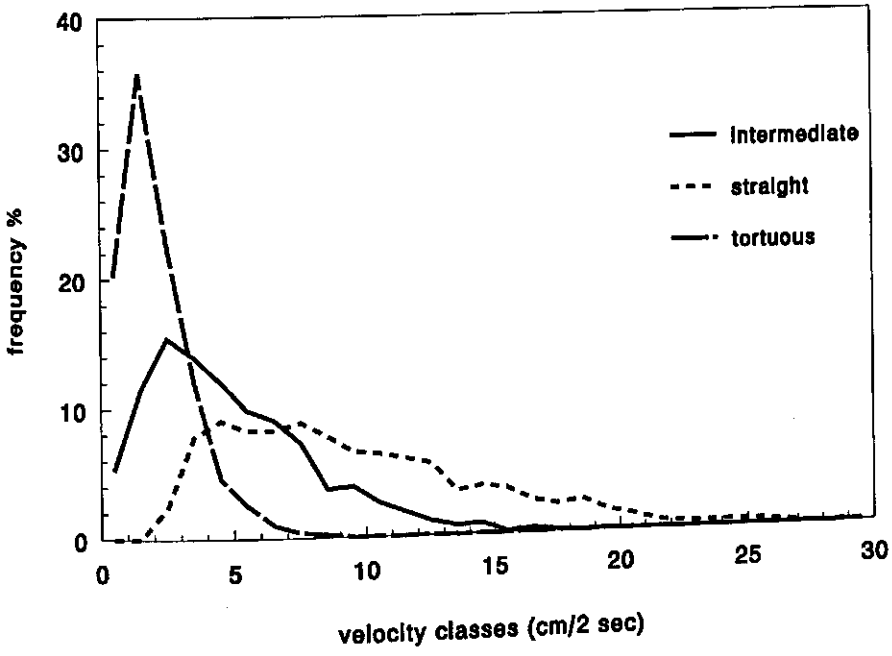

FIG. 2.10 Frequency distribution of walking velocity for three walking types.

that tortuous walk appears to have the narrowest distribution. The frequency distribution of the other types are highly leptokurtic and largely overlap, straight walk showing more time steps with a high speed than intermediate walk.

Relationship between velocity and windingness.

When the velocity is correlated with the turning rate, it appears that the mean turning rate decreases significanly ($r=0.65$, $P<<0.01$) with increasing speed. However, the variation is high (fig 2.11). The relationship between velocity and average turning angle per cm shows less variation. The relationship would be a perfect hyperbole, if the turning rate was constant for all velocities. In fig. 2.12 a hyperbole (Y1) with $x=0.55$ as limit is not fitting well through all the points. Most of the turning angles of tortuous walk are positioned left of the curve. This may be an indication that tortuous walk is another walking type. A power curve (Y2) offers the best fit through all the points. This curve has a limit at $x=0$ which indicates that the beetle turns around on the spot. The turning angle changes gradually and continues from 360 to almost zero degrees with increasing speed.

From each track the frequency distribution of the turning rate per 2 sec. time step was made. A Tukey distribution was fitted to the angle frequency distribution and thus for each track the appropriate standard deviation and the kurtosis were calculated (according to Sabelis, 1981). Using all the analysed tracks, relationships were estimated between walking velocity per 2 seconds (V) of the beetle

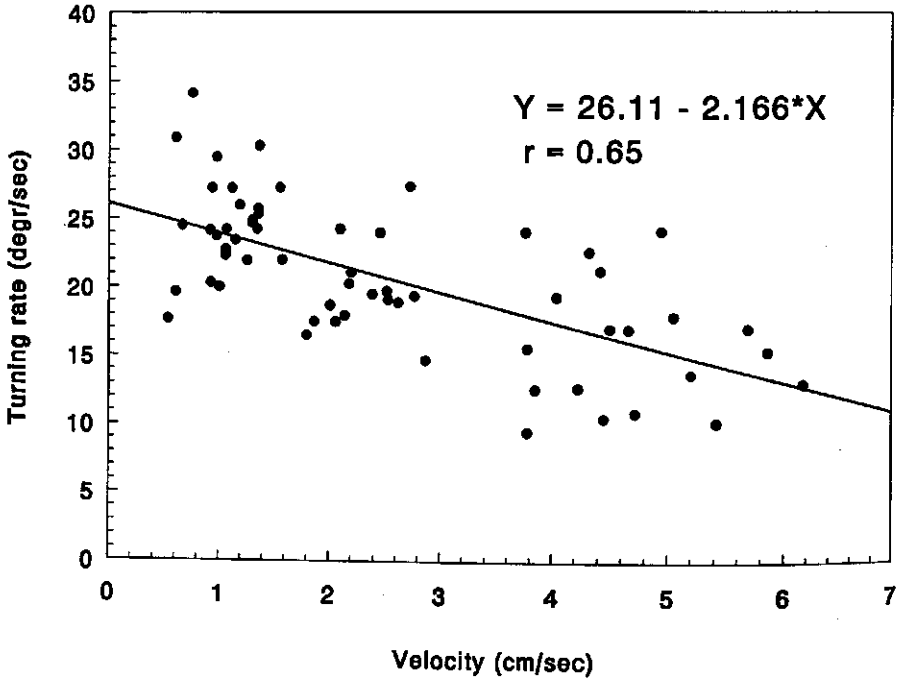

FIG. 2.11 Relationship between walking velocity and turning rate.

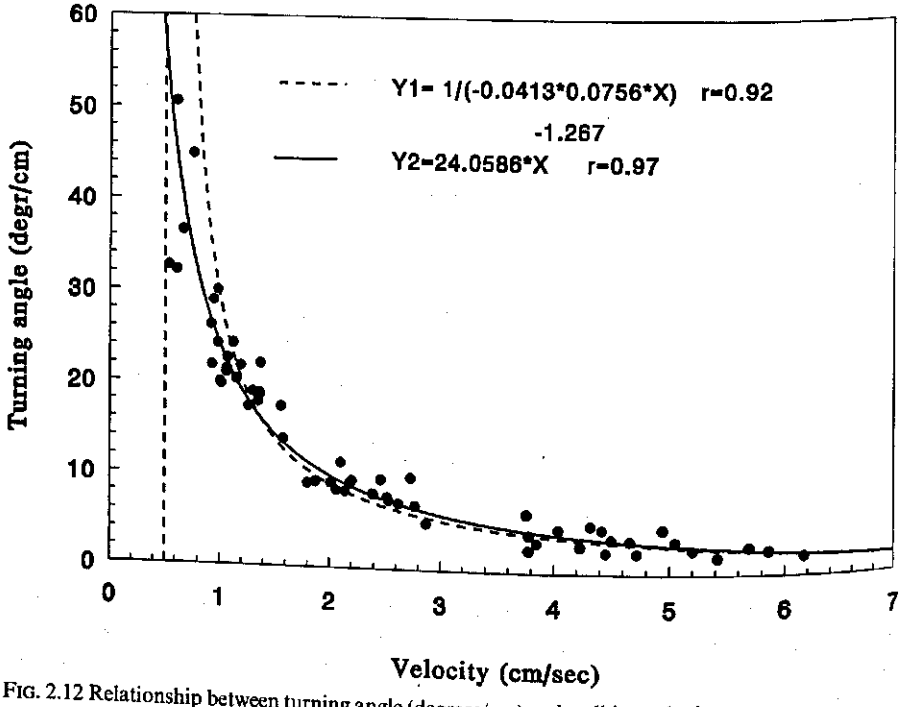

FIG. 2.12 Relationship between turning angle (degrees/cm) and walking velocity.

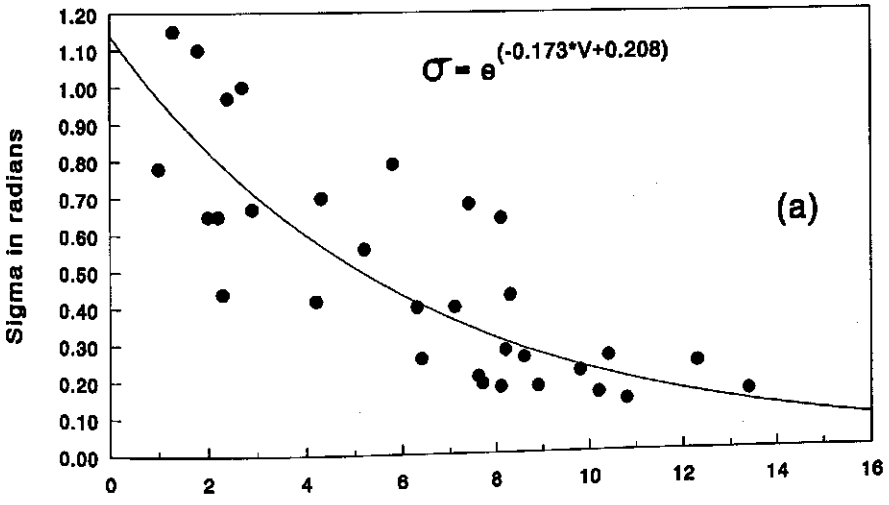

FIG. 2.13a Relationship between the SD of the frequency distribution of the turning rate of a walking track (fitted with the Tukey distribution) and average walking velocity.

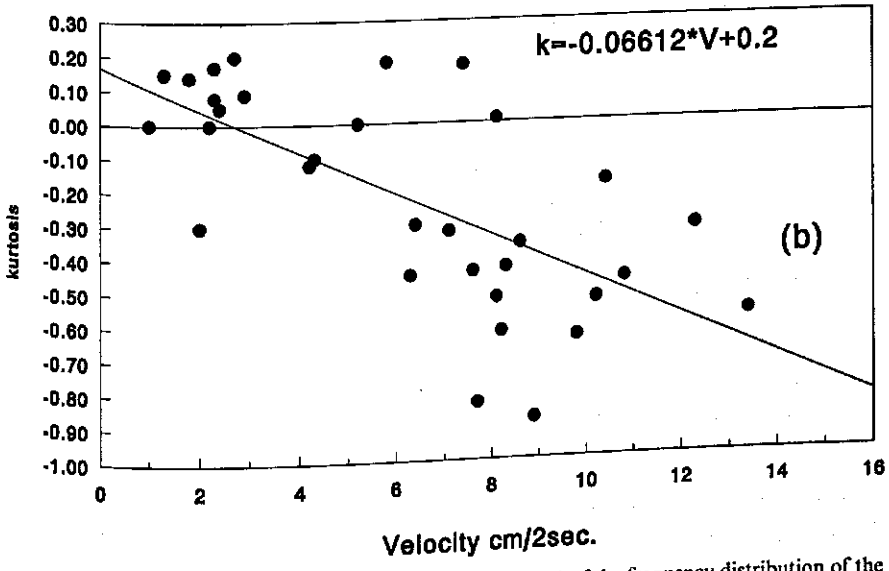

FIG. 2.13b Relationship between kurtosis related parameter K of the frequency distribution of the turning rate (fitted with the Tukey distribution) and walking velocity.

and its standard deviation (σ) and kurtosis (K) of the turning rates frequency distribution. A significant relationship was found (fig 2.13 a+b). The faster the beetle moves the narrower the distribution and the smaller the standard deviation of it, and the more negative kurtosis.

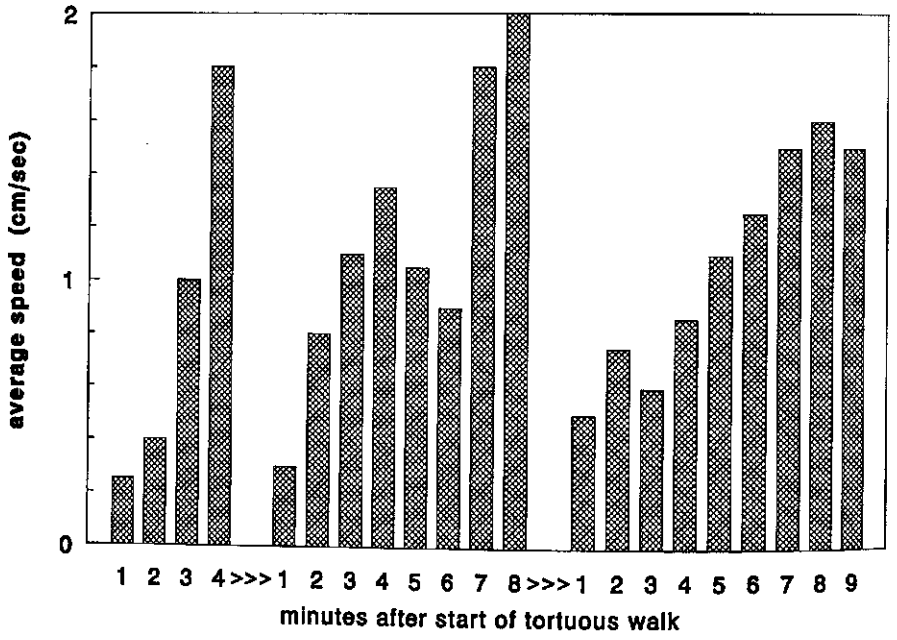

FIG. 2.14 Example of increase of walking speed in tortuous walk after prey consumption.

This gives the following expressions:

$$\sigma = \exp(-0.173*V+0.208) \qquad r^2=.7 \quad (p<0.01) \qquad (5)$$

$$K = -0.0661*V+0.2 \qquad r^2=.49 \quad (p<0.01) \qquad (6)$$

Duration of tortuous walk.

After prey consumption the velocity of the beetle gradually increases and when no other prey is found rapidly the track straightens out and either becomes intermediate walk or the beetle stops walking or reaches the edge of the arena. An example of such an increase of speed during the course of a typical tortuous walk track is given in fig. 2.14. The time span of tortuous walk appeared to be a function of the relative satiation level (fig. 2.15). When the gut is almost empty this behaviour may last for about 11 minutes, but when the relative satiation level exceeds 80% it does not occur anymore.

Concentration

The concentration parameter r decreases with the tortuousity of the track (fig. 2.16). When all the walking tracks are taken for estimation of the correlation between walking velocity and concentration this relationship shows to be significant ($r=.61$ for $n=67$, $p<<0.01$). The combined walking patterns (table 2.2) show no significant difference between the mean values of straight and interme-

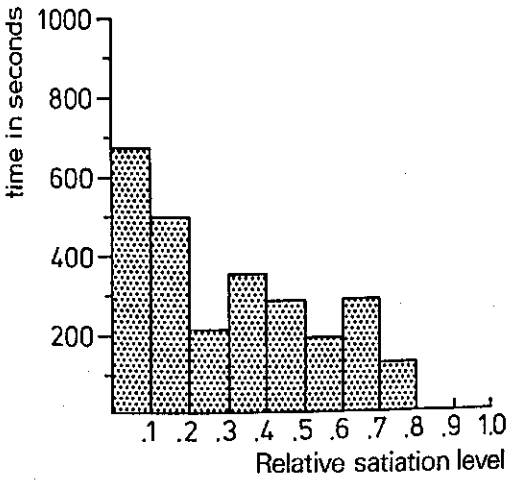

FIG. 2.15 Relationship between duration of tortuous walk and relative satiation level.

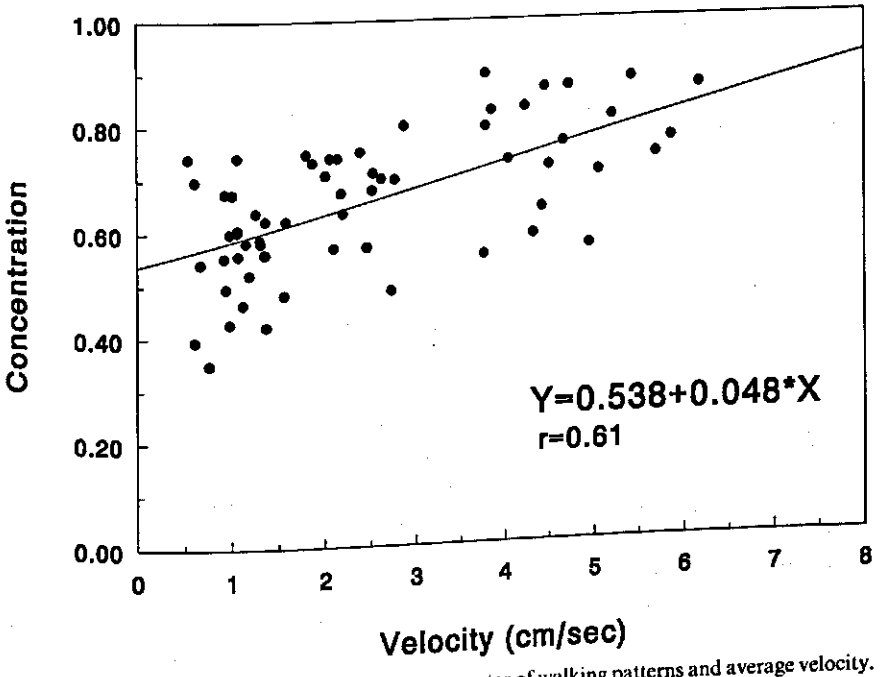

FIG. 2.16 Relationship between concentration parameter of walking patterns and average velocity.

diate and between intermediate and tortuous walk but it does between straight and tortuous walk.

Field observations.

Beetles walking in the arena could be observed rather easily by eye. On the

video they were more difficult to follow, especially when they walked in the vegetation. This hampered the registration of the tracks and limited the number of tracks which could be followed. At least one track per beetle was analysed. The results are given in table 2.3. The speed of walking in the field was usually lower than found in the laboratory, both for hungry beetles and for those with some gut filling. After prey consumption in the field, tortuous walk occurred also but at a lower velocity.

When a beetle was placed in the arena together with prey clusters of ± 10 maggots, it could be observed also that during sunny weather the beetles took the maggots from the cluster and dragged them to a shaded place in the vegetation. After prey consumption they returned in a rather straight way to the prey cluster to capture another prey. This process was repeated untill satiation. When it was cloudy the beetles stayed in the cluster until satiation. When more beetles were placed in the arena in the prey clusters often fights between beetles could be observed. Then dragging away of prey from the prey clusters occurred more often.

TABLE 2.3. Observations on velocity (cm/sec), turning rate (degr.sec), turning angle (degr/cm) and concentration of beetles walking in the field. The temperature varied between 17-23 °C. The results are grouped for two satiation levels: hungry beetles (RSATL < 5%, straight walk) and beetles with some gut filling (RSATL > 5%, intermediate walk), and for tortuous walk. (n = number of beetles, SD = standard deviation between the tracks, SE = standard error of the mean of the tracks).

		Speed		Turning rate		Turning angle		Concentration	
	n	cm/sec	SE	degr/sec	SE	degr/cm	SE	mean	SD
RSATL < 5% (straight)	9	4.3	0.4	16.2	5.1	4.8	1.2	0.74	0.15
RSATL > 5% (intermediate)	8	1.6	0.25	22.2	7.0	13.8	4.2	0.63	0.10
Tortuous walk	6	0.9	0.15	28.5	10.0	32.4	11.2	0.55	0.12

2.2.3 Discussion

Observation of walking tracks with the help of video equipment is a nice but also a very laborious technique. In the laboratory the tracks could be followed rather easily. The field observations gave more problems. It was especially difficult to indicate the timesteps correctly. The time lag between the moment of hearing the time signal and drawing the time mark on the plastic sheet attatched to the monitor was a source of errors. This time lag is in the order of 0.3-0.5 sec. If the time lag would be constant there is no problem, but because of its variability it may result in an error of about 10-20% of speed estimates. At low velocities marking give other problems, because distances are small and the marks come too close together by which the velocities estimated have to be considered cautiously.

Pauses smaller then 2 seconds have been omitted. They occurred irregularly and in fact do decrease the calculated average velocity of the track. Brunsting

(1983) got the same problems during his observations of displacement of *P.oblongopunctatus* in the laboratory, but he even included pauses up to 30 seconds into the activity pattern.

When we correct his measurements adequately the speed of active, well fed beetles appeared to be: at 7 °C 0.85 cm/sec, 10 °C 1.1 cm/sec, 16 °C, 1.9 cm/sec, 20 °C 2.2 cm/sec. and at 25 °C 3.4 cm/sec. These velocities are about the same for fed beetles of *P.coerulescens*. As beetles of both species are of about the same size this could be expected (Evans, 1977). Just as in *P.oblongopunctatus* also in *P. coerulescens* a raise of temperature increases the speed of locomotion as was observed by Mossakowski and Stier (1983). They did experiments with hungry beetles and forced them through a tunnel and found at 10 °C 1 ± 0.2 cm/sec, at 15 °C 3 ± 0.5 cm/sec, at 20 °C 5.8 ± 1 cm/sec, at25 °C 8.5 ± 1 cm/sec and at 30 °C 9 ± 1.5 cm/sec. The velocity at ± 20 °C is about similar to that found in my observations for hungry beetles.

In this analysis of the walking pattern spatial and temporal components of the walking pattern are blended. To get insight in the effect of velocity on the structure of the path both its relationship with the turning rate (degrees/sec) and the turning angle (degrees/cm) have been considered. From the observations it is quite clear that the turning angle depends on the speed of walking. The turning rate on the other hand is for most of the tracks almost constant. But at extreme low and high velocities the rate is respectively higher or lower. This results in a significant negative correlation between turning rate and velocity (fig. 2.11). when all the tracks are involved. Therefore, the turning angle (= turning rate/speed) becomes relatively smaller as the speed increases, otherwise the product of turning angle and velocity would result in a constant value (= angle/sec). This is mainly due to the relative high turning rate made at a low speed and the low turning rate at high speed. At low speed this results in a strong winding searching pattern. This is what is usually referred to as 'area restricted search'. This offers an argument for the hypothesis that the tortuosity of the track may be determined by more factors than by low speed alone. It may also be that at low velocities, after prey consumption, both an extra internal or external stimulus makes that the the distribution of the turning rate becomes wider and the average rate becomes higher. This extra high turning rates may be initiated by the remains of the prey (external stimulus) or by a stimulus from the crop expansion. When no other prey is discovered this stimulus may wane so that the beetle returns to the speed it had before the previous feeding.

Differences between field and laboratory observations in *P.coerulescens* especially hold for the walking velocity. This was most probably caused by the vegetation density which was much higher in the field than in the laboratory experiments. Structure and density of vegetation together with the roughness of the soil surface (Mossakowski and Stier, 1983) are important factors that influence the speed and thus the walking pattern of the beetles. Although velocity in the field was lower than in the laboratory the same three walking patterns could be observed both in laboratory and field. This is a valid indication that in this beetle these walking patterns are general, and that walking speed is mainly gov-

erned by the hunger level in combination with temperature, soil surface and vegetation structure.

2.3 Reaction distance

2.3.1 Method

Reactions of beetles towards prey were observed in an arena. These reactions could be: a sudden stop with distinct waving of the antennae, a sharp change in direction towards the prey, biting the prey or just investigating the prey with antennae and maxillae. When a beetle showed a reaction towards a prey this was called a discovery.

2.3.2 Results

In an arena most hungry beetles observed showed reactions when they touched a prey item (maggots of 2 mg). The percentage of beetles being in the immediate vicinity of a prey and reacting with a sharp turn or with distinct antenna waving decreased with increasing distance. Between a distance greater than zero but smaller than 1 cm, 75% showed reactions. Between 1 and 2 cm, 40% reacted, and this decreased to 30% when the distance between prey and predator was between 2 and 4 cm. When the distance exceeded 4 cm no reaction of the beetles was observed (fig 2.17).

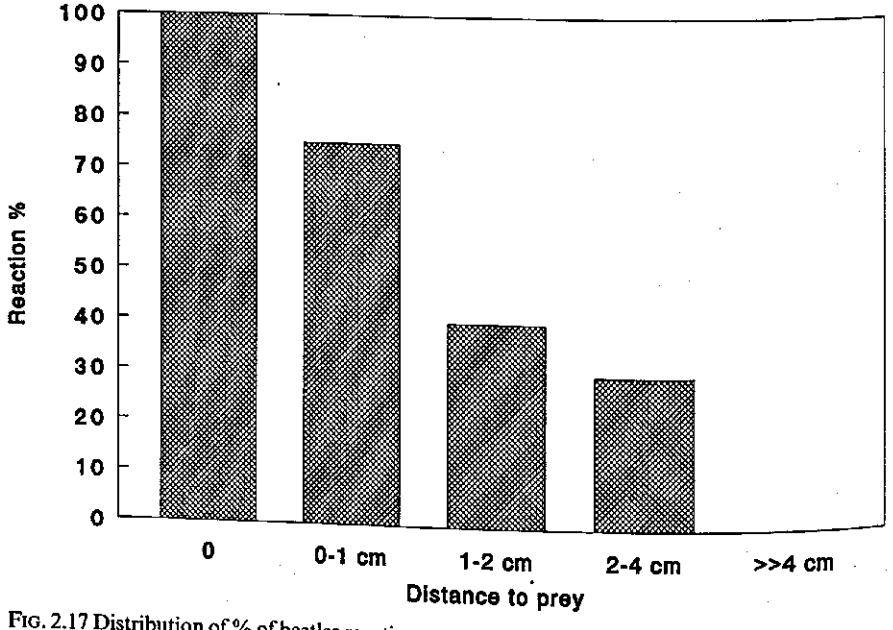

Fig. 2.17 Distribution of % of beetles reacting to prey depending on distance to the prey.

2.3.3 Discussion

P.coerulescens is a diurnal beetle with reasonably developed eyes which are able to observe movements of objects in its neighbourhood (Pers. observations). This suggests that hunting by eye may be a means of tracing prey. Antenna waving is often observed in the immediate vicinity of the prey, which suggests that odours may also be involved in prey searching. However, preliminary experiments on the walking sphere at the Department of Entomology (for description of apparatus see Thiery & Visser, 1986) with *P.coerulescens*, did not show reactions to odours of maggots, contrary to the carabid *P. madidus* that inmediately reacted by changing its walking direction. The observation of small prey seems to be restricted to distances up to 4 cm, but from 0 to 4 cm the proportion of beetles reacting decreased sharply. Although the beetle often changed direction in the immediate vicinity of a prey it is difficult to distighuish this from an accidental turn, which is also possible, of course. The number of observations is not high enough to give a clear picture. The chance to make such a turn by accident must be known. This can be computed from the observed turning rate frequency distribution. The observed angle directed to the prey must be compared with the chance to make the same turn by accident.

Reaction distance may be influenced by size and movement of the prey, but the latter factor has not been investigated. The beetle surely is not a specific eye hunter such as the carabid *Notiophilus biguttatus* (Bauer, 1975, 1981,Bauer et al., 1977, Ernsting, 1977, 1978). If vegetation hampers sight only short vision is important, and running into a prey just by random movement and making contact with mouthparts and antennae may be an obvious way of prey discovery. Nevertheless, it must be stressed that each enlargement of the reaction distance will have a positive effect on the discovery rate with prey. Each observation of prey by eye at a greater distance than the prey diameter is increasing the efficiency of searching. In the case of *P. coerulescens* doubling the reaction distance should theoretically double the rate of dicovery. But this also depends on the satiation level, because this determines the speed and thus whether the beetle will walk more ore less winding, which in its turn determines the degree of recrossing of the walking path and therefore the effectiveness of the searching expressed as the encounter rate.

The reaction distance was measured from the head of the beetle to the outside of the prey. When predator and prey are considered objects with a specific diameter the real reaction distance of a predator to a prey consists of the prey radius plus the predator radius plus the above mentioned distance (see also Skellam, 1958). The predator has a lenght of about 1 cm and a width of 0.5 cm, a 2 mg maggot measures about 0.5 cm in length and is 0.25 cm wide. As an average for the distance of discovery between prey and predator another cm can be added. Instead of the beetle diameter (1 cm) one can also think about taking the maximum distance between the antennae tips but the average reaction distance then will also be between 1 and 2 cm.

It is not known whether or not hunger elicits an effect on the reaction distance. The results of the few experiments do not give substantial evidence that hunger

is involved. It seems a matter of chance whether or not within a distance of 0-4 cm a beetle discovers a prey.

2.4 Success ratio

Experiments were executed in the laboratory with *P. coerulescens* to assess the relationship of RSATL of the beetle with a few prey types it may encounter in the field.

2.4.1 Method

The observations were executed in large Petri dishes (diam 20 cm) with loamy sand on the bottom. A beetle of known weight and satiation level was placed in the dish with a specific prey item. The following prey types were tested: maggots of the blow fly (*Calliphora* sp.) (2-4 mg), larvae of the Heather beetle *Lochmea suturalis*, earthworms (2 cm long) and Leather jackets (larva of *Tipula* sp., 1 cm long). When the beetle didn't react to the prey after 40 contacts with prey the observations were stopped. Then the discovery rate was considered to be close to zero (smaller than 1/40). After consumption of the prey the beetles were weighed. Later on they were used again. Maggots and Heather beetle larvae were tested over more levels of satiation than earthworms and Leather jackets.

To get an impression of the eagerness of a beetle trying to kill a prey also the attack ratio was measured. The attack ratio differs from the success ratio by that only those discoveries are involved in which the beetle tries to kill the prey by biting. Some observations were also executed with wolfspiders (*Lycosidae*) and ants (*Myrmica* sp.) as prey because they were often found in the gut of *P.coerulescens* (Hengeveld, 1980).

2.4.2 Results

The succes ratio of the beetle with the maggots is found to be clearly related to the relative satiation level. Maggots appear to be very attractive to the beetles even at a high relative satiation level. The attack and the succes ratio are high and run similar even at high satiation levels (fig 2.18a). An attacked maggot is always succesfully attacked. The Heather beetle larvae are also attractive at high satiation levels but an attack is not always followed by subsequent killing of the prey (fig 2.18b).

When earthworms and Leather jackets are encountered a different result is found (fig. 2.18c and d). Earthworms are attacked heavely, they seem to be rather attractive but in most cases the earthworms escape from the attack by giving a strong lash with their body, while also the slime gives problems to the beetle. This behaviour results in a low succes ratio. Leather jackets are also easily attacked, but the skin of the larva is so tough that only with the highest effort, the mandibles of the beetle can penetrate. After a few fruitless attacks the beetle mostly leaves this prey almost unharmed, thus resulting in a low succes ratio.

Wolfspiders are too rapid for the beetle, they always escape and cannot be

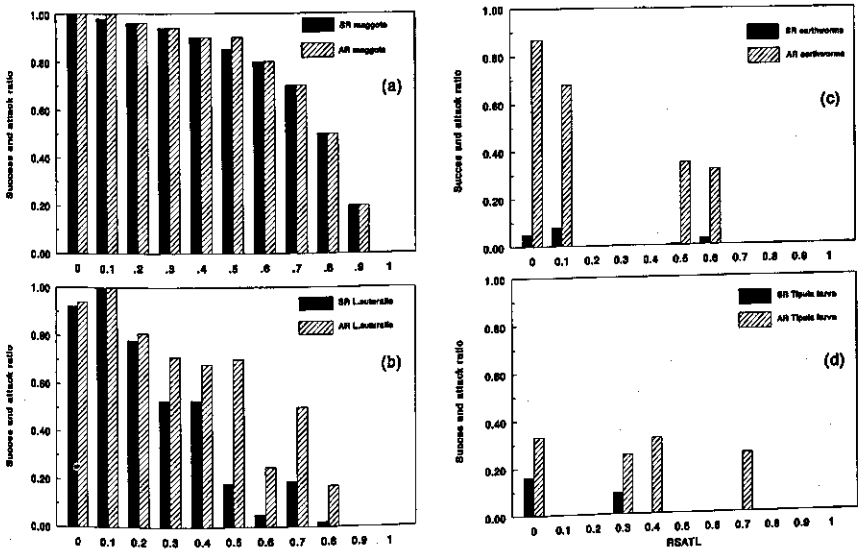

FIG. 2.18 Relationship between both success and attack ratio with relative satiation level of *P.coerulescens* when A) maggots, B) Heather beetle (*L.suturalis*), C) earthworms, D) leatherjackets (*Tipula* sp.) were offered as prey.

captured. The same holds for the ants. The latter attack the beetle furiously, which tries to get rid of them as soon as possible.

2.4.3 Discussion

P.coerulescens is a general predator of all kind of prey (Hengeveld, 1980). Aphids, lepidopterous larvae and diptera form an important part of its diet but also remains of Lycosidae and ants were found. Lepidopterous larvae, maggots and aphids are prey types with a soft body that hardly can defend themselves, which will result in high successs ratio's when discovered by a beetle. This is supported by the experiments with the maggots and with the heather beetle larvae. The experiments show that defense reactions of prey are important esp. in earthworms and that counterattack of ants is even more effective. The rapid wolfspiders escaped by their higher speed. The observation of remains of these two prey types in the gut of *P.coerulescens* must therefore be from dead or injured specimens. Other less rapidly moving spider species may be an easier prey to get by the beetle.

2.5 VALIDATION OF PREDATION IN AN ARENA

Validation of predation and egg production of this carabid under field conditions is hardly possible, because of experimental difficulties. For instance to

get a reliable average of predation a great number of repetitions is necessary and since field conditions change continuously this cannot be reached by direct observations. Egg production can be measured directly by sieving of the soil, but therefore the beetle has to be disturbed by placing it in another arena and this may influence the predatory behaviour negatively. Nevertheless, to get at least some observations of predation in aggregated prey distributions these were made under constant environmental conditions in an artificial arena in the laboratory.

2.5.1 Methods

Observations were carried out in an arena of 100*150 cm. The soil consisted of loamy sand with light vegetation and some leaves and small pieces of bark under which the beetles could hide. The temperature was about 22 °C and the observations were recorded with video (see chapter 2). Only laboratory-reared female beetles, which hatched in late summer and were kept cool at 12 °C and which were not fed before in their adult stage were used in the experiment. A single beetle was used per observation. Before each observation the beetle was set at 20 °C for one day and weighed just before it was placed in the arena. The observational period lasted $1^1/_2$ hour. The observations occurred between 10:00 and 14:00 o'clock, because of diurnal rhythm in locomotory activity of the beetle (chapter 2). Each day one beetle was observed. The prey was *Drosophila* maggots of 2 mg each, which were arranged in two clusters of 7 prey in a hexagonal way with one prey in the centre and placed 10 cm apart. The place of the clusters was randomly chosen but more then 50 cm apart. The maggots were kept at their place in the cluster by a microneedle through the outer parts of their skin.

2.5.2 Results

In the beginning it usually took half an hour before the beetles found the first prey. They walked rather straight and spent a lot of time running around the edge. Capture of the first prey took 36.7 $\pm$ 32.5 minutes (X $\pm$ SD). After capture and consumption of the first prey others followed rapidly. The beetle changed its walking behaviour into an intensive search by walking tortuously and 'border running' did hardly occur anymore. The time between captures without the time needed for consumption (the handling time) in the same cluster was about 4.3 $\pm$ 4.6 minutes (X $\pm$ SD n = 42). The interval time between prey capture in another cluster was 7.5 $\pm$ 5.7 minutes (X $\pm$ SD n = 7). The handling time took 171 $\pm$ 38 sec per prey (n = 57). No relationship between handling time and hunger level could be found. The average prey capture per beetle for the observation period was 5.7 $\pm$ 3.7 (X $\pm$ SD).

2.5.3 Discussion

For most beetles the time needed to capture the first prey is extremely long compared to the following periods needed for the successive captures. This was mostly due to running behaviour along the borders of the arena and to the

straight walking behaviour in that period. This border behaviour may be a consequence of straight walking on such a small surface. It is striking to see that the border behaviour disappears after capture of the first prey. The increase of windingness appeared to be very effective in capturing successive prey even in another prey cluster. Another point is the individual difference in capture succes between the beetles, it varied from zero to 11 prey captured. Whether this occurs by accident or depends on individual differences in behaviour can be solved by simulation of predatory behaviour in an arena as has been done in the next chapter.

3.0 SIMULATION

3.1 DEVELOPMENT OF SIMULATION MODELS

To simulate predation rate and the resulting egg production at different densities and distributions of the prey a model was constructed that integrates the most important components of predation and egg production of the beetle. To analyse the effect of the various components of behaviour this was done in three steps.

1. A model of walking behaviour and prey encounter was developed that simulates the walking patterns and prey discovery at different prey densities and distributions. With this model the importance for the searching efficiency of various components of walking behaviour, resulting in the three observed walking patterns, can be studied. This also offered the possibility to investigate at which prey distribution the various types of walking behaviour are most profitable for the beetle.
2. Integration of the relationship between relative satiation level (without the influence of ovary size) and locomotory activity, succes ratio, walking speed and duration of tortuous walk into the previous model, to study the effect of satiation on predatory behaviour.
3. Integration of ovary growth and egg production into the relative satiation model, resulting in a complete model that, for one beetle at several distributions and densities of the prey, simulates predation and egg production over a season.

3.1.1 Simulation of walking behaviour and prey discovery

A general description of the simulation model of walking behaviour and prey discovery is given below. An annotated computer program listing is given in appendix I.

The following aspects are incorporated in the model:

a) Walking velocity.
b) Standard deviation and kurtosis of the frequency distribution of the turning rate and their relationship with walking velocity.
c) Duration of tortuous walk.
d) Prey cluster scanning and individual prey scanning.
e) Reaction distance to prey.
f) Prey density and prey distribution.

The aspects from (a) to (d) are properties of the beetle, (f) concerns prey pro-

perties and (e) concerns properties of both. In this model satiation effects are not yet incorporated.

Velocity and turning rate.

The average speed of the beetle is introduced as a forcing variable at the beginning of the simulation. Beetles do not walk with a constant speed but show variations in velocity. Therefore each time step a value is taken at random from a uniform distribution around this average value (the speed in a track varied randomly around the average speed with a standard deviation of 50% of the mean as this was observed to occur in the individual tracks of the beetles (chap. 2)). The direction of walking is calculated by drawing randomly a direction from the experimentally established distribution of the turning rate. This is done again at each timestep, and the next angle is added to the former direction which then gives the new direction (fig.3.1).

As the speed (V) of the beetle is known (for each time step this is the distance between two sets of coordinates XP_1,YP_1 and XP_2,YP_2 it is possible to calculate the new coordinates of the beetle with the cosine rule.

$$XP = XP + COS(DIR)*V$$
$$YP = YP + SIN(DIR)*V$$

The walking direction (DIR) of the beetle depends both on the former direction and on the turning rate (A) drawn randomly from the Tukey distribution.

$$DIR = DIR + A$$
$$A = AV + SIGMA * (P^{KURT} - (1-P)^{KURT})/KURT$$

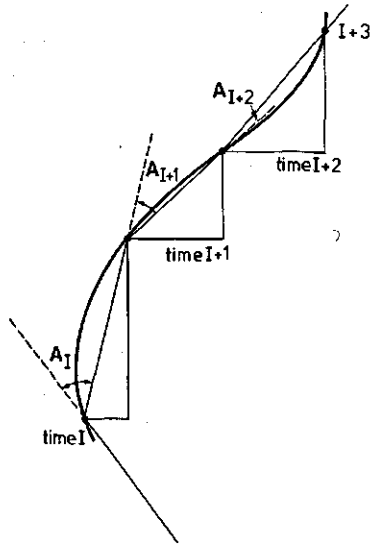

FIG. 3.1 Turning rate (A_I,A_{I+1},A_{I+2}) at consequetive timesteps.

This formula calculates the turning rate/2 sec as a function of the average (AV), the standard deviation (SIGMA) and kurtosis (KURT) of the turning rate distribution (see Chapter 2.).

The model simulates the walking of beetles in an arena of a specific size. The moment the beetle reaches the border of the arena it will rebound into the field.

Duration of tortuous walk.

Just after consumption of a prey, the beetle resumes searching at a very low speed. When no new prey is encountered the speed increases gradually to the speed before consumption or to a level that corresponds with a specific level of satiation. In the discovery model the duration of tortuous walk is kept constant at 300 seconds being the average duration of tortuous walk. During this period the speed gradually increases to the speed at which the beetle was walking before prey consumption. Parallel with the increase of speed the distribution of the turning rate changes from wide to narrow because the speed determines the SIGMA and Kurtosis parameter of the TUKEY distribution.

Prey distribution and prey encounter.

In the program the distribution of the prey can be arranged such that it may vary from random to very aggregated. This is done by putting the prey in discrete prey clusters of a specific size. The numbers of prey in each cluster, the number of clusters and the size of the clusters can be varied. The prey is considered to be immobile. In the clusters they are randomly distributed, and the clusters themselves are also randomly distributed in the arena. The arena is a square which can be varied in size. The clusters are circular.

The area of discovery.

In the model, the beetle is represented as a circular object with a specific radius. The prey is considered in the same way. Together with the distance of prey discovery they constitute the reaction distance (radius predator + radius prey + discovery distance) which varies between 1 and 2 cm. When the beetle is walking it covers a path with a width of 2 times the reaction distance in which it can discover a prey (the area of discovery). In the model prey discovery in the area of discovery is calculated by giving each prey in the cluster coordinates relative to a new coordinate frame. This frame is perpendicular on the moving direction of the beetle during the time step (fig 3.2).

When a beetle moves from one position to the next an area is covered consisting of a strip of 2 times the reaction distance in width but also consisting of the half of a circle at the start and end of the step. When the beetle moves to the next position with a change in direction a portion of the area is covered twice (fig 3.3). Double counting of prey present in that area has to be avoided.

Two situations can be distinguished (fig 3.4, I and II)

I) The distance a beetle covers during one time step (V = the speed per timestep) is larger than its reaction distance.

In this case three area's can be distinguished (fig 3.4, I).

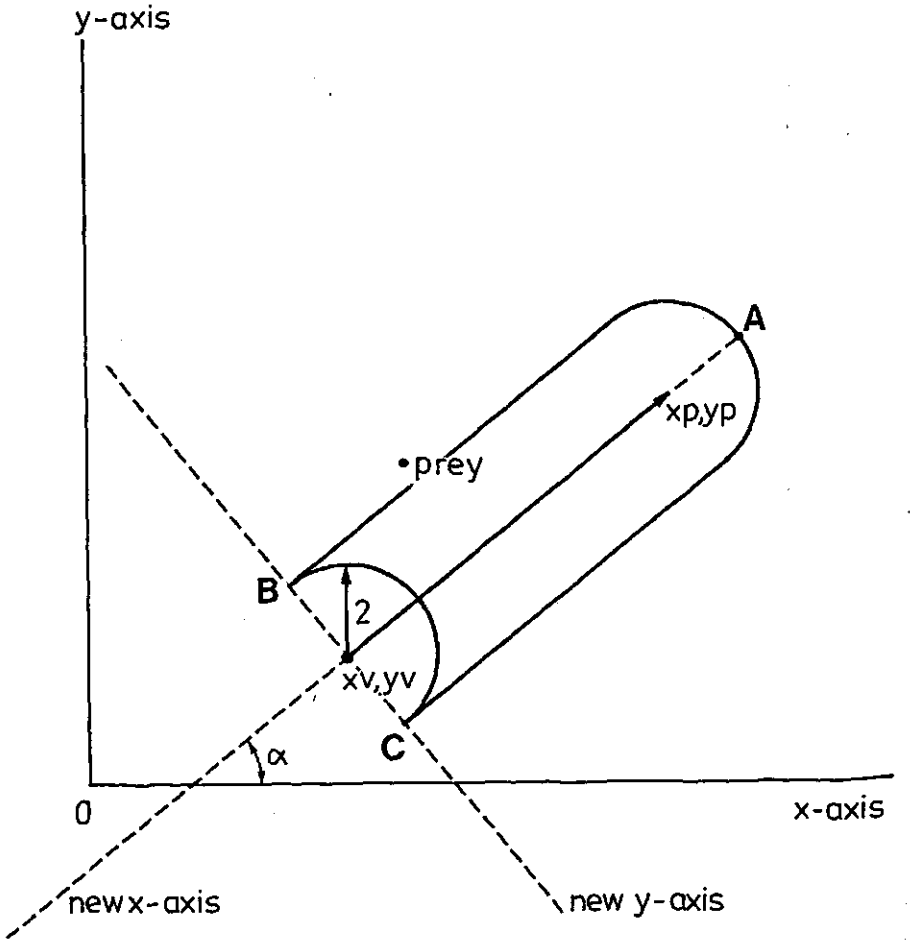

FIG. 3.2 A new coordinate frame is constructed, to determine whether a prey is in the beetles area of discovery. For a number of points the coordinates are given in this new frame. xv,yv=(0,0). xp,yp=(V,0). A=(V+radius,0). B=(0,radius). C=(0,-radius).

A) X-coordinate is smaller than reaction distance
B) X-coordinate is larger than reaction distance but smaller than V
C) X-coordinate larger than V

The prey items located in each part of the area of discovery must be scanned separately to see which one has already been discovered in the previous time step (for details of the program see appendix I).

II) The distance a beetle covers during one time step is less than its reaction distance (fig. 3.4.II). In this case only those prey items further away than the reaction distance from XV,YV and closer to XP,YP than the reaction distance (the white area in the figure) are considered to be discovered.

In this model the discovered prey are put back into the cluster with a new

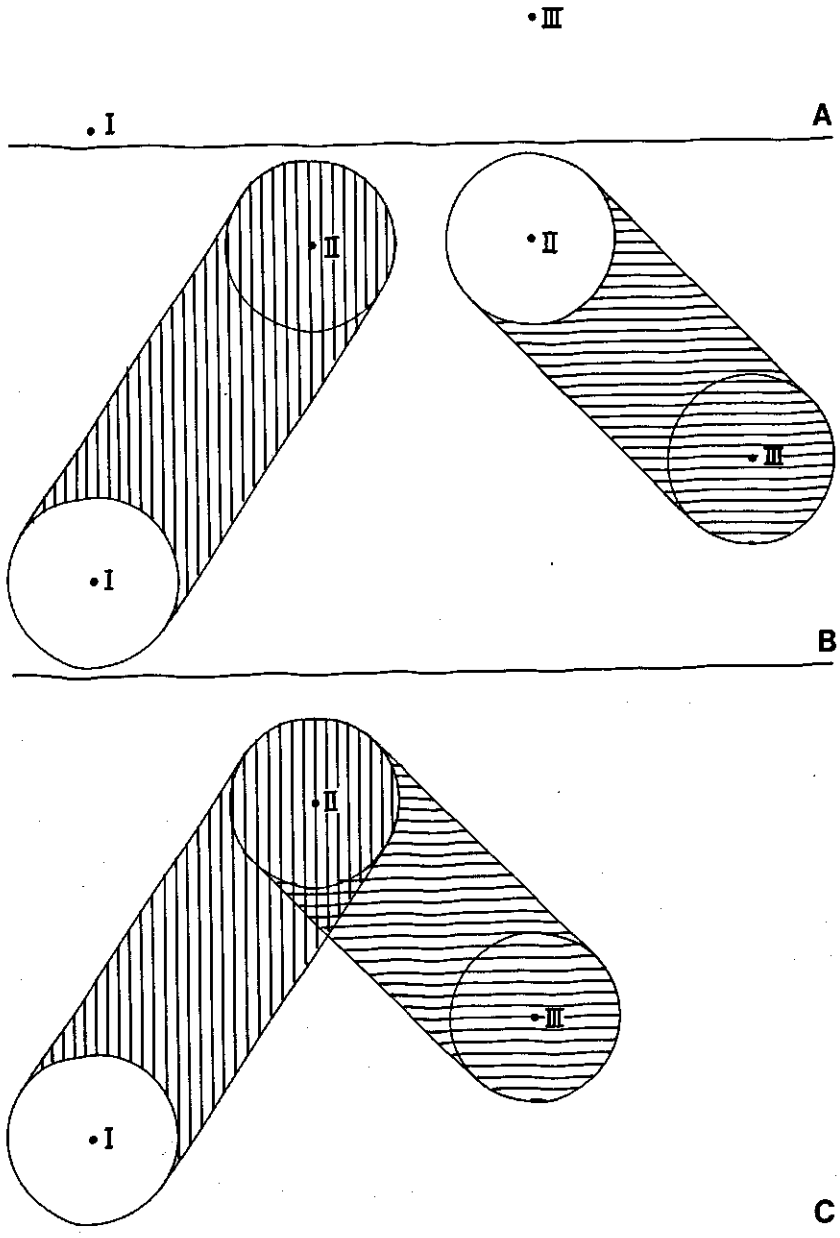

FIG. 3.3 A, location of the beetle at three consecutive timesteps I,II,III. B, area searched from times I to II and II to III. C, area searched from time I to III. The double hatched area is covered twice.

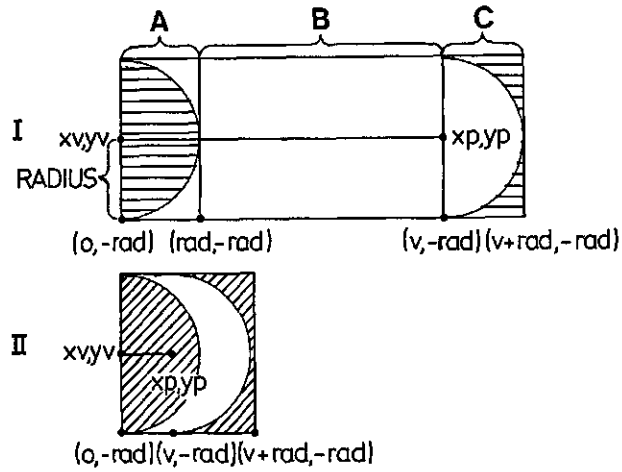

FIG. 3.4 Prey located in non-hatched areas is encountered by the beetle. Two situations are shown: I) The speed > RADIUS, II) The speed < RADIUS. xv,yv is the former position of the beetle and xp,yp is te new position of the beetle. Coordinates given in the figure are the new coordinate frame (see text).

set of coordinates if the prey density has to remain constant, or they are removed from the cluster when this is not necessary. For the calculation of a functional response of a predator to prey density the average density in the field has to remain constant. If the prey remains at the same spot the chance of encountering the same prey twice or more is very high especially when the speed is low and the prey density in the cluster high. This may give erroneous high rates of discovery.

Cluster scanning.

It is less laborious to first determine which cluster is within the reaction distance of the beetle and subsequently to scan only the prey of that cluster than to scan all prey in the field each time step. To determine whether or not a cluster is within the reaction distance of the beetle the coordinates of the centrally located prey of a cluster are used. If the distance measured between the center of the beetle and the center of the cluster is smaller than the sum of the reaction distance of the beetle and the cluster radius, only then the distance to each individual prey in that nearest cluster will be measured. If this condition is not fulfilled the next walking step will be taken and cluster scanning will start over again.

3.1.2 Coupling motivational state and searching behaviour

To analyse the searching behaviour in relationship to the motivational state of the beetle the following relationships were integrated into the searching model:

a) Locomotory activity (TWALK), b) Succes ratio (SR) and c) Walking velocity

(V) all with respect to the relative satiation level (for the appropriate values see chapter 2).

In this simplified model a fixed maximum gut capacity is used and RSATL is only determined by ingestion and by gut-emptying. Prey size is given as a fraction of the maximum gut capacity. Thus each time a prey is consumed RSATL is increased with that fraction. Gut emptying is simulated with the relative gut emptying rate found at 20 °C (Mols, 1988).

a) Calculation of the level of locomotory activity.

The time a beetle spents walking during a specific timestep can be calculated from the relations found in the experiments concerning the relationship between the relative activity coefficient (AC=(actual activity)/(maximum activity of hungry beetles per time period)) and RSATL (chapter 2). Per timestep the activity period can be calculated with:

$$WALK = AC*FREQ*MAXACT$$

WALK = The total time a beetle is locomotory active during a timestep.
AC = The relative activity coefficient related to the relative satiation level.
FREQ = The fraction of the total daily locomotory activity realized during that timestep.
MAXACT = The duration of locomotory activity of a hungry beetle expressed in hours per day at 20 °C

In the motivational model the timestep of integration (DELT) is a quarter of an hour, which is sufficient to calculate the decrease of RSATL by digestion. The walking part of the program is running during that quarter for TWALK seconds.

b) Success ratio and RSATL

The relationship between the success ratio and RSATL determines the chance of a discovered prey to be captured. The relationship found for maggots is used in the model (see chap 2.)

c) Velocity and RSATL

When RSATL exceeds 5% the average walking velocity decreases from about 5 cm/sec to an average of 2.5 cm per sec (fig 2.12). This is included into the model.

d) Duration of tortuous walk.

Each prey consumption is followed by tortuous walk. During that period the velocity is adapted to the value that corresponds with the actual RSATL. The duration depends on RSATL according to figure 2.19. Thus when the beetle is still very hungry after consumption of a small prey tortuous walk may last

11 minutes during which the speed increases slowly to the level of 5 cm/sec. When RSATL is about 50% tortuous walk is shorter (about 4 minutes) and than speed returns sooner to the level of 2.5 cm/sec. When RSATL exceeds 80% tortuous walk does not occur any longer.

3.1.3 Simulation of searching, predation and egg production

In this extended model the relationship of locomotory activity with RSATL and with the diurnal rhythmicity is combined with the complete motivational part including egg production and with the searching and predation part. RSATL is governed by ingestion and egestion and by the egg load. One run of the model concerns the simulation of searching, predation and egg production during a whole season, which takes about 35 days at 20 °C.

3.2 Simulation experiments

I) Simulation of searching independent of motivation.

Simulations were done with the searching model (appendix 1) in which only walking behaviour was incorporated. The goal was to investigate the range of prey distributions and densities at which the walking behaviour of *P. coerulescens* is most profitable. The distributions varied from random to extremely aggregated. The overal prey density per arena was varied over a wide range depending on the simulation experiment. Prey cluster size was investigated from 5, 10, 20, 30, 40, 80, 160 to 320 cm diameter. Prey number in the cluster was varied from 5, 10, 20, 40 to 80. All different combinations of cluster diameter and prey/cluster were tested.

The effect of the following characteristics of walking behaviour were analysed in the simulations:

1) Speed in a range varying from 1 to 5 cm per sec in the random prey distributions, and average speeds of 2.5 and 5 cm per sec in the aggregated distributions. The latter were chosen because they resemble the average speeds found in beetles with food in the gut and in hungry beetles respectively.
2) The effect of having tortuous walk after consumption of a prey item.

The beetle's discovery rate with prey per hour was used as output variable of the simulations.

The number of repetitions of the simulations was dependent on the aggregation of prey. The stronger the aggregation the more simulations were needed to obtain reliable values of the discovery For 5-20 prey/cluster 50 runs were necessary and for more than 20 prey/cluster 100 runs, because in the latter case only few clusters were present in the arena when the overall prey densities were kept low.

II) Simulation of searching and predation coupled to motivation.

Simulation runs were made for periods of one hour. For each run in sequence prey was replaced in the arena with the same density and distribution, but not

at the same place. In the simulations the beetles were considered to be active during the whole period. With the results of the simulations functional response curves could be constructed. This is done for different prey densities and prey distributions, varying from random to strongly aggregated with the same cluster diameters and prey number per cluster as mentioned before.

In aggregated prey distributions simulations were done with:

a) Constant prey density. A captured prey was randomly replaced at another place in the cluster.
b) Decreasing prey density by removal of captured prey. By this procedure local depletion of prey occurs, which is a natural phenomenon in predators. As a consequence prey density in the arena does not remain constant. Thus no normal functional response curves can be constructed in this way. It is to be expected that at locally high prey densities the average density/m^2 will not change much after a capture but at locally low prey densities local removal of prey may exert a negative influence both on the discovery rate and on the predation rate.

III) Simulation of searching, predation and egg production.

Simulations were done at constant temperatures with random as well as with aggregated prey distributions. The prey is replaced every day. The overall prey density varied from 0.125 to 16 prey/m^2 for random prey distributions and from 0.125 to 8 for aggregated prey distributions. The aggregated distributions were done with 20 prey/cluster, and the cluster diameters used were: 5, 10, 20, 30, 40, 80, 160, 320 cm. The prey density in the clusters with 20 prey per cluster depends on cluster surface and is respectively: 11088, 2546, 636, 283, 159, 39.8, 9.94, and 2.48 prey/m^2. Reaction distances of 1 and 2 cm. were tested in the simulations. The effect of TW and of prey depletion was tested in random prey distributions and in aggregated distributions at prey densities ranging from 0.25, 0.5 and 1 prey/m^2.

IV) Simulation of dispersal.

The beetle *P.coerulescens* only rarely flies, thus dispersal almost exclusively occurs by walking. Therefore, dispersal of the beetle depends both on walking speed, on windingness of the walking track, and on the duration of locomotory activity. These are determined again by the motivation of the beetle, which in turn depends on prey density and distribution. With the help of the searching model it is possible for each walking speed to simulate dispersal of the beetle from a fixed point in the environment. The dispersal is measured as the linear displacement from the starting point. This linear displacement is simulated for the walking velocities ranging from 1 to 6 cm/sec for the time periods 1, 2, 4, 8, 16, 32 and 64 minutes and for 5.4 hours as the latter is the maximum period of activity per day for a hungry beetle. Each velocity-time combination is repeated 100 times.

V) Simulation of the validation experiment.

Simulation was done in an area with the same surface as in the experiment (see chapter 2.5). Two clusters with 7 prey, each were placed at random in the arena. The complete model was run for the appropriate part of the day: Start at 11 pm for 90 minutes. As a comparison the model was also run with 14 prey placed at random in the arena. The captured prey items were not replaced. The simulation model was adapted for this small arena by including walking along the border of the arena into it. The moment the beetle reaches the border of the field it was not rebounded into the field but it followed the border depending on the choice of the subsequent angle. When an angle is chosen that should lead the beetle outside the field the border will be followed, other angles will bring the beetle back into the field again. This approach is an assumption, but as no quantitative information was available about behaviour of the beetle in the field to borders this was chosen. It results in patterns that resemble the walking behaviour observed in the neighbourhood of borders and obstacles.

3.3 Simulation results

The simulated walking pattern was analysed in the same manner as the real walking patterns. The turning rate at different walking speeds obtained in this way were the same as those found for the real tracks. This was also the case with the concentration parameter. In was concluded that the model simulated the walking patterns correctly. Therefore, the simulation experiments were carried out as planned.

3.3.1 Searching without motivation.

a) Random prey distributions.

The discovery rate per hour of the beetle with randomly distributed prey with and without performance of tortuous walk after each discovery is shown in fig 3.5 (a and b). In both cases the discovery rate increases steadily both with increasing velocity and with increasing density of the prey. When the velocity exceeds 2.5 cm/sec the discovery rate increases strongly because of the decrease of windingness. When prey is randomly distributed tortuous walk has an inhibiting effect on the discovery rate. This effect becomes stronger both when prey density and walking velocity increases. At low velocities (< 1 cm/sec) the path is so winding that a further decrease of speed caused by tortuous walk, and consequently followed by an increase in windingness has hardly any influence on the discovery rate anymore since the linear displacement is very low. The difference in discovery rate between walks with and without tortuous walk increases with prey density and depends on walking velocity. At a speed of 5 cm/sec the difference at a prey density of 1 prey/m^2 is about 11% and increases up to 45% at 5 prey/m^2 and becomes greater at higher prey densities. In table 3.4.1 the simulations are given for $V = 5$ and 2.5 cm/sec at an increasing range of prey densities. The

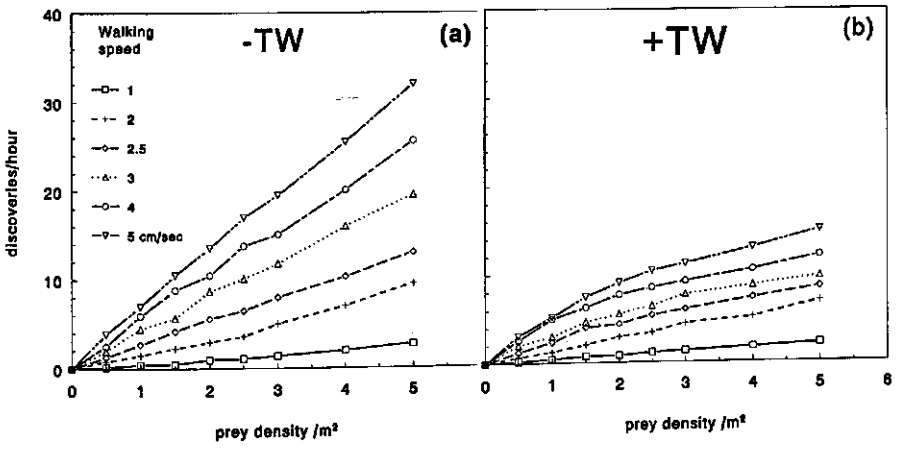

FIG. 3.5 Discovery rate (discoveries/hour) with randomly distributed prey, simulated for different walking velocities (cm/sec) of the beetle, a) without and b) with tortuous walk after prey encounter.

coefficient of variation (SD/mean) is about similar for tracks with and without TW.

The efficiency of the walking track can be expressed as the distance covered per discovered prey (= path length/discoveries). When a comparison is made between tracks with and without tortuous walk than it appears that up till a prey density of 8 prey/m² the efficiency is approximately the same for both tracks. Above this prey density TW becomes more and more inefficient, because by the high discovery rate the amount of time spent in TW increases, thus the average walking speed decreases more and more resulting in a walking patteren that becomes more and more winding. Recrossing occurs more often and this decreases the efficiency of the track.

b) Aggregated prey distributions.

If in aggregated prey distributions a discovery is *not* followed by tortuous walk the mean discovery rate is the same as in random prey distributions. Only the standard deviation of the discovery rate per hour depends on the cluster type (prey density in the cluster and cluster size). The coefficient of variation increases both with a decreasing number of clusters and with increasing prey density per cluster (for an example see fig.3.6). The smaller the cluster and the higher prey density in the cluster the higher the standard deviation of the discovery rate. At a high prey density in the cluster the number of clusters per area decreases (because the overall prey density per m² in these simulations remains constant), thus the distance between the clusters increases and therefore a beetle needs more time to cover this distance. Therefore, long periods between discoveries will be followed by series of short periods when the beetle is in a prey cluster. Tortuous walk after prey discovery increases the discovery rate, but the

TABLE 3.4.1. The effect of tortuous walk on the discoveries per hour at two walking velocities (V = 5 and 2.5 cm/sec). Simulations without motivation and and success ratio. Prey is randomly distributed and the density is kept constant. A discovered prey is placed elsewhere in the arena. Reaction distance = 2 cm. Averages are based on 50 runs; path+/path is the ratio of the pathlength with and without TW; disc+/disc- is the ratio of discoveries with and without TW.

	coefficient						
	Disc-overies	variation		pathlength		path/	ratio
prey density/m^2	average	SD	sd/disc	average	path SD	discoveries	disc+/disc-
V = 5 cm/sec −TW							
0.05	0.30	0.51	1.70	18000	100	60000	1
0.1	0.74	0.72	0.97	18000	100	24324	0.97
0.25	1.60	1.25	0.78	18000	100	11250	0.97
0.5	3.36	2.00	0.60	18000	100	5357	0.93
1	6.60	3.12	0.47	18000	100	2727	0.89
2	13.39	3.16	0.24	18000	100	1344	0.61
4	25.74	4.72	0.18	18000	100	699	0.50
8	49.00	6.97	0.14	18000	100	367	0.38
16	98.00	13.6	0.14	18000	100	184	0.26
32	191.70	12.9	0.07	18000	100	94	0.18
V = 5 cm/sec +TW							path+/path-
0.05	0.30	0.58	1.93	17779	459	59263	0.99
0.1	0.72	1	1.39	17505	706	24313	0.99
0.25	1.56	1.1	0.71	16891	756	10828	0.96
0.5	3.12	1.42	0.46	15795	1002	5063	0.94
1	5.86	1.73	0.30	13940	1124	2379	0.87
2	8.16	1.43	0.18	12501	917	1532	1.14
4	12.82	2.51	0.20	9974	1208	778	1.11
8	18.72	2.55	0.14	7881	919	421	1.15
16	25.24	2.76	0.11	5798	600	230	1.25
32	33.70	3.21	0.12	4347	353	129	1.37
V = 2.5 cm/sec −TW							disc+/disc-
0.05	0.15	0.27	1.80	9000	60	60000	1
0.1	0.26	0.56	2.15	9000	80	34615	0.85
0.25	0.76	0.89	1.17	9000	80	11842	0.87
0.5	1.48	1.13	0.76	9000	80	6081	0.80
1	2.62	1.66	0.63	9000	80	3435	0.85
2	5.32	2.65	0.50	9000	80	1692	0.76
4	10.28	3.30	0.32	9000	80	875	0.70
8	20.50	5.14	0.25	9000	80	439	0.53
16	43.78	8.19	0.19	9000	80	206	0.37
32	85.78	11.11	0.13	9000	80	105	0.25
V = 2.5 cm/sec +TW							pathd+/path-
0.05	0.15	0.44	2.93	8933	194	59553	0.99
0.1	0.22	0.42	1.91	8905	159	40477	1.17
0.25	0.66	0.74	1.12	8756	261	13267	1.12
0.5	1.18	1.06	0.90	8548	399	7244	1.19
1	2.22	1.33	0.60	8233	444	3709	1.08
2	4.06	1.52	0.37	7547	532	1859	1.10
4	7.20	1.94	0.27	6591	585	915	1.05
8	10.96	2.50	0.23	5647	577	515	1.17
16	16.22	2.16	0.13	4335	395	267	1.30
32	21.38	2.86	0.13	3410	346	159	1.52

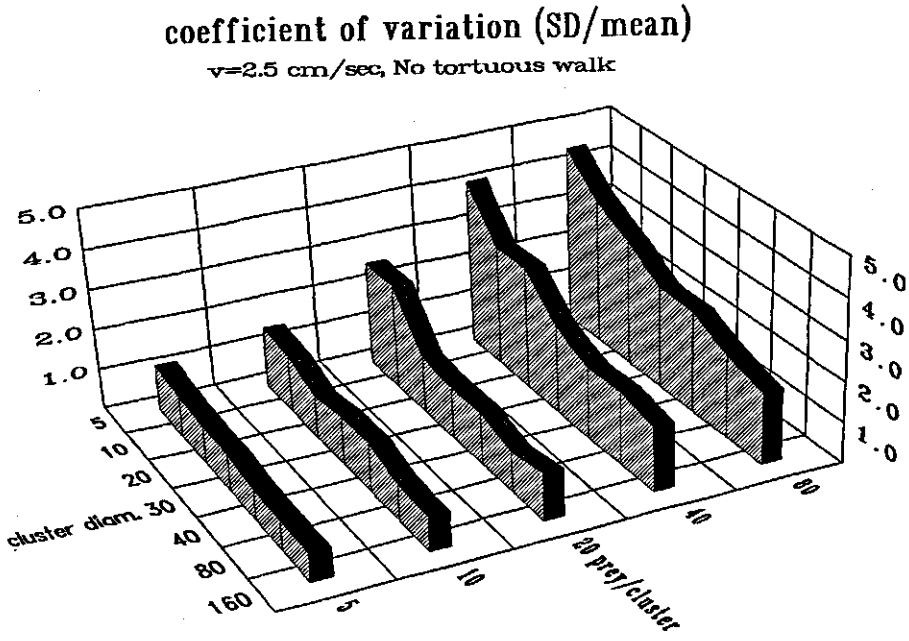

FIG. 3.6 Coefficient of variation (SD/mean), without tortuous walk, of prey discoveries when prey is distributed aggregated. In that case the mean discovery rate equals that with random prey distributions. Overall prey density is 1 prey/m^2.

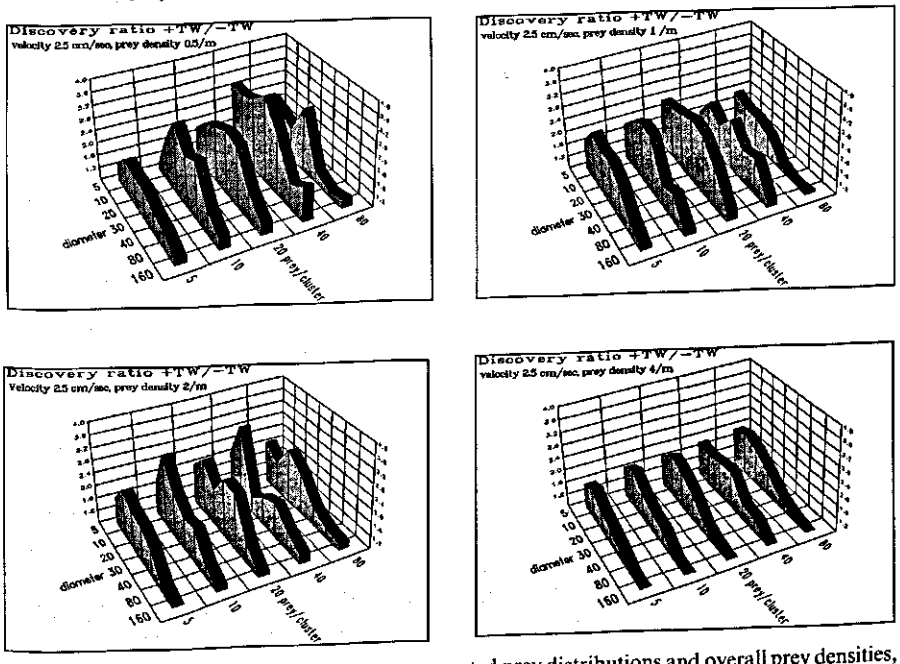

FIG. 3.7 Effect of tortuous walk in different aggregated prey distributions and overall prey densities, expressed as a ratio of the discoveries with and without tortuous walk after prey encounter.

size of the effect depends both on walking velocity, on cluster size, and on prey density in the cluster. To show the positive effect of tortuous walk in aggregated prey distributions, the ratios of discovery rates per hour between walking tracks with (+TW) and without tortuous walk (–TW) are given in figures (3.7 a to d) for 4 different prey densities.

The figures show an optimum for the positive effect of tortuous walk that depends on the walking velocity as well as on the cluster size and prey density in the clusters. In general, increase of the average prey density decreases the positive effect of tortuous walk, because after each discovery the walking speed decreases thus decreasing the average walking speed over the whole searching period. When V = 2.5 cm/sec tortuous walk shows its highest profit at intermediate cluster diameters from 10 to 40 cm.

The efficiency of the walking pattern (path length/discovery rate) is demonstrated in fig 3.8.a,b for V = 5 and 2.5 cm/sec. These figures show that at the average prey density of 0.5 prey/m^2 the effort for the beetle to discover a prey is minimal between small clusters crowded with prey and large clusters that almost appraoch a random prey distribution. In small crowded clusters it takes a longer walk to reach a cluster, because the distance between the clusters is long. In large clusters the prey density in the clusters is so low that tortuous walk becomes less profitable also. Both for walking speeds of 5 and 2.5 cm/sec it shows that prey in clusters of an intermediate size are discovered with the lowest cost in terms of walking distance. Simulations done at higher average prey density show that the lowest effort shifts more to the smaller clusters and to the higher number of clusters per arena.

3.3.2 Searching and predation coupled to motivation

1) Random prey distributions.

The effect of the success ratio on predation is clearly shown in fig (3.9 a and b). At increasing prey density the discovery rate steadily increases, while the predation rate is levelling off to approximately 12 captures per hour at the highest prey density. This effect is mainly caused by a decreasing success ratio when satiation level increases, although at low prey densities the walking speed also influences the form of the curve. At the start of the simulation walking velocity is 5 cm/sec but after capture of the first prey the velocity decreases to 2.5 cm/sec. Therefore the first prey will be captured at a rate which is twice that of the second prey. At prey densities below 1 prey/m^2 no difference can be found between the discovery rate and the capture rate as almost each discovered prey will be captured. At prey density 4/m^2 the discovery rate curve seems to bend upwards when TW is involved. This is caused by the decrease of the duration of tortuous walk when the beetle becomes more and more satiated, and which is absent above 80% of RSATL. Above this satiation level the walking speed remains constant thus from that prey density the discovery rate increases linearly with prey density.

When prey density is not kept constant after capture of a prey it decreases

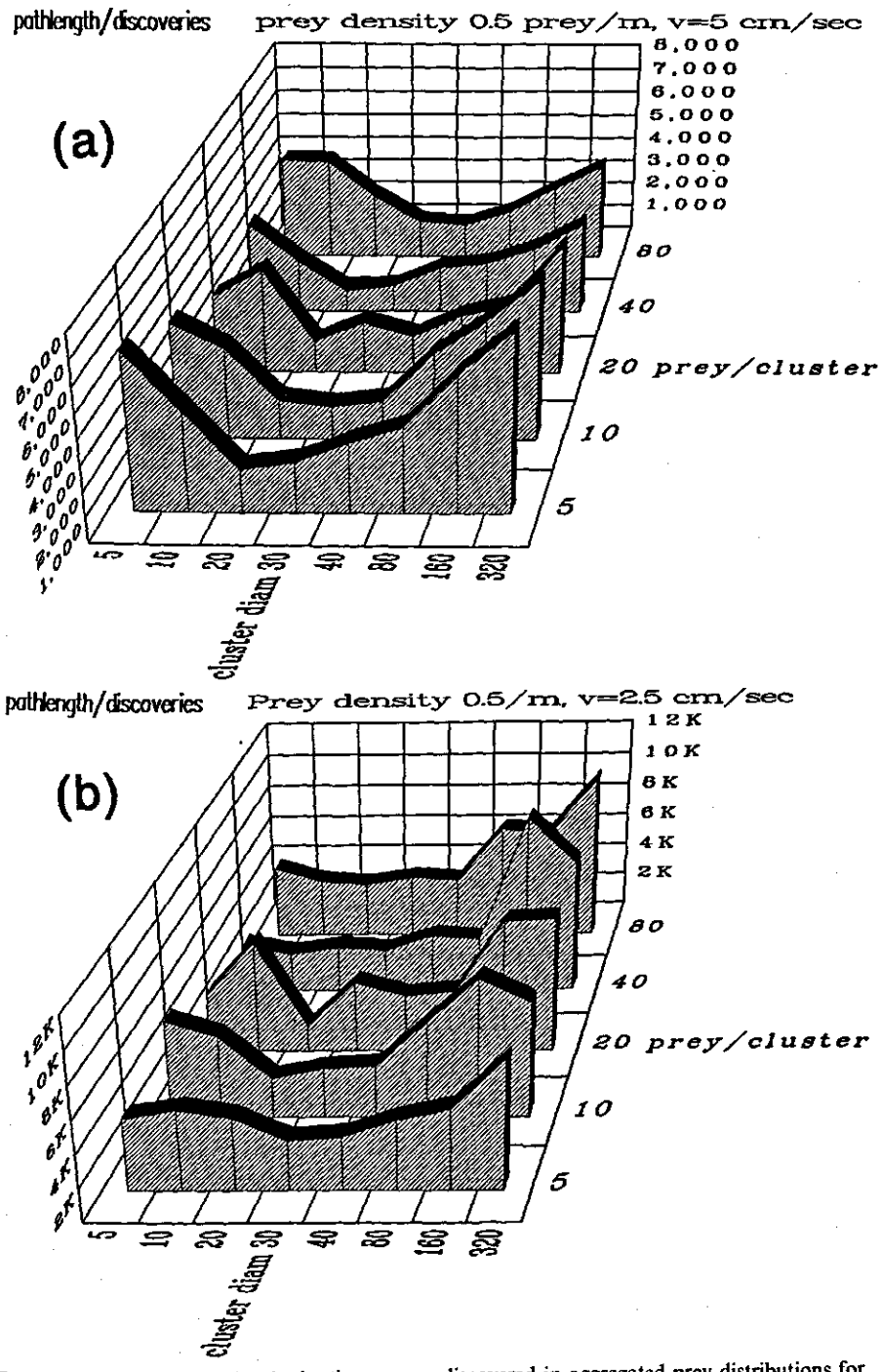

FIG. 3.8 Distance walked by the beetle per prey discovered in aggregated prey distributions for two walking velocities: a) 5 cm/sec, b) 2.5 cm/sec. Overall prey density is 0.5 prey/m^2.

slowly after each capture, which leads to a slightly lower discovery rate, but it hardly influences the capture rate (fig. 3.9 a and b), because the prey is replaced every hour.

When the reaction distance is halved from 2 to one this decreases the discovery rate also with 50%, but as the capture rate levels off at increasing prey density the effect of decreasing reative distance becomes smaller at increasing prey density.

2) Aggregated prey distributions.

Figures 3.10 (a to d) and 3.11 (a to d) show the effect of walking behaviour in situations of constant and decreasing prey densities respectively caused by predation in relation to cluster diameter, and prey number per cluster, at two average prey densities viz. 0.5 and 1 prey/m^2. To illustrate the difference between random prey distributions and aggregated distributions the discovery and the capture rate of random prey distributions for these two prey densities are given by the horizontal lines. It shows clearly that both discovery rate and capture rate at these two prey densities are significantly higher when the prey is aggregated. It also shows that this strongly depends on the cluster diameter as small, but larger than 5 cm diameter, clusters, result in higher discovery rates than large clusters and extremely small clusters. Prey depletion does affect the discovery rate at cluster diameter up to 80 cm and when the prey density per cluster is high. This can be explained by the increase of the distance between the clusters. The capture rate is much lower than the discovery rate and seems only affected by local prey depletion when prey number per cluster is low. This is because the discovery rate remains sufficiently high. This is only the case when the arena is sufficiently large in relation to prey density (> 100 m^2) to overcome a serious decrease in overall prey density. When the clusters have a high prey number (thus only a few clusters per arena) the capture rate decreases to the average

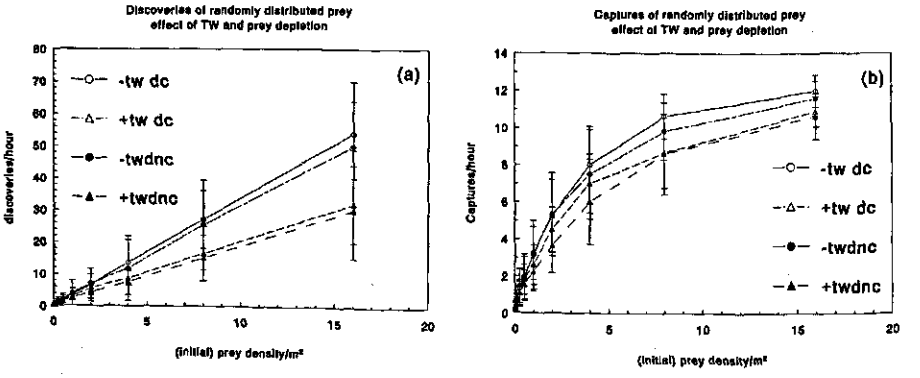

FIG. 3.9 Discoveries (a) and captures (b) when prey is randomly distributed. Effect of tortuous walk (+ or –TW), and effect of prey depletion (density constant = dc, density not constant = dnc) are shown.

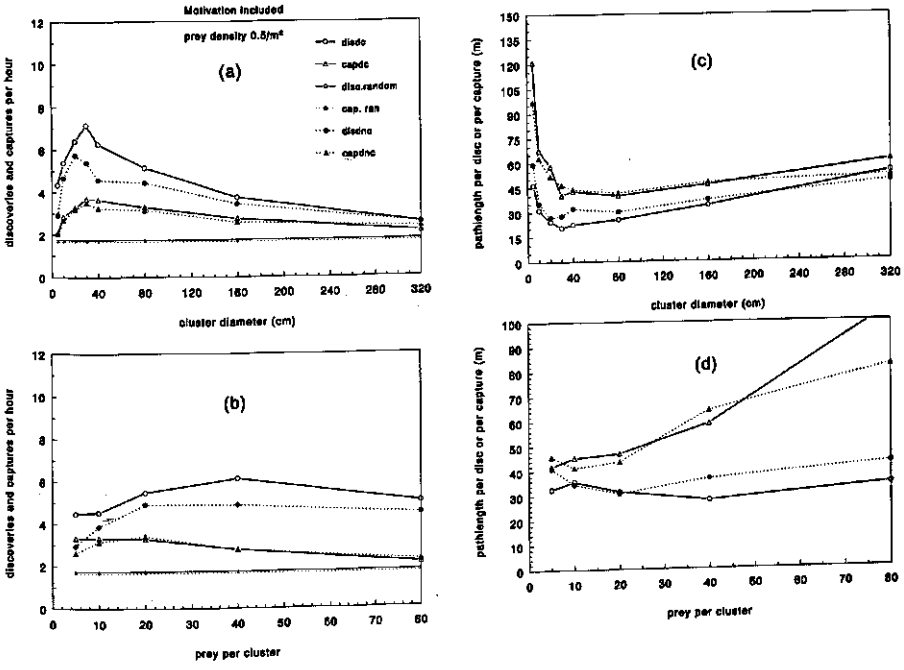

FIG. 3.10 Effect of cluster diameter (a,c) and prey/cluster (b,d) on discoveries, captures and the distance walked per prey in aggregated prey distributions at an overall prey density of 0.5 prey /m^2 at constant prey density (dc) and with depletion of prey (dnc) by the beetle. The values for the random prey distribution are given for comparison.

value of the random prey distribution, because of the satiation of the beetle and of the long distance between the clusters. Once a prey cluster is reached the beetle cannot eat more then up to satiation, the success ratio decreases strongly and although more prey are discovered they will not be captured. The same can be said for the pathlength walked per prey discovery or per prey capture (fig 3.10 and 3.11 c and d). The searching is most effective at intermediate cluster sizes (10-80 cm diameter). When clusters are smaller and heavely crowded long distances have to be walked per prey discovery or per prey capture, and above 80 cm the distance increases to the distance walked as for random prey distributions

3.3.3 Searching, predation and egg production

Random prey distributions.

Prey density.

The discovery rate in relationship to prey density is shown in fig 3.12

Whether or not prey density is kept constant after predation of a prey seems

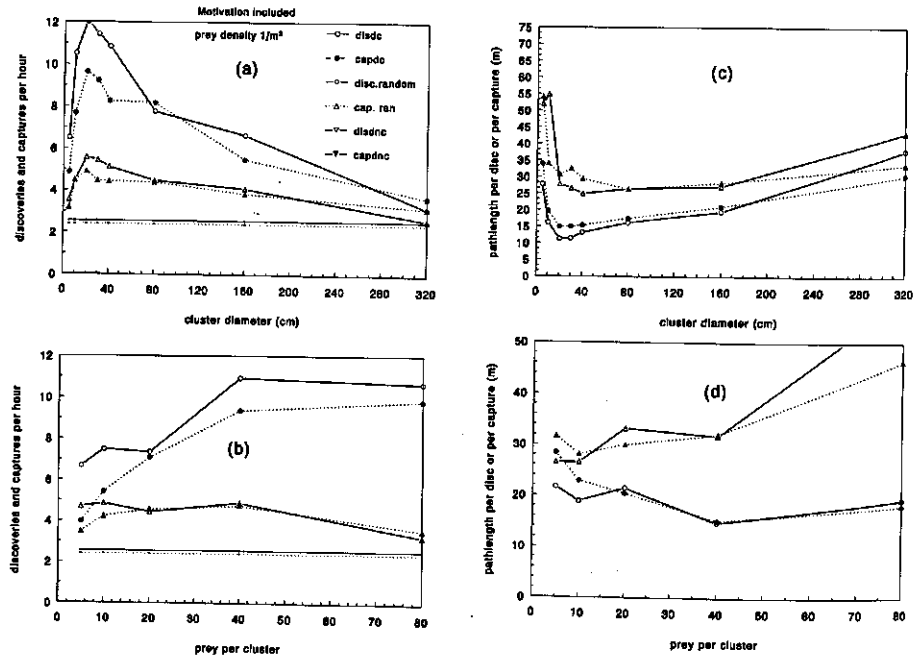

FIG. 3.11 Same as Fig 3.10 but with overall prey density of 1 prey /m^2.

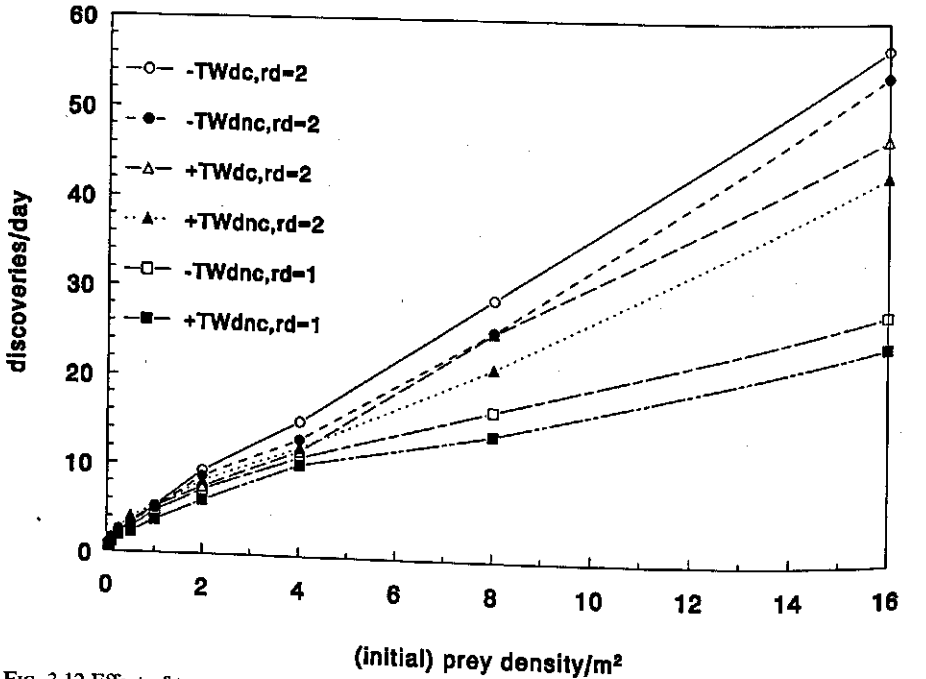

FIG. 3.12 Effect of tortuous walk (+ or –TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on number of discoveries per day for random prey distributions of increasing density.

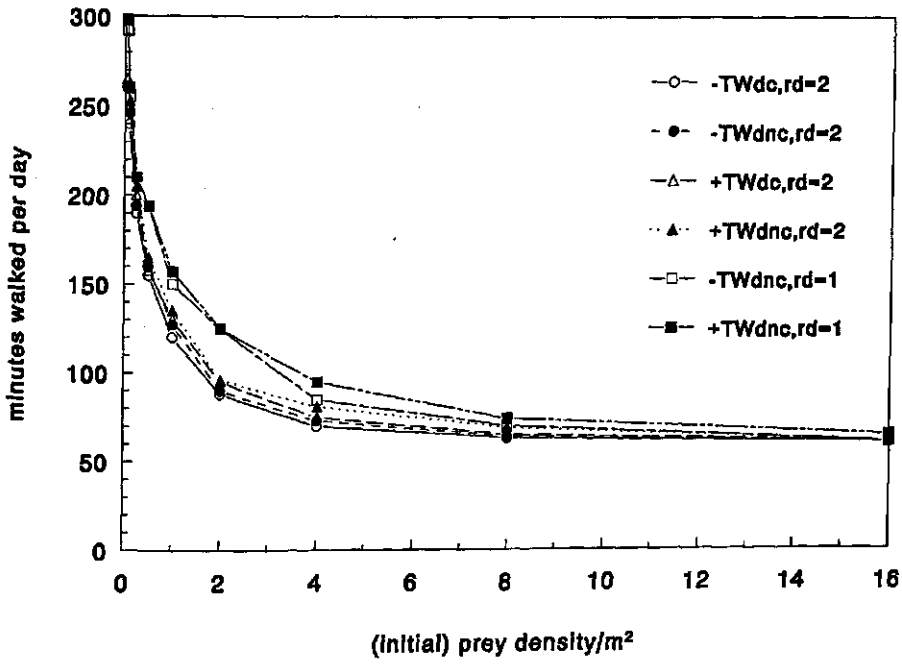

FIG. 3.13 Effect of tortuous walk (+ or -TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on locomotory activity, expressed in minutes per day, for random prey distributions of increasing density.

hardly to affect the discovery rate when prey is replaced daily. Even on this time scale local prey depletion does not seem to play an important role. At low prey densities (smaller than 4 prey/$m^{2)}$ the curves increase like a power curve. Above this density the dicoveries increase almost linearly with prey density. This can be explained by the switch of the walking speed from 5 to 2.5 cm/sec when RSATL exceeds 5%.after the first prey capture. At low densities more time is spent by walking at high speed. As prey density increases this high speed is replaced by intermediate speed and in the mean time the total locomotory activity is decreasing. Above 4 prey/m^2, almost all the walking is done at an average speed of 2.5 cm/ sec. and locomotory activity does not decrease much anymore (fig. 3.13).

Capture and consumption rate per day follow a Holling 2 curve (fig 3.14 a and b) and the same can be observed for the egg production per season (fig.3.14 c). No strong effect of prey depletion either on capture and consumption rate as on egg production can be observed. The interval of prey replacement is too short for that.

Tortuous walk: Tortuous walking has only a small influence on the discovery rate when prey density is below 1 prey/m^2. Above this density the negative effect

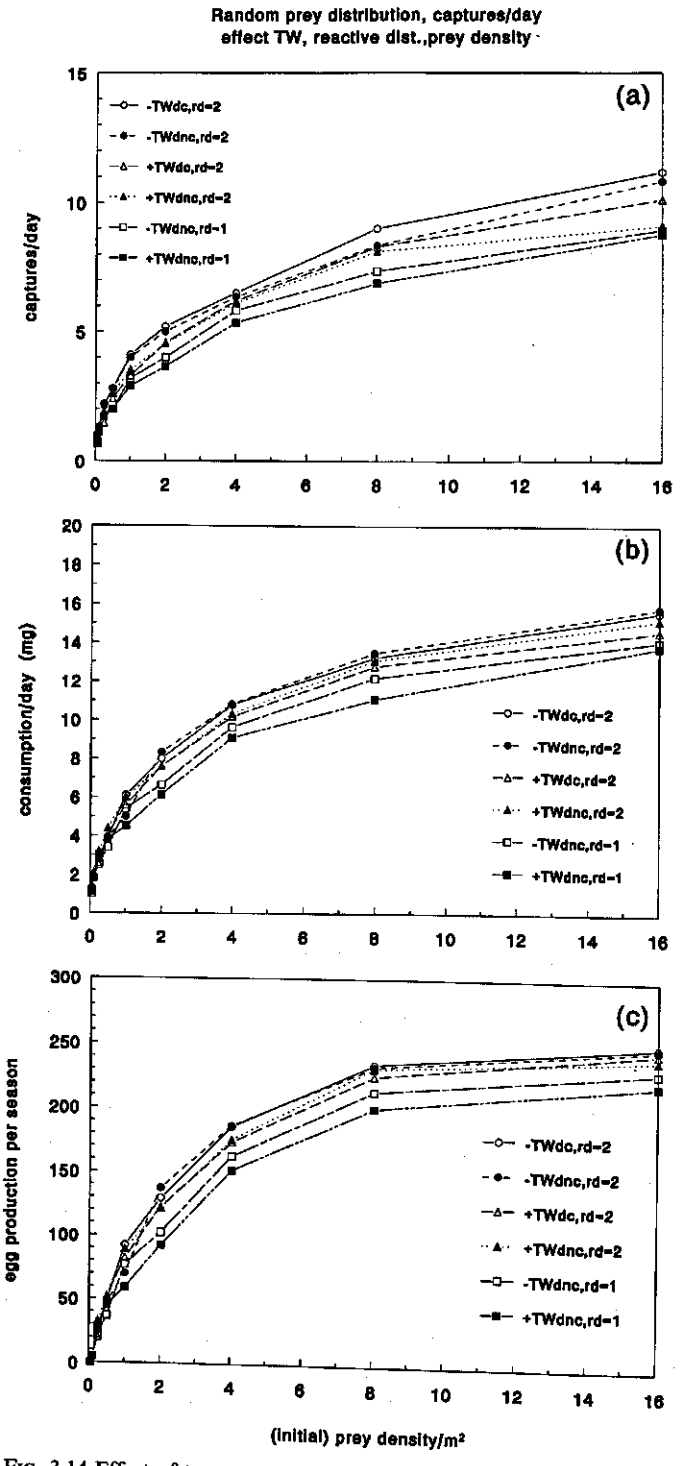

FIG. 3.14 Effect of tortuous walk (+ or –TW), prey depletion (dc or dnc) and reaction distance (rd = 1 or 2 cm) on captures per day (a), on the consumption/day (b), and on the egg production per season (c) for random prey distributions of increasing density.

of tortuous walk is increasing up to 20%. With tortuous walk the pathlength per day is shorter and locomotory activity is approximately 5% higher than in behaviour whithout tortuous walk. Thus locomotor activity is only partially compensating the effect of lower prey capture when tortuous walk is performed.

Concerning predation, consumption and egg production the difference resulting from behaviour with and without TW is small. Generally having TW in random prey distributions results in a lower predation rate. Per prey density the effect is not significant. The negative effect of TW on egg production is greatest between 1 and 8 prey/m^2

Reaction distance. Up to prey density 4 prey/m^2 halving the reaction distance from 1 to 2 cm has only a small effect on the discovery rate. Up till this density locomotory activity is almost complete compensating the effect of the decreased reaction distance. Above this density the effect of reaction distance becomes more and more important up till about 50% at 16 prey/m^2. This effect can be explained by the form of the locomotory activity curve in relationship to prey density (fig. 3.13). Compensatory effects are strong up to 4 prey/m^2 , above this prey density locomotory activity remains almost constant.

Above prey density of 1 prey/m^2 the effect of halving the reaction distance on the capture rate is about 15%. Below this density no difference can be observed. For consumption and egg production (fig.3.14 b and c) the same effects can be observed because they are a direct result of prey capture.

Aggregated prey distributions.

Since predation rate is hardly affected by local prey depletion when prey is replaced once per day this schedule is used further on for the simulations of searching and predation in aggregated prey distributions.

Cluster diameter: In fig 3.15 the influence of cluster diameter is given on discovery rate, capture rate and consumption per day for 20 prey/cluster and a reaction distance of 2 cm.

Prey discovery is clearly influenced by the cluster diameter. The discovery rate is always higher in clustered then in random prey distributions. The lower prey densities show the highest discovery rate in clusters with 30 cm diameter, but when the prey density increases this shifts to clusters with a smaller diameter.

Generally it can be stated that at low overall prey densities ($<$ 1 prey/m^2) prey clustering results in higher capture rates compared to random prey distributions. At higher prey densities only the very small clusters result in a higher capture rate than the others and random prey distribution. At higher overall prey densities the intercluster distance is shorter which makes the small (high density) clusters becoming better attainable. The larger clusters give capture rates that are similar to those found at a random prey distribution. Up till an overall prey density of 1 prey/m^2 prey clusters of 20, 30 and 40 cm diameter prey are utilized better resulting in higher consumption rates. Above this overall density the capture, consumption (fig 3.15) and egg production rates (fig 3.16)

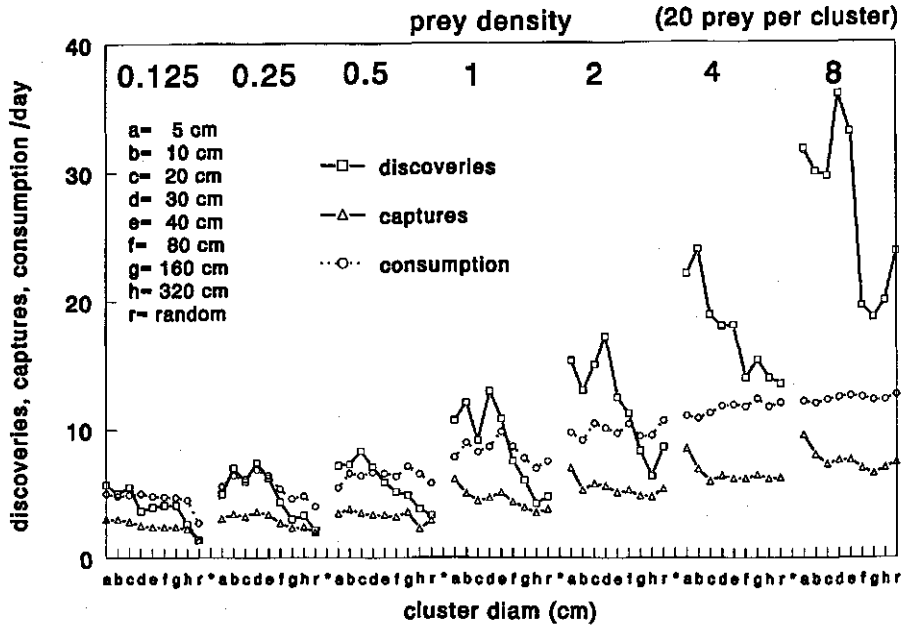

FIG. 3.15 Effect of prey cluster diameter on discoveries, captures and prey consumption (mg) per day for different overall prey densities. The number of prey/cluster is 20. The captured prey was removed from the field.

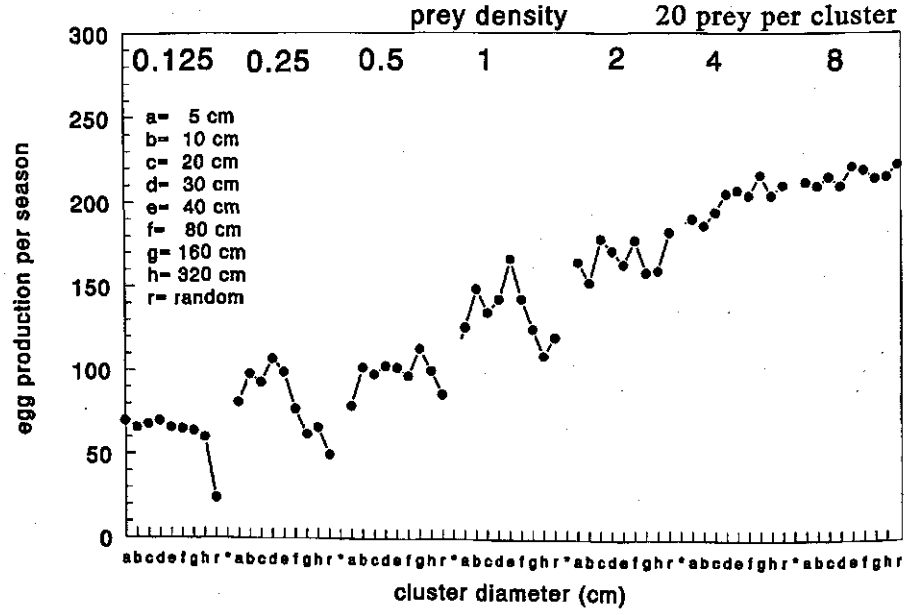

FIG. 3.16 Effect of prey cluster diameter on total egg production per season for different overall prey densities. The number of prey/cluster is 20. The captured prey was removed from the field.

are not different from those in random prey distributions. The high capture rate in the very small clusters at high prey densities do not result in high consumption rate because of rapid satiation in those clusters. Thus profitability, expressed in capture rate, consumption and egg production, of the beetle's behaviour occurs only in aggregated prey distributions at low overall prey densities (smaller than 1 prey/m^2).

Walking behaviour: When walking behaviour is considered (spending of time and walking types fig 3.17), it is found that in aggregated prey distributions at low overall densities high activity and much high speed walking is alternated with days with low activity spent in a prey cluster. High speed walking occurs especially at low overall densities and when clusters with small diameters are available. The time spent in high speed walking not only decreases with overall prey density, because the chance to discover and capture a prey increases, but also with increasing cluster diameter, because the distance between prey clusters is shorter. The fraction of time spent in tortuous walk is very short when the prey density in the cluster is high, because once in a prey cluster captures follow each other rapidly, thus leaving less time to complete the whole duration of TW. When prey clusters with the same amount of prey items become larger the distance between the prey in the cluster increases thus giving the beetle more space and time to complete its tortuous walk. Therefore more time will be spent walking tortously when the clusters are larger. When the prey distribution

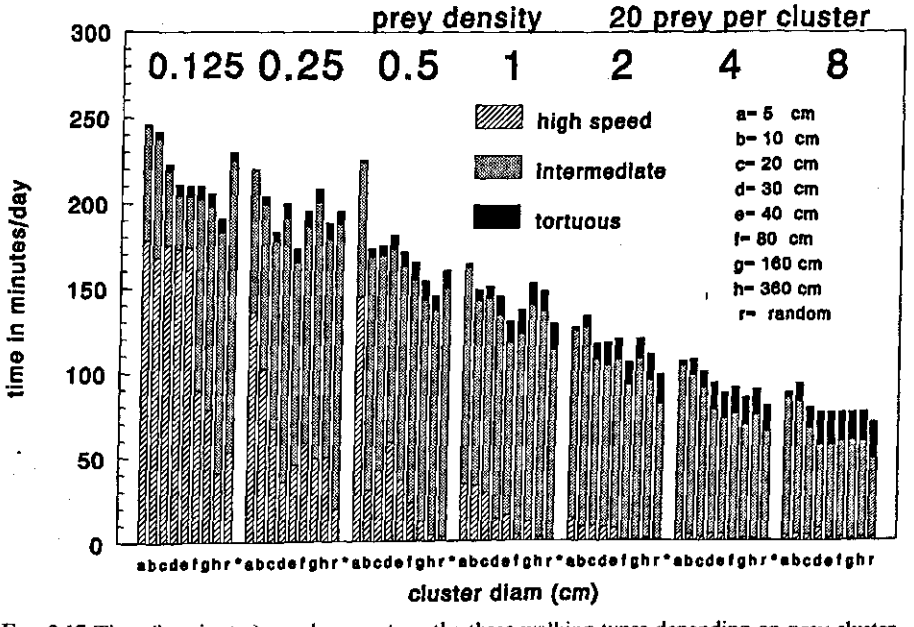

FIG. 3.17 Time (in minutes) per day spent on the three walking types depending on prey cluster diameter (with 20 prey/cluster) and overall prey density.

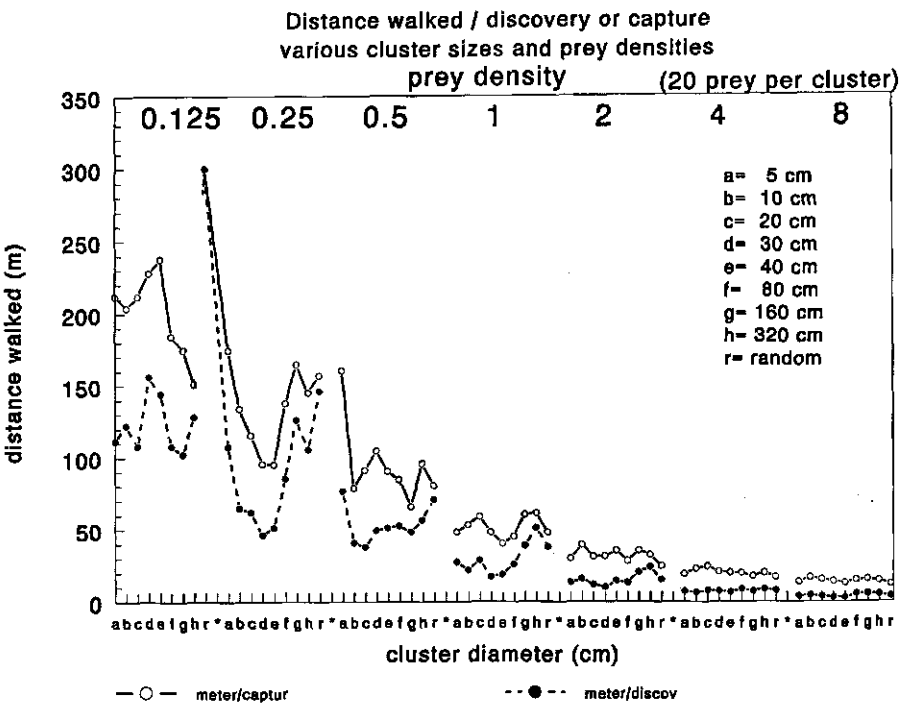

FIG. 3.18 Distance walked (m.) per discovery or per capture depending on prey cluster diameter (20 prey/cluster) and on overall prey density.

approaches randomness the fraction of time spent in tortuous walk is generally longer compared to aggregated prey distributions.

Simulations with the complete model have also been done without performance of tortuous walk to see to what extent having this behaviour is advantageous with respect to prey discovery and prey capture and to egg production in aggregated prey distributions. The results are that the positive effect of TW is only present at very low overall prey densities (< 1 prey/m^2) and that it is inversely related to prey density. For prey densities 0.25, 0.5 and 1 prey/m^2 performance of TW compared to non-performance gives resp 38%, 23% and 2% higher number of discoveries per day, this resulted in resp 32%, 18% and 0% increase in captures/day and a 120%, 16% and 3% higher egg production. The strong effect on egg production at the lowest prey density is because performance of tortuous walk in such poor food situations leads to such an increase of the capture rate that the metabolic threshold (a consumption of 2 mg/day) leading to egg production is exceeded. Therefore, in such poor food situations walking tortuously after prey capture is extremely important.

The average distance which has to be covered by the beetle between two discoveries or two captures depends both on the cluster diameter and on the overall prey density (fig 3.18). The figure shows that only at low densities to 1 prey/m^2

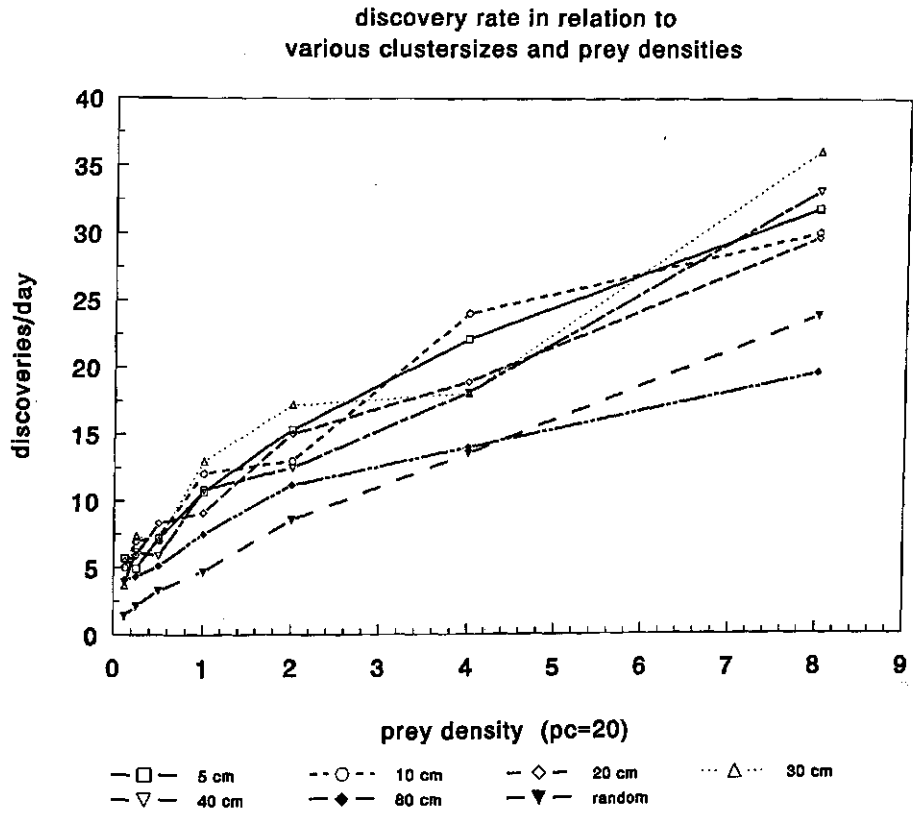

FIG. 3.19 Discoveries per day in relation to overall prey density and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

and with small cluster diameters between 10 and 40 cm the behaviour is most profitable because than the shortest distance has to be covered. At higher prey densities such a minimum is not observed anymore.

Prey density: To show the positive effects of the combined behavioural components of discovery and predation in clustered prey distributions as compared to random prey distributions the functional (fig 3.19 and 3.20) and numerical respons curves fig 3.21 are given. These show that especially at overall low prey densities the behaviour of the beetle shows its greatest profitability in clustered prey distributions. Small clusters are more heavily attacked than larger ones, which leads to a higher consumption and egg production. When overall prey density exceeds 1 prey/m^2 it depends on the cluster size whether the prey clustering offers still any advantage for the beetle.

Reaction distance: Decreasing the reaction distance from 2 to 1 cm when prey

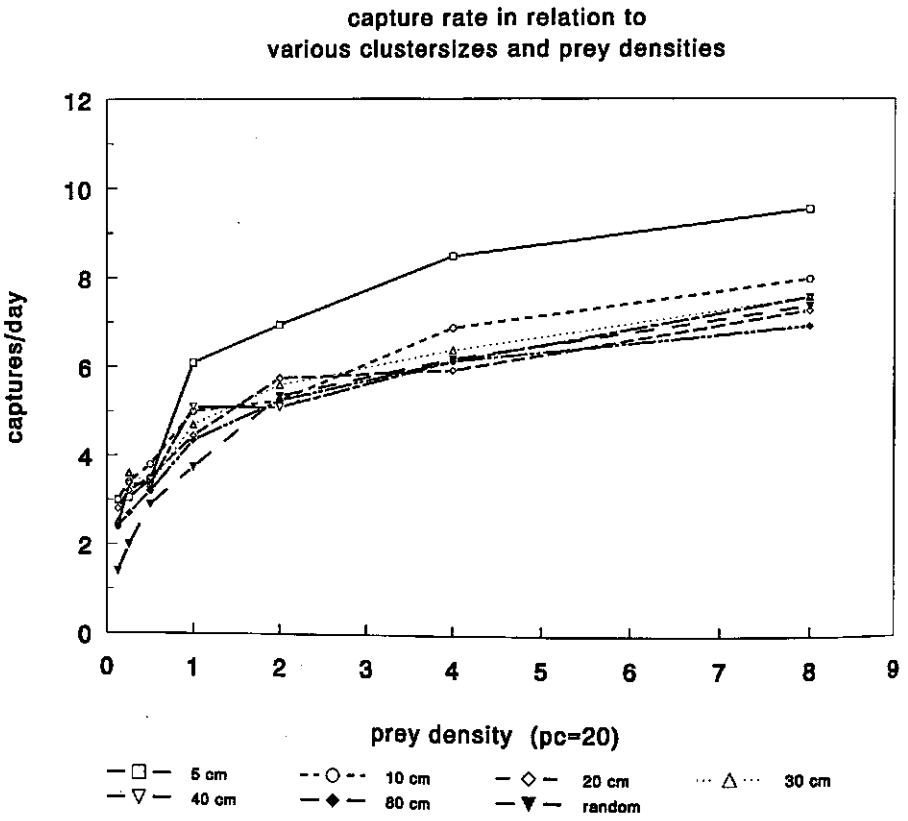

FIG. 3.20 Captures per day in relation to overall prey density/m^2 (functional response) and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

is aggregated highly decreases discovery rate (30%) but less so predation rate (15%) and egg production (13%). The greatest effect is found at low overall prey densities in small clusters. This is in contrast with random prey distributions where no effects of changing reaction distance could be observed at such low overall prey densities. In aggregated prey distributions and low overall prey densities more time is spent in straight walk, which is effective because of the smaller amount of recrossings as compared to intermediate walk. But it also results from the fact that in clustered situations the most important capture is the first one. Then the chance to find the first prey is the chance to find a cluster and because behaviour changes and the prey density in a cluster is higher than the overall prey density the next prey will be discovered sooner. Therefore, because of this phenomenon, reaction distance must be considered relative to the cluster size and thus a change of reaction distance from 2 to 1 is relatively small with respect of the size of a cluster. A constraint in this predatory behaviour is that, once a cluster is discovered, satiation is reached soon, because of the high prey

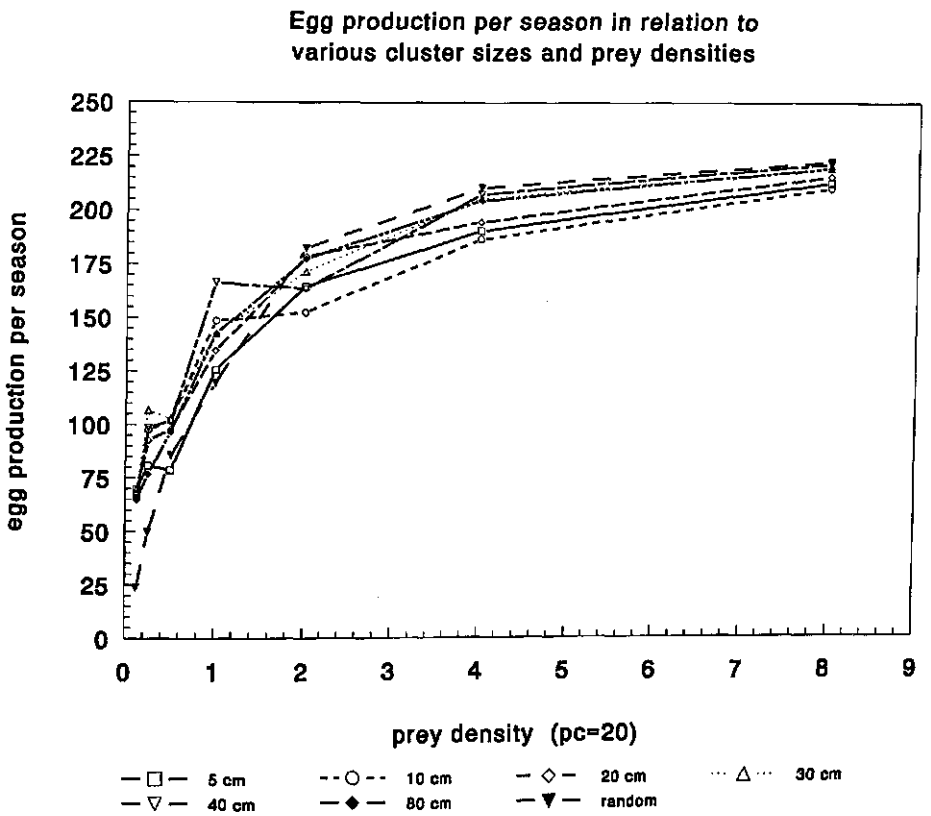

FIG. 3.21 Egg production per season in relation overall prey density (numerical response) and prey cluster diameter (20 prey/cluster). The largest clusters (160 and 320 cm diameter) are omitted because their results are the same as for random prey distribution.

density in a cluster, leading to a relative small effect on capture rate, when reaction distance is halved. When prey clusters are very large, residence time in such clusters becomes longer. In such cases reaction distance becomes more important because the longer the beetle has to deal with the prey density and prey distribution in that cluster, the more the daily capture rate will be determined by the local situation instead of by the overall prey density.

3.3.4 Dispersal of beetles as a result of walking behaviour

The relationship between velocity and linear displacement (Ld) is given in fig.3.22 This figure shows that linear displacement strongly depends on the speed and therefore on the windingness of the track. Tortuous walk keeps the beetle almost on the spot, while intermediate walk gives a linear displacement of approximately 2-3 meters/hour, and high speed walking leads to a displacement of about 6-12 meters/hour. According to the figure linear displacement is dependent on the velocity and is proportional with the square root of the

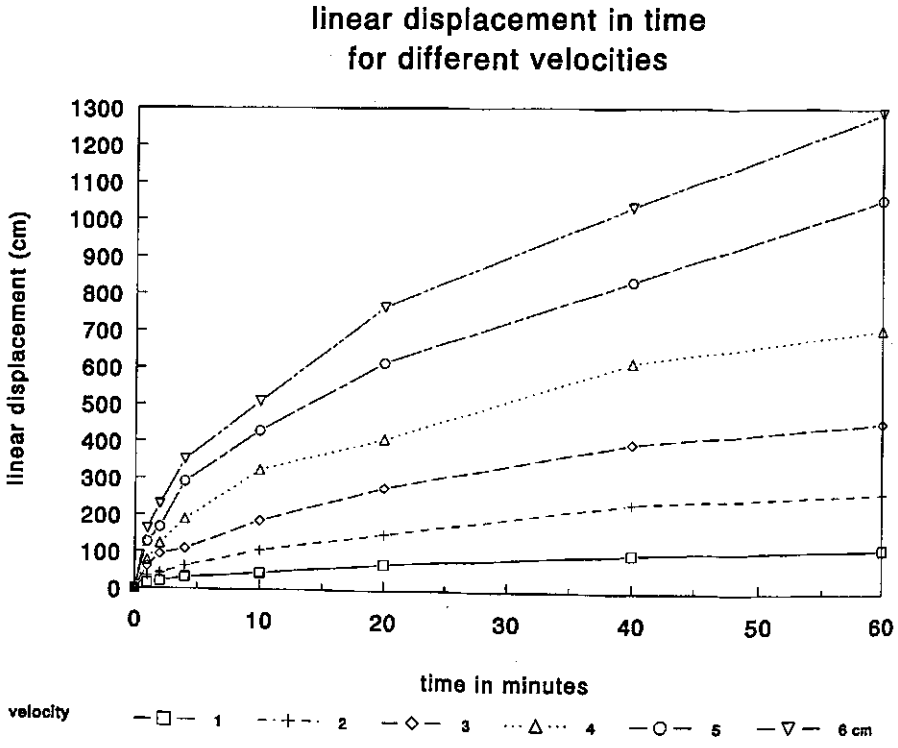

FIG. 3.22 Linear displacement of the beetle in time for different walking speeds. (cm/sec)

walking time according to:

$$Ld = a\sqrt{t} \qquad (1)$$

For each velocity the constant (a) is calculated with linear regression. The relationship between the walking velocity (V in cm/sec) and the constant (a) follows closely a power curve according to:

$$a = 1.82\ V^{1.385} \qquad r^2 = .99 \qquad (2)$$

Combining equations (1) and (2) results in a general equation with which the linear displacement of the beetle can be calculated for each walking velocity and for each time period (in seconds):

$$Ld = 1.82\ V^{1.385} * \sqrt{t} \qquad \text{(cm)}$$

With this relationship it is possible to calculate the daily linear displacement of the beetle for each relative satiation level as this results in a specific duration of the locomotory period (see fig.2.4) and in a specific walking speed (fig 3.23)

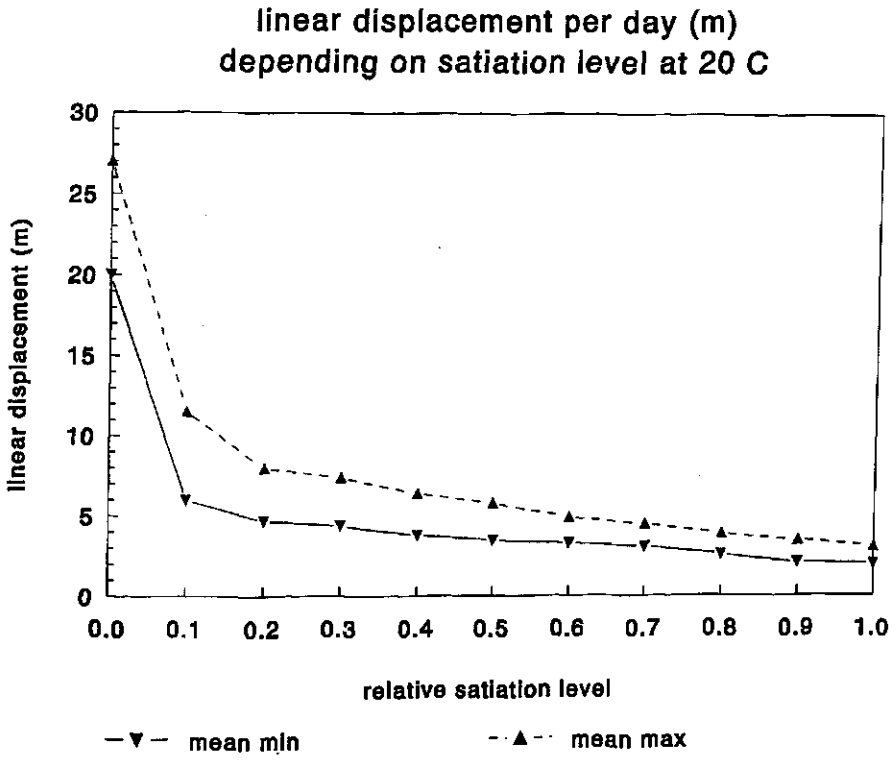

FIG. 3.23 Range of linear displacement per day (min and max) depending on RSATL at 20 °C. Calculated with formula using v ± 0.5 (resulting in min. and max ld)

In this figure it is shown that hungry beetles have an average daily linear displacement that varies between 17 and 23.5 meter. From 0.1 < RSATL <0.6 this distance varies between 4-9.5 meter and well fed beetles show a displacement of 2-4 meter.

Discussion.

The dispersal of the beetle is determined by its walking behaviour. In areas with a low prey density more time will be spent in high speed walking thus this will lead to leaving an area which is unsuitable and reaching another one that is more profitable in the fastest way. The moment a more profitable area is reached both locomotory activity and speed decrease because the RSATL decreases, resulting in a longer stay in the profitable area. This supports the work of Baars(1979) who measured daily distances covered by radioactively labeled *P.coerulescens* in two different habitats: a poor Molinia field and a mosaic type of heathland. He found two distinct patterns of movement in individual beetles. There were periods, sometimes very prolonged, during which the beetles only covered small distances (average 2.5 m ranging from 0-13 meter) in continually

changing directions which he called 'random walk' that alternated with periods in which long distances were covered (average 22 m ranging from 2-87 m)in a more or less constant direction, which he called 'directed movement'. In the Molinia field the beetles performed shorter periods of 'random walk' than in the mosaic field. The duration of 'directed movement' was about equal, but the distances covered during 'directed movement' were larger in the Molinia field nl. 28 m compared to 17 m in the mosaic field. These distances measured at warm days (maximum temp. 24-28 °C) come closely to those calculated for hungry beetles with an average temperature of 20 °C. The alternation of periods with short distances to periods with long distances supports the idea of the beetles reacting to clustered prey in the field. In this view the Molinia field should have prey clusters that are smaller or occupied by lower prey densities than those in the mosaic field. Although alternating periods of low and high temperature may give the same results, the observation that at the same day beetles could be observed that only covered short distances while others walked large distances is not in agreement with that. Simulations of searching behaviour with clustered prey at constant temperatures show the same alternation of long and short distances at low overall prey densities. This also supports the hypothesis that daily linear displacement to an important level is determined by the prey distribution and prey density in the field.

By Okubo (1980) much attention is given to the relationship between the dispersal of organisms and diffusion processes. Diffusion is defined as a' basically irreversible phenomenon by which matter, particle groups, population, etc spread out within a given space according to individual random motion. When this theory is applied to the beetles it can get the following meaning:

1. The netflux of beetles over a line of one meter and per time unit (for example the border between an unprofitable and a profitable area) equals the diffusionconstant multiplied with the difference in beetle density over that distance.
2. The difference in density is determined by the immi- and emigration of the beetles.
3. If the diffusion constant is different for the 2 areas this will lead to a concentration of beetles in that area with the lowest diffusionconstant.

With the information above and assuming that walking is at random it is possible to calculate the diffusion constant D from the walking behaviour in the following indirect way:
$D = \lim_{t->\infty} (Ldis)^2/(2t)$ This holds when a track is simulated long enough such that the D is constant in the end. This leads to the following equation for the diffusion constant in relation to the walking velocity:

$$D = 5840 * V^{2.738} \qquad (cm^2/hour)$$

With the diffusion constant the general spread of a population beetles over an area can be calculated. This offers a tool to estimate the exchange of individuals of different local populations in dependence of walking characteristics, food

TABLE 3.2. Calculation of diffusion constant D with help of the walking program at different walking speeds.

v cm/sec	D (m^2/hour)	SD
1	0.6	.025
2	3.7	.15
3	10.6	.43
4	26.6	.97
5	51.7	1.9

level and temperature as these determine mainly the walking behaviour. It can also be used the other way around to estimate the general food level of a location once the individual walking characteristics of a species are known in relationship to surface structure and temperature by measuring the immi- and emigration.

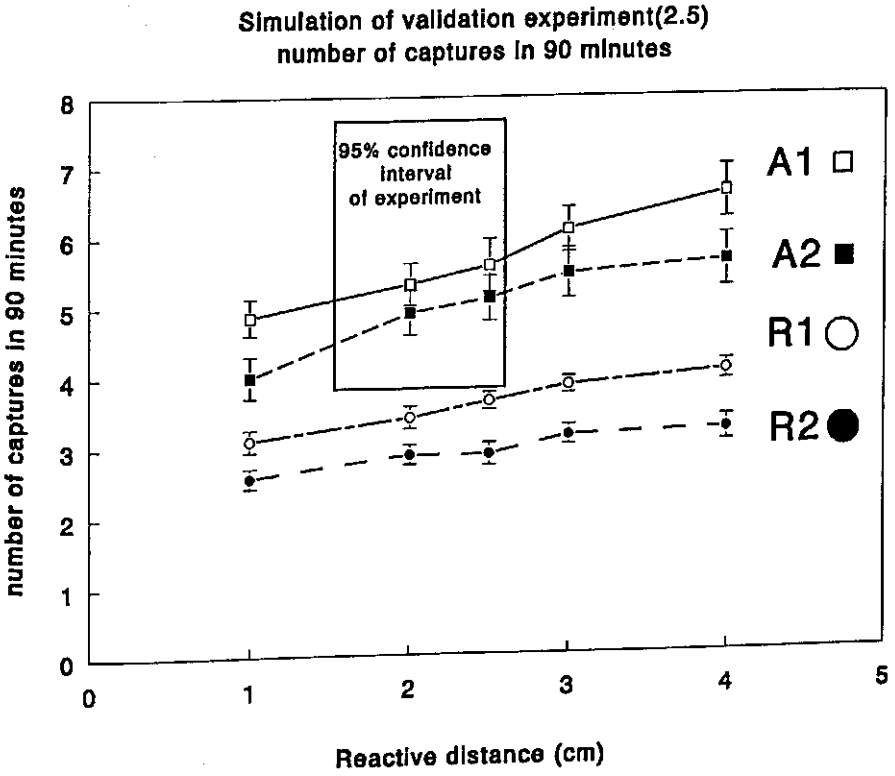

FIG. 3.24 Results of the validation experiment (± 95% confidence interval) in an arena of 100*150 cm.(chapter 2.5) compared to results of simulation for aggregated prey (A) and randomly distributed prey (R) related to reaction distance. Prey content is 5% (A1,R1) or 10% (A2,R2) of MAXGUT respectively.

3.3.5 Comparison of validation experiment and its simulation

The mean result of the observations, 5.7 ± 3.7 prey captured/period (10 beetles) (see chapter 2.5) and its 95% confidence interval of the mean are give in fig. 3.24 together with the results of the simulation (average of 100 runs). Because only 10 beetles were observed the confidence interval is quite large. Nevertheless, the results of simulations with clusterd prey agree rather well with the observations. Simulations with randomly placed prey show a significantly lower predation rate. Since the maggots offered in the experiment differed slightly in weight, effects of variations in prey weight on the capture rate were simulated by offering prey with a weight of 5% or 10% of the maximum gut capacity of the beetle. By feeding on heavier prey satiation occurs sooner resulting in a lower capture rate, but even this remained within the 95% confidence interval of the experimental results.

Reaction distance of the beetle is not exactly known therefore simulations have been carried out on a range of reaction distances (ranging from 1 to 4 cm) to test the effect of it on predation rate. Changing reaction distance has only a minor effect on predation rate. Probably this is mainly due to prey depletion in such a small arena, because after each prey capture it is more difficult to get the next one. The type of prey distribution has a much stronger effect on predation rate than the reaction distance. Concerning prey depletion, the difference with the results of previous simulations, where effects on capture rate by prey depletion hardly occurred, is due to the size of the arena. In a large arena local lower densities of prey are easily compensated for by the beetle as it walks relatively large distances. In a small arena the beetle is kept at the same location were prey density decreases rapidly by predation.

4.0 GENERAL DISCUSSION

The ultimate aim of this study was to investigate the impact of spatial distribution and density of prey on the predatory behaviour and resulting egg production of the carabid beetle *Pterostichus coerulescens* L. Firstly the driving force ('the motivation') behind foraging behaviour was studied, secondly the most important components of foraging behaviour were identified, and thirdly the relationships between the behavioural components and motivation were quantified. Mols (1988) showed that in addition to the emptiness of the gut the size of the ovaries and of the ripening eggs had to be taken into account, because they limits gut expansion and thus determine the relative satiation level of the beetle and also the rate of change of the satiation level. The latter depends both on the gut-emptying rate and on the egg deposition rate, because egg laying has an effect on the extent of expansion of the gut. Because of the clear influence of the size of ovaries and eggs in *P. coerulescens* the definition of motivation differs from that found for predatory mites (Fransz, 1974; Rabbinge, 1976, Sabelis, 1981), where gut size was considered to be constant. Next, the relative satiation level was related to the components of predatory behaviour. The most important components are: locomotory activity, walking velocity and turning rate, reaction distance to the prey, and success ratio. The implications of the relationships found for predation and egg production in relation to the spatial distribution of the prey, are discussed below.

4.1 PREDATORY BEHAVIOUR AND PREY DISTRIBUTIONS

An important factor determining the predation rate of a predator is the way it searches for its prey. Firstly, the prey habitat has to be located, and then the prey itself has to be found. In *P.coerulescens* this takes place by walking as the beetle rarely flies. Lastly the suitability of the prey has to be established once it has been encountered. However, *P.coerulescens* is a polyphagous predator accepting all kinds of prey (Hengeveld, 1980). Therefore, search for a specific prey habitat is hardly necessary. Its preference for a specific locality will mainly be influenced by other factors such as soil type and structure, vegetation and microclimate (Heydemann, 1955). Sandy soils with a low humus content, open and dry localities with sparse vegetation where sunlight can easily reach the soil, are preferred. When it has found such a habitat it will look for food. This food may include aphids (mostly highly aggregated), larvae of Diptera feeding in the litter (random to aggregated), caterpillars (random to aggregated) and also larvae of the heather beetle (*Lochmea suturalis*), usually highly aggregated.

Thus, the beetle has to deal with prey with all kinds of spatial distributions. Prey density in the beetle's habitat, may be temporarily very low, as in poor heathland and moorland, or sometimes excessively high as during heather beetle outbreaks. In previously cultivated land prey density may be moderate to high depending on the nitrogen content of the soil. From experiments and simulations, it appeared that the beetle was adapted to such varying prey distributions, and can respond to them by changing its behaviour.

4.1.1 The advantage of specific walking behaviour

In the experiments we observed that the beetle may show three distinct types of walking. A) Walking at high speed when it is hungry, B) walking at an intermediate speed when it has something in its stomach and C) a slow very winding walk after eating of a prey. High-speed walking is very useful when large distances have to be covered. It only occurs when the beetle is hungry, disturbed, or when trying to escape from enemies. It is profitable when prey is aggregated or when large prey is randomly distributed at a low density. In these situations high-speed walking between the clusters results in a substantial increase in predation because the distance between them is covered in the shortest time. The time between encounters with clusters is more than halved, because at higher speed the beetle walks straighter. Intermediate speed is advantageous in prey clusters, because it results in a longer stay in the clusters where there is a good chance of meeting the next prey. Tortuous walk (TW) is only profitable if prey are aggregated (Chapter 3.3.1); with randomly distributed prey it is disadvantageous as it decreases the discovery rate because the high degree of recrossing results in a low linear displacement. If the duration of TW could remain constant it would have more effect as the prey density increased. However,the duration of TW is not constant, rather it depends on RSATL and decreases as the satiation level increases. This means that at increasing prey densities it will have less and less effect untill it disappears above a RSATL of 80%.

Considering the rate of discovery that results from the walking behaviour without the feedback of the motivational part, sizes of clusters can be found in which TW behaviour is more useful. Tortuous walk was of most use within clusters smaller than 30 cm diameter. The high degree of recrossing at velocities of below 3 cm/sec decreases the effectiveness of the search (area searched/distance walked). On the other hand, because of this intensive search, a small area will be inspected very thoroughly. Of course, this is only profitable when prey is aggreggated.

The effectiveness of this walking pattern can be estimated by simulating the discovery rate of the beetle at different walking speeds and with randomly distributed prey. The outcomes of these simulations can be compared with estimations calculated with the Skellam formula (Chapter 1.1), where the effect of turning resulting in recrossing is not included. The differences between the results of simulation and of calculation with this formula gives an estimate for the effect of recrossing. The more winding the path, the more recrossings and the lower the effectiveness. The effectiveness is estimated by dividing the simu-

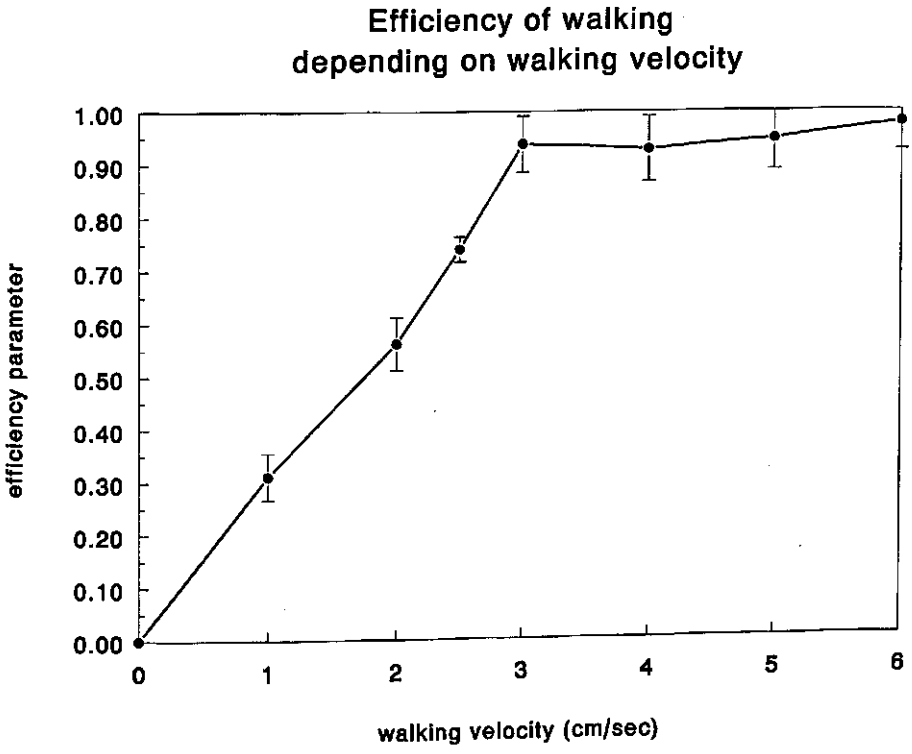

FIG. 4.1 Searching efficiency parameter (E_{ff}) calculated from results of the stochastic searching model and the Skellam model (see text) offers a correction factor for the windingness of the walking track.

lated results by those calculated with the Skellam formula. This is illustrated in fig 4.1, which shows that the effectiveness of the walking pattern depends on the speed of walking. Therefore, the efficiency of tortuous walk is very low. That, nevertheless, it is profitable in clustered prey distributions must be attributed wholly to the compensation by the increased time spent in prey clusters, only then does it result in a higher predation rate and in a higher egg production.

When no motivation is included Skellam's formula provides an easy way of estimating discovery rates, but for the beetle it highly overestimates the discovery rate below a speed of 3 cm/sec. This effect shows that Skellam's formula can only be used for rather straight walking patterns, unless a necessary correction for recrossing, depending on turning rate and thus on speed, is included. The second restriction is that it only can be used for the estimation of predation for periods with constant behaviour, because changes in behaviour are not included in it.

When walking behaviour is coupled to motivation, it may be concluded that the searching behaviour of *P.coerulescens* is adapted to various types of prey distribution, but that it shows its greatest profitability at overall low prey densities with aggregated prey. Especially when the prey is small, i.e. 5-10% of the maximum gut size, tortuous walk is very profitable.

But how will the situation be in the field with varying temperatures, rain, and varying structures of both soil surface and vegetation? Walking velocity is positively related to temperature (Mossakowski & Stier, 1983). If the relationship between velocity and turning rate remains the same at different temperatures, the model takes care of the effect of fluctuating temperatures. But if the relationship changes this has to be carefully studied before reliable statements about the the field situation can be given.

The influence of soil surface structure and vegetation was only incorporated to a small extent into the experiments. Dense vegetation and a rough surface hamper walking speed and increase the turning rate so that these may deviate a lot from the relationship established experimentally between velocity and turning rate. On the other hand, the agreement between the dispersal found in the field (Baars, 1979) and that found by simulation indicates that this effect could be less important than that of the temperature.

By sampling, we can estimate prey density and prey distribution in the field, but what we assess, may differ completely from what the beetle experiences. Also between various prey species differences in availability will be very difficult to assess, if not impossible. This makes it difficult to make a direct comparison between the results obtained by simulation and those estimated from the field, and also to predict predation rates in relation to 'real' prey densities and distributions. However, a rough estimate of the total prey situation may be obtained using the state variables of the beetle, such as weight of the adult beetle and number of eggs in the ovaries, to calculate at which overall prey consumption the values of these state variables can be reached. The mean and variance of these individual state variables of the beetles in relationship to the locality where they were caught represents the food available at that particular time and place. The variation in beetle weight in the field may thus give an indication of prey consumption and consequently of prey availability and prey clustering. Prey quality is an essential element in food availability as it is difficult to consider apart. But it may obscure the interpretations of the beetle weight, because prey quality influences the motivation and egg production. Nevertheless, the model may be used as a tool to illustrate how the different prey densities and distributions led to the distribution of the internal states of the beetles in the field.

4.1.2 The effect of locomotory activity

Two factors significantly influence the locomotory activity, namely temperature (Thiele, 1977), and the hunger level of the beetle. As the locomotory activity of the beetle decreases like a hyperbole with the increase of the satiation level, thus decreasing strongest at low satiation levels, this points to an adaptation to clustered prey. By decreasing its locomotory activity after consuming a prey (even a small one), the beetle stays longer in a location profitable for feeding. While resting it digests the prey and produces eggs of it. In combination with the slow and tortuous walk this is highly profitable. In contrast, long periods of locomotory activity together with high speed walking during periods of hunger increase the chance of finding places where food is more abundant.

In the experiments, locomotory activity differed highly between individuals. This variation was strongly correlated with egg production. Because high egg production results from a high intake of food and its rapid and efficient conversion, it may be hypothesized that the relative rate of gut emptying (RRGE) and the efficiency of food conversion (EFF) (See Mols, 1988) are the most important variables on an individual level. The energy used by the beetle for walking depends on its locomotory activity and walking speed (Alexander et. al, 1977, Delcomyn, 1981, 1984, 1985, Heath et al.1982, Herreid et al., 1981) thus an increase of activity and speed is only advantageous, if it enhances the discovery rate of prey. We have no information about the difference in energy usage between high-speed walkers and intermediate-speed walkers. Respiration experiments showed no difference in relative weight loss between starved and non-starved beetles, so that these differences may be small. Egg production as a result of ingestion, digestion and respiration is a good measure of energy surplus. Therefore it can be used to show the differences between the beetle's searching effort in randomly and aggregated prey distributions.

Because of differences in individual locomotory activity, we may also talk about 'active' and 'lazy' beetles as high and low egg producers respectively. A 'lazy' beetle may remain longer under the cover of litter etc and thus may have a lower chance of being victim to a predator. Different strategies of survival may be represented: a) Being active and thus increasing the chance of finding extra prey and increasing egg production but with a higher risk of being discovered by an enemy and being eaten itself, or b) being lazy resulting in a lower egg production, but having the chance of surviving longer. Which of these strategies is most successful will depend on the predation pressure. It could also be hypothesized that 'lazy' beetles, because of a lower metabolic rate, can better survive periods with an extremely low prey availability (during a dry spell) than 'active' beetles.

Locomotory activity and temperature.

To simulate locomotory activity at field temperatures, its relationship with temperature must be known. From the results of the experiments in Chapter 2 and from field data (Baars, 1979) the following reasoning can be used to get an estimation of this relationship.

In the observations done at 12°C the beetles hardly showed any activity. Although locomotory activity was very low, feeding and egg production still occured at a low level (Mols, 1988). Therefore, not 12 but 10°C was considered to be the thermal threshold for locomotory activity.

To estimate the maximum locomotory activity at other temperatures, the maximum locomotory activity at 20°C is taken as a reference, and the factor ACTEMP was introduced. ACTEMP is the locomotory activity relative to the maximum locomotory activity at 20°C, which is given the value of ACTEMP = 1. At 10°C ACTEMP =0. Above 20°C ACTEMP was not known because observations were lacking. Therefore, to get rough etimates of the relative activity at other temperatures, we used the catches of pitfall traps set in springtime,

when no young beetles emerge, and corrrelated them to air temperature (Baars, 1979). The catches at different temperatures were scaled to those of 20 °C, and thus the estimates of ACTEMP were obtained (table 4.1). At temperatures above 22 °C pitfall catches decreased and above 30 °C became zero. This is a rough estimate of course, because we only related trap catches to temperature, assuming that other factors have the same effect on activity.

TABLE 4.1 Relative locomotory activity (ACTEMP) estimated as a function of temperature (degrees Celcius).

Temperature	ACTEMP	Temperature	ACTEMP
10	0	22	1.2
12	0.1	25	0.75
15	0.5	30	0.15
20	1.0	35	0

Observations showed that locomotory activity of the beetles in the arena in the field almost decreased to zero when temperature was near to or above 30 °C.

Locomotory activity and pitfall trapping

Another field of interest is the estimation of population density by means of pitfall trapping, where the locomotory activity of a beetle plays an especially important role; the number of beetles captured reflects their locomotory activity. As stated earlier we learned that the change of locomotory activity is governed by temperature and by satiation level. Beetles with a high locomotory activity are caught sooner than beetles with a low one. Hungry beetles have therefore a higher chance of being caught by a pitfall trap than those who are full. In good feeding areas, pitfall captures will underestimate the real population density, while in poor feeding areas they will overestimate it. This hypothesis is supported by Chiverton (1984), who found that significantly more female *P.melanarius* were caught in plots treated with insecticides than in the untreated control plots. The females from the treated plots had a lower gut content than females from untreated plots.

Estimations of state variables based on dissection of beetles caught in pitfall traps, such as gut content and the number of eggs in the ovaries, both of which are highly related to how much food they can get, will severely underestimate the beetle's weight, average gut content and the average number of eggs number in the females of the population. Estimations of the quantity of food available in the field, based on the condition of the beetles caught in pitfall traps underestimate the real food situation. To get an impression of the real distribution of the different feeding conditions of beetles in a field population, the frequency distribution of the numbers caught over specific feeding conditions, needs to be corrected for their chance of being captured, which for hungry beetles is 5 times higher than for satiated beetles.

4.1.3 The effect of success ratio

The success ratio for different kinds of prey, depends on the satiation level of the beetle. As this ratio decreases with increasing level of satiation it largely determines the shape and level of the functional response curve (especially when prey handling time is relatively short with respect to the total searching time). This is also found with other predators (Fransz, 1974; Rabbinge, 1976; Sabelis, 1981). The relationship between success ratio and RSATL is specific for each kind of prey. Preferences for different kinds of prey may be found by comparing the success ratio – RSATL curves, as these are hunger dependent. Thus, for polyphagous predators the difference in the succes ratio -RSATL relationship between different kind of prey may explain the preference for particular kind of prey at a specific satiation level.

4.1.4 The effect of reaction distance

In the simulations, reaction distances are 1 and 2 cm. The simulations show that in random prey distributions reaction distance plays a substantial role, because discovery rate is linearly related to it. When the prey distribution is aggregated, differences in reaction distance do not result in the same change in discovery rate. Simulations showed that doubling the reaction distance from 1 to 2 cm results neither in a doubling of discovery rate (42%), nor in doubling of captures/day (17%). When the prey is clustered, it is only profitable for the beetle to increase its reaction distance to about the radius of the prey cluster. *P.coerulescens* is diurnal and hunts by eye and it does not seem to orient itself from a distance by olfactory queues. In preliminary experiments on a walking sphere it showed no reactions to a stream of air with maggot odour, while a nocturnal hunting species (*Pterostichus madidus*) reacted immediately. Hunger may have an effect on reaction distance in *P.coerulescens*; however, the results of a few experiments, give no reliable evidence of this.

4.2 Predation and egg production

From the results of simulations using models in which all the important behavioural components were included and connected with the motivation model, the following can be concluded concerning daily predation and egg production:

(1) In random prey distributions, the predation per day is about the same whether the beetles perform tortuous walk after prey consumption or not. Although tortuous walk normaly will lead to a lower predation rate this is partly compensated for by a small increase in locomotory activity.
(2) In aggregated prey distributions, the advantage of the walking behaviour is much more striking when the discovery rate is considered alone than when predation rate is taken into account.

Predation and egg production are only higher when the prey density is low and prey is aggregated. With more than 1 prey/m^2 no difference could be found between aggregated and random prey distributions. It may be hypothesized that

predatory behaviour of the beetle is adapted to clustered prey occurring at low densities.

(3) Below overall prey densities of 1 prey/m^2, the beetle is most adapted to small prey clusters (up to 40 cm), resulting in higher prey capture, consumption and egg production. However, within this range of small cluster diameters the beetle can reach a similar rate of predation and egg production. In the simulations the distance between the clusters decreases with the decrease of the prey density in the clusters, so that over this range of cluster sizes, differences in prey density and distance are more or less compensated for by the change of the beetle's searching behaviour.

(4) Although prey capture is always higher when the clusters are very small (< 10 cm)(fig. 3.15), this does not result in a higher prey consumtion and egg production. In small prey clusters, prey is encountered rapidly after each other, therefore satiation is reached very soon, and as a result only a small part of each captured prey is consumed. This decrease in prey utilisation has a negative feedback on egg production.

By its wide range of behavioural reactions in relation to the relative satiation level, the beetle is able to adapt to the prey distribution encountered. At low prey densities and small cluster sizes (smaller than 40 cm) a high locomotory activity, straight walk alternating with tortuous walk, are responsible for an optimal result. When prey density as well as cluster size increase, intermediate walk replaces straight walk more and more, locomotory activity decreases and tortuous walk becomes less important.

It is of interest to compare this simulated behaviour with that found in the field by Baars (1979) for the same species. He observed periods in which beetles day after day covered long distances (straight walk) alternating with periods in which only short distances were covered. To a great extent this behaviour can now be explained by the relationships between behavioural components of the beetle and its motivation; because in simulations the same pattern is found for low overall prey densities and aggregated prey distributions.

4.3 Dispersal

In poor habitats, such as those of *P.coerulescens* dispersal is important, leading to the exchange of individuals between subpopulations. From experiments and by simulation we learned how *P.coerulescens* can cope with a low prey density in a mozaic landscape with alternating rich and poor prey patches.

Both from Baars' (1979) field experiments and the results of calculations using walking behaviour components, such as velocity, turning rate and locomotory activity, we can predict the dispersal power of this species. Linear displacement calculations agree rather well with Baars' field observations (Chapter 3.3.4). Dispersal is governed by temperature and food; temperature has a direct influence (Massakowski et al., 1983) on walking speed and locomotory activity (Chapter 2.2), but also an indirect influence via the rate of change of the motiva-

tional state. The relative amount of food in the gut has a direct effect on walking speed and locomotory activity. When the beetle is in a prey cluster linear displacement of the beetle is low (2-4 meter), outside prey clusters it increases and when no prey is found, daily distances can vary between 17 and 24 metres. This high-speed walking behaviour may last only for a few days e.g. depending on temperature for about a week in June, because after that period eggs are resorbed and the beetles become 'spent' (van Dijk, 1979) producing no more eggs for the rest of the season. Roughly, this implies that distances between clusters must not be more than about 45 metres. If there is food available between clusters, the distances may be much larger.

Fieldwork and simulations may help to derive guidelines for nature conservation to predict for this and other species how far they can walk between suitable pieces of landscape or habitats, and whether it is necessary to help them by constructing corridors or stepping stones between such areas. Such information can thus help to increase the attainability of suitable sites for certain species and increase exchange between subpopulations.

4.4 Coupling predation to population models

In predator-prey population models, the interaction between the growth of the prey population and the predator population is obtained by the functional and numerical response of the predator to its prey. According to Solomon (1949), functional response is defined as the number of hosts succesfully attacked per natural enemy (a predator or a parasitoid) as a function of host density. Thus it describes the way a predator or parasitoid responds to the changing abundance of its prey by killing or parasitizing more or fewer prey as it becomes respectively easier or more difficult to find.

The numerical response is defined as the reaction of a predator/parasitoid to the changing abundance of the prey by: (1) Producing more or fewer off-spring when the prey is respectively easier or harder to find and to consume. (2) Migrating to or aggregating in areas with higher prey densities.

The functional response is also a numerical response, if the eggs are laid in or near a host, as occurs with most parasitoids, the adults of which do not consume the prey. In predator models, a factor is used that converts the number of prey consumed into the number of offspring produced. In agricultural systems, the functional response is a commonly measured characteristic of natural enemies of crop pests. The failure of natural enemies to keep pest density below the economic threshold has been associated with a rapid increase in pest density which overwelms the enemies functional and numerical response (Murdoch et al., 1985). This may be due to the satiation of the predator, or to limitations of the handling time, or the time-lag in the egg production in the case of predators. Therefore, by knowing the functional and numerical responses of a natural enemy, it is theoretically possible to predict its contribution to the dynamics of a pest population, and identify the density at which the pest would escape control by the beneficial enemy (O'Neil, 1990).

4.4.1 Functional response models

In predator-prey population models, simple descriptive models of the functional response are preferable as they are easy to understand and, unlike the stochastic models, do not need much computer time. One may ask, what models are available to describe the functional response of a general predator like *P.coerulescens* appropriately, and is it possible to apply them?

Holling (1966) describes 3 types of functional response models for random prey distributions (see appendix II).

Type 1 response: When a predator kills a constant proportion of the prey the relationship between prey density and number of prey killed is linear until a plateau is reached were the number of successful attacks remains constant. The plateau represents the maximum predation rate. That rate is physically determined.

Type 2 response: Just as in the type 1 response a saturation level is reached, but in a gradual way. This is probably the most widespread type of response. If we realise that a predator or parasitoid only has a limited amount of time, this type is easy to understand. Some of this total time (T) is needed for searching for prey while another part, collectively referred to as 'handling time', is used for the pursuit, attack and consumption of prey. At increasing prey densities (N_0) the time available for searching (T_s) decreases as more time is used for the handling of prey (T_h). This leads to Holling's ' disc equation' for the calculation of the number of prey killed (N_e)

$$N_e = a'*T*N_o/(1+a'*T_h*N_o)$$

a' = the searching efficiency or relative rate of successful attack.

Holling assumpes that when a predator or parasitoid searches for prey it does not change its behaviour during the whole searching period. The number of prey encountered is an instantaneous rate which only holds for short periods when the prey density remains constant. In case of predators, this is not true because when prey is killed it is removed from the population. In case of parasitoids, it is assumed the parasitoid searches in such a way that a host is only encountered once, thus the number of prey encountered equals the number of prey parasitized. This only holds for a short observation period. It can also be said that the parasitoid searches systematically. What we see in most experiments is that parasitoids do not avoid previous parasitized hosts thus that they encounter a host more than once. To account for this effect, the approach of Nicholson and Bailey (1935) can be used (see Rogers, 1972). They assume that:

- Searching is random and does not change during the observation period, thus each prey has an equal chance of getting parasitized in a certain period.
- Parasitoids do not discriminate between parasitized and unparasitized hosts.
- Parasitoids to not interfere with each other.
- The parasitization time is zero (i.e. no handling time)

then the chance of a host being encountered is a Poisson process. The chance

of having no encounters (and thus no parasitization) equals the zero term of the Poisson distribution. Including the 'Disc equation' in the Nicholsons competition equation leads to the 'random parasite' or to the 'random predator equation'.(See appendix II).

Type 3 response: If a predator reacts to an increase in prey density by increasing the proportion of prey it kills over a specific range of prey densities, this results in a sigmoid curve. This type of response is caused by a number of predatory characteristics, and it may be found in predators which are capable of learning.

Prey aggregation

Prey often has an aggregated distribution, resulting in predators that search for them in an adapted way. In functional response models instead of using the zero term of the Poisson distribution the zero term of the negative binomial distribution is used for expressing the proportion of prey that escapes from predation (Crawley, 1992): $P_0=(1+/k)^{-k}$
thus 1-P_0 is the proportion that will be predated. k is the aggregation parameter. As k gets large (> 10) the negative binomial approaches the Poisson distribution. For small values of k (< 1) the distribution of predator attacks is highly aggregated. As the degree of aggregation increases, the value of k decreases and the zero term gets bigger. This means that a larger proportion of the prey escapes predator attack.

The type II and III functional response models and the random parasite and predator equations (see appendix II) predict that the number of hosts or prey attacked increases at a diminishing rate as the prey density increases. It is possible to use these models to describe the same experimental results, although in this way different estimates of the searching efficiency and the handling time will be obtained. This is because the disc equation assumes that the predator searches systematically for its prey and does not waste any time in re-searching part of the arena, whilst the random predator equation assumes that the predator searches at random. The values of the parameters can be obtained by linear regression of the experimental results. Although this all seems clear we soon get into trouble when the real handling time is measured experimentally. It may appear to deviate substantially from the calculated value which shows that searching efficiency (a') and handling time (T_h) stand for more then they are meant to. This may imply that the predator or parasitoid does not searches randomly, that T_h is not constant, that the locomotory activity changes with prey density, or that the searching velocity changes with prey density etc. In such cases it is better not to estimate a' and T_h from the data of the functional response experiments, because they apply only to these specific experimental conditions. When conditions are changed, the functional response changes. It is better to estimate their value from behavioural observations of the predator or parasitoid during the process of searching and predation or parasitization.

From the stochastic simulations, we learned that for *P. coerulescens*, especially at low prey densities, different Holling II response curves can be constructed

for each prey distribution. Using the negative binomial zero term for aggregated prey in the Random predator equation model seems not to be appropriate, because it results in a lower predation when prey is aggregated than when prey is randomly ditributed. This result is in complete contradiction with the stochastic simulation experiments of *P. coerulescens* (Chapter 3), where it was found that the functional response of the beetle, which, both for random and aggregated prey distributions looks like a Holling II response curve, is steeper when prey was aggregated,and thus predation higher, than when it was randomly distributed. Therefore, using the $(1\text{-}P_0)$ term of the negative binomial, seems not to be appropriate for estimation of predation in aggregated prey distributions, because changes in behaviour are not accounted for. This agrees with Murdoch et al. (1989, 1990) who say, that rearrangement of predators to prey aggregations during the season makes the functional response curve steeper. That result is good for biological control but not for the stability of the predator-prey system.

For aggregated distributions a solution can be found by dividing the searching time into periods when the predator is either present inside or outside a prey cluster, because of possible changes in behaviour of a predator/parasitoid. This mostly results in complex models involving the behaviour of both predator and prey.

4.4.2 From behavioural components to functional response

To include real behavioural components in the functional response models, Skellam's extented formula for calculation of the predation rate offers a solution (Chapter 1.1; Sabelis, 1981). This model uses behavioural components for the calculation of predation, which can be measured separately, such as: the walking velocity, the effectiveness of walking depending on windingness, locomotory activity, reaction distance and success ratio; all in relation to external and internal conditions. If the handing time (T_h) is included in the searching time (T_s) the equation can be extended to:

$$N_{pred} = T_s/\{1/(a'*N_o) - T_h\}$$
$$a' = V*D**E_{ff}*Sr$$

If the handling time is inluded in the resting time

$$N_{pred} = a'*N_o*T_s = a'*N_o*A*T$$

The assumptions are:

- The predator walks randomly with respect to the prey
- The velocities of prey and predator are mutually independent and the resultant velocity is $V = \sqrt{(V^2pred + V^2prey)}$. If this is not the case (for example when the predator follows the trail of a prey) the formula is not applicable.
- The behaviour does not change.

If the handling time is difficult to measure and relatively short with respect to the exposure time (T), it is easier to measure the active searching period T_s

directly and ignore T_h. If T_h is relatively long (and therefore strongly influences T_s) it is better to measure both. In predators handling time may be very variable as it may depends on satiation level and prey size (Mols, 1988) and sometimes also on a digestive pause (Holling, 1966).

For inclusion of specific searching behaviour, like tortuous walk, searching time should be divided into periods with and without tortuous walk.

As these are instantanious rates they can be substituted in The Nicholson & Bailey equation to get a Random predator or Random Parasite equation.

Then we obtain equations in which behavioural characteristics are included, thus the vague variable 'a" is now replaced by biologically clear variables. The problem remains that predator behaviour (especially walking speed, locomotory activity and prey acceptance) changes according to local differences in prey density. Therefore this approach is only be applied to short periods when it can be assumed that behaviour is constant. A disadvantage is also that population models including these functional response models with changing behaviour cannot be solved analytically but only numerically.

4.4.3 From individual predator models to population models

The stochastic searching model (Chapter 3) may be useful for analysing the effect of walking behaviour at different prey densities and prey distributions at the individual predator level. The model can be extended to population level by bringing in more beetles and by making the stationary prey distribution and prey density dynamic. This will lead to a complete stochastic model which can be used to estimate the effect of the beetle as a control agent of a specific pest, for example, aphids in cereals. However, many simulation runs and a large amount of computer time are needed, due to the stochastic nature of the model for walking behaviour and the small time step (2 sec). Another approach uses the average predation values for individual beetles, calculated with the stochastic model as input for the predator-pest model; assuming that the outcome from average input values is identical to the average outcome with variable input values. This is generally only true when the variation in input parameters is small or when the model has linear relationships between its variables. However, there is a large variation between individual beetles, especially at low prey densities, while several relationships (e.g. the functional response) in the model are non-linear and depend on prey distribution. Thus averages cannot be used as inputs in the simulation. A solution for this problem is offered by compound simulation (Fransz, 1974; Rabbinge et al, 1989). Therefore, the beetle population is divided into three classes according to the types of walking behaviour. Each class is split into two subclasses, for beetles inside and outside a prey cluster. Thus beetles belong to one of six classes. Within a walking class the beetles are assumed to behave identically. The stochastic model of the individual beetle is replaced by relationships, calculated from a large number of runs with this model, which estimate time spent within a prey cluster as a function of walking velocity and cluster diameter (fig 4.2). The discovery rate with prey clusters and with prey within a cluster can be approximated with the extended Skellam model.

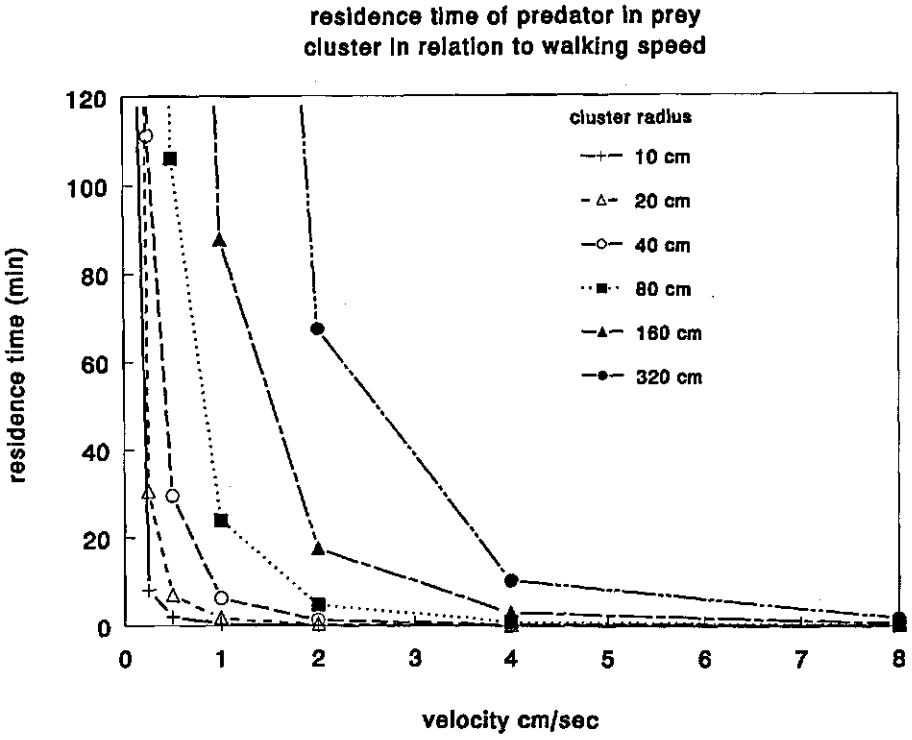

FIG. 4.2 Residence time of the beetle in a prey cluster depending on walking speed and prey cluster size.

Each time step, the population model is run for each class of beetles separately and beetle numbers in each class are adjusted according to motivation dependent behaviour and the residence time in the cluster. When beetles (or fractions of the beetle population) shift from one class to another also all contents of the state variables of the motivational part also shift to the next class, and are averaged with those that are still there (fig 4.3). In this way, a stochastic model of an individual beetle is replaced by a deterministic model in which the motivational state of all beetles in a class changes by the average state in that class. Prey numbers may be distributed randomly or clustered and can be calculated with a population growth model. For example an aphid growth model in cereals (Rabbinge et al., 1979, Rabbinge & Carter, 1984, Carter, 1985). Preliminary simulations with this model show that *Pterostichus cupreus*, the dominant carabid species in cereals on clay soil, which is very closely related, and similar in size to *P.coerulescens,* may have a considerable impact on aphid population growth. The relationships found for *P.coerulescens* were used in the model, therefore the conclusions were based on the assumption that *P.cupreus* behaves similar to *P. coerulescens.*

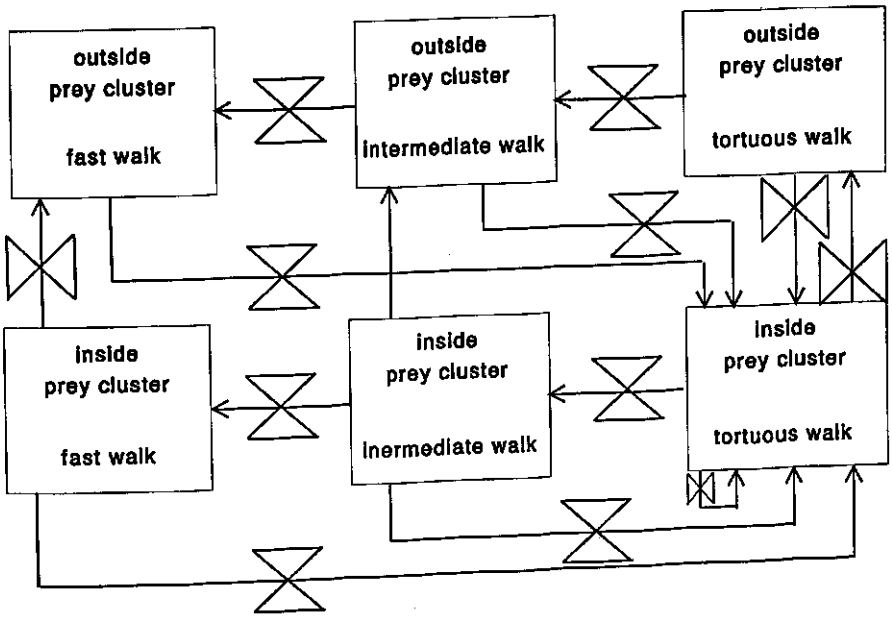

FIG. 4.3 Division of the states of the beetle according the type of walking behaviour and being inside or outside a prey cluster used in the compound model of the beetle population.

4.5 METHODOLOGY OF EVALUATION OF POTENTIAL PREDATORS FOR BIOLOGICAL CONTROL

The relationships found in *P.coerulescens* between both motivational state and behaviour and the prey density and distributions of its prey may lead to a list of recommendations on how observations and experiments should be carried out when a potential predator is evaluated for use in biological control and which factors have to be taken into account.

1. From the research on the motivational state of the beetle in Part I of this study (Mols, 1988), it is clear that we need to quantify the physical and physiological properties of a predator.
   a) Gut capacity in relation to predator size and room in the abdomen,
   b) Satiation level for different physiological stages of the predator (reproductive or not),
   c) Gut emptying rate.
   d) Metabolic needs, both in reproductive and non-reproductive state.

e) Uptake and conversion efficiency in relation to prey type.
f) Egg weight

2. For the estimation of searching and predation rate the following behavioural components are necessary.
   a) Walking behaviour (walking speed and turning rate) and duration of specific walking behaviour (e.g. intensive search)
   b) Relationships of behavioural components, like locomotory activity, succes ratio and reaction distance with internal variables like the satiation level.
3. Validation experiments concerning the motivational part and the functional response.
   a) Independent egg production experiments under controlled food conditions.
   b) For functional response experiments, the area of observation must be related to the radius of action (walking distance per day) of the predator. If this is not the case, border effects will strongly influence the outcome of the experiments.
   c) The experiment must be long enough for the predators to adapt to the prey density and prey distribution such that feed back mechanisms show their effect. Historical effects like gut content, fat quantity, ovary size and number of eggs in the oviduct strongly determine the predatory capacity (e.g. effect of egg load on the expansion of the gut). Not doing this overestimates the advantage of the predator. As the predator becomes older, the responses to internal and environmental stimuli may change, resulting in a difference in predation.
   d) Experiments to find out the functional response of a predator, especially at low prey densities and also when the prey is clustered need many repetitions. To obtain confident averages the number of repetitions required is often so high that this is not practical, because of the time and space needed and above all the stochastic nature of the material. Nevertheless, if they are carried out, results will be very arguable. Functional response curves carried out with standardized predators only hold for that type of standardization, meaning that different standardizations result in different functional responses. The results of an experimentally established specific functional response of a predator are only indicative for its predatory capacity. Therefore simulation models incorporating the behaviour of the natural enemy may be a better tool for estimating its functional responses.

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APPENDIX I THE SEARCH MODEL

APPENDIX I

Simulation of walking behaviour and discovery.

The direction of walking is calculated by drawing randomly a direction out of the turning rate distribution. Each timestep this is done again and the next angle is added to the former direction which then gives the new direction. This is accomplished by drawing a random number out of a uniform distribution between 0 and 1.

```
P = RAN(IS)
```

IS is a seed number needed for the random generator. P is used in the following equation:

```
A = AV + SIGMA*(P**KURT-(1.-P)**KURT)/KURT
```

Which is the Tukey distribution (Montfort et al. 1976) given in chapter 2.
The angle is now added to the former direction giving the new direction of the beetle.

```
DIR = DIR + A
```

As the speed of the beetle is known it is possible to calculate
the new coordinates of the beetle (XP,YP)

```
XP =XP + COS(DIR)*V
YP =YP + SIN(DIR)*V
```

The moment the beetle reaches the border of the field it will follow it when angles are chosen that should lead the beetle outside the field, other angles lead the beetle back into the field again.

Duration of tortuous walk.

Just after consumption of a prey, the beetle resumes searching at a very low speed. If no new prey is discovered the speed increases gradually to the speed given at the start of the simulation. In reality this will be the speed belonging to a specific level of satiation. The duration of tortuous walk is thus the time from the end of consumption when searching is started until the speed equals the value before the prey was discovered. Parallel with the increase of speed the turning rate distribution changes from wide to narrow, as the speed determines the SIGMA and Kurtosis parameter of the TUKEY distribution.

Prey distribution and prey discovery.

In the program the distribution of the prey can be arranged such that it may vary from random to very aggregated. This done by putting the prey in discrete prey clusters of a specific size. The numbers of prey in the cluster, the number of clusters and the size of the clusters can be given a specific value. The immobile preys are located in NC clusters, which are randomly distributed through the model field. Within a cluster IC preys are randomly located. Therefore, NC*IC preys are present in the field. The model field is a square with sides of UNIT length (expressed in cm.). The clusters are circul with a diameter of CLUNIT.

The distribution of prey through the field can be arranged as follows:
Random distribution: 1) Put one cluster in the field with the same diameter as the field length and place all the prey randomly in that cluster or 2) take as many clusters as prey are needed and place one prey in each cluster.

Aggregated distributions: Aggregation of prey increases by both decrease of the number of clusters per field and by decrease of the cluster size and consequently increase of the number of prey per cluster.

Procedure of prey location.

First the centers of the clusters are randomly placed in the field, and stored in two arrays. The X(L) and Y(L) memories, with the L being a multiple of IC, and in the CCX(I) and CCY(I), with I running from 1 to NC. The coordinates stored in the latter arrays are used to determine the distance from the beetle to the cluster centre. This procedure is needed for cluster scanning. Obviously it is less laborious if firstly the nearest cluster is determined and subsequently the prey of that cluster have to be scanned than to scann all the preys in the total field each time step. To determine which cluster is nearest, it is necessary to identify that cluster. The centrally located prey of a cluster is used as identification mark. Subsequently the preys are randomly located around the center of the cluster in a square with dimensions CLUNI*CLUNIT. To acquire a circular cluster, the preys located in this square are shecked to see if they are within a distance of 0.5*CLUNIT from the center. This is tested by calculating the distance from the prey to the center. If this distance is greater than 0.5*CLUNIT the prey is disgarded and a new prey is selected. The prey distribution is accomplished in the following program section:

```
 Do 1 I    = 1, NC
 L         = IC*I
 X(L)      = RAN(IS)*UNIT
 Y(L)      = RAN(IS)*UNIT
 CCX(I)    = X(L)
 CCY(I)    = Y(L)
 DO 1 J    = 1, (IC-1)
 M         = IC*(I-1)+J
11 XM      = RAN(IS)
 YM        = RAN(IS)
 X(M)      = X(L)+(XM-0.5)*CLUNIT
 Y(M)      = Y(L)+(YM-0.5)*CLUNIT
 DIST      = SQRT(X(M)-X(L))*(X(M)-X(L))+(Y(M)-Y(L))*(Y(M)-Y(L))
 HCLUNI    = 0.5*CLUNIT
 IF (DIST.GT.HCLUNI) GO TO 11
1 CONTINUE
```

Cluster scanning.

First the program determines which prey cluster is nearest to the beetle.

```
    DO 4 L =1, NC
    DIST1 =SQRT((CCX(L)-XP)*(CCX(L)-XP)+(CCY(L)-YP)*
           (CCY(L)-YP))
    DIST  =AMIN1(DIST1, DIST)
    IF(DIST.EQ.DIST1) L1= L*IC
 T4 CONTINUE
```

Prey is only located in the clusters, thus the beetle can only discovery a prey within a certain distance from the cluster center. The sum of the reaction distance of the beetle and the cluster radius form this distance (CLDIST). As standard reaction distance 2 cm is taken.

```
 RADIUS     =2.0
 CLDIST     =0.5*CLUNIT+RADIUS
   IF(DIST.GT.CLDIST) GO TO 6
```

If the distance is greater than CLDIST, for all clustres, the beetle did not find any cluster. Hence, the program will skip the next section in which the individual prey in the neares cluster are scanned.

The area of discovery.

In the model, the beetle is represented as a round object with a radius of 2 cm. When a beetle moves from one position to the next an area is covered consisting of a strip of 4 cm width but also consisting of a halve circular start and end area. When the beetle moves to the third position with a change in direction a part of the area is covered twice (fig 3.3). This indicates already that a winding walking track never reaches 100% searching efficiency even if they do not seem to cross.

Prey discovery in the area of discovery is calculated in the model by giving all the prey in the cluster coordinates relative to a new coordinate frame. This frame is perpendicular on the moving direction of the beetle during the time step.

The coordinates of the preys can be determind with the formula's:

```
Xnew = (Xold-XV)*COS(alpa)+(Yold-YV)*SIN(alpha)
Ynew = (Yold-YV)COS(alpha)+(Xold-XV)*SIN(alpha)
```

These new coordinates given to the preys in a specific prey cluster and the scanning of preys located in the area is programmed as:

```
      DO 5 J      =1,IC
      I           =L1-IC+J
      DX          =X(I)-XV
      DY          =Y(I)-YV
      CX(J)       =DX*CSDR+DY*SNDR
      CY(J)       =DY*CSDR-DX*SVDR
      IF(CX(J).LE.(V+RADIUS).AND.CX(J).GE.0.) GO TO 15
      GO TO 5
15    IF(ABS(CY(J)).LE.RADIUS) GO TO 16
      GO TO 5
16    NL          =NL+1
      B(NL)       =J
5     CONTINUE
```

Two situations can be distinguished.

a) The distance a beetle covers during one time step is larger than its reaction distance.
In this case three area's can be distinguished.

A) X-coordinate is smaller than reaction distance
B) X-coordinate is larger than reaction distance but smaller than V
C) X-coordinate larger than V

The prey located in area A must be scanned to see which ones have already been discoveryed in the previous time step; viz. all the prey located in the half circle. The selection takes place by determining the distance from the prey tp the XV,YV. If the distance is smaller than reaction distance the prey is discarded. From the prey located in area C, only those within a distance reaction distance from XV,YV are retained, whereas all prey in area B are saved.

Determination whether a prey is located in area A,B or C

```
    DO 71     =1,NL
    AM        =B(J)
    IF(CX(AM).LE.RADIUS) GO TO 17
    GO TO 18
17  D         =AM
    GO TO 71
18  IF(CX(AM).GT.V) GO TO 19
    GO TO 20
19  E         =AM
    GO TO 71
20  NF        =NF+1
    F(NF)     =AM
71  CONTINUE
```

The chance that a prey will be located in B is much greater than the chance to locate a prey in sector A or C. The preys located in B are stored in the F(NF) memory. A and C can maximally contain 1 prey each.

In the next section of the program it is prevented that in two consequetive time steps the same prey is scored in part A and C. This part of the program may be omitted if the prey is removed after an discovery or when it is not sessile.

```
    IF(D.EQ.0) GO TO 21
    DIST1   =SQRT(CX(D)*CX(D)+CY(D)*CY(D))
    IF(DIST1.LT.RADIUS) GO TO 21
    G         =D
21  CONTINUE
    IF(E.EQ.0) GO TO 22
    DIST2   =SQRT((CX(E)-V)*(CX(E)-V)+CY(E)*CY(E))
    IF(DIST2.GT.RADIUS) GO TO 22
    H         =E
```

The selected prey from sectors A, B and C are potential prey, and they are put in memory POT(CNT). In fact these are all the prey discoveryed by the beetle in one time step.

```
22   CONTINUE
    IF(G.EQ.0) GO TO 23
    I     =L1-IC+G
    CNT     =CNT+1
    POT(CNT)=I
23   CONTINUE
    IF(NF.EQ.0) GO TO 24
    DO 24 J =1,NF
    I     =L1-IC+F(J)
    CNT     =CNT+1
    POT(CNT) =I
24   CONTINUE
    IF(H.EQ.0) GO TO 25
    I =L1-IC+H
    CNT =CNT+1
    POT(CNT) =I
25   CONTINUE
```

b) The distance a beetle covers during one time step is less than its reaction distance.

In this case only those prey at larger distance than the reaction distance from XV,YV and closer to XP,YP than reaction distance are also put in memory POT(CNT) and can also be considered as discoveryed.

```
      DO 8 I        =1,NL
      AM            =B(I)
      DIST3         =SQRT(CX(AM)*CX(AM)+CY(AM)*CY(AM))
      DIST4         =SQRT((CX(AM)-V)*(CX(AM)-V)+CY(AM)*CY(AM))
      IF(DIST3.GT.RADIUS.AND.DIST4.LE.RADIUS) GO TO 41
      GO TO 8
41     NF           =NF+1
      F(NF)         =AM
8      CONTINUE
      IF(NF.EQ.0) GOTO 43
      DO 43 J       =1,NF
      I             =L1-IC+F(J)
      CNT           =CNT+1

      POT(CNT)     =I
43     CONTINUE
```

In the discovery model the discovered prey are given new coordinates in the cluster. The average density in the fields remains constant. If this is not done the chance of discoverying the same prey in sector B is very high when the speed is low and the prey density in the cluster high. This may give erroneous high rates of discovery.

APPENDIX II

Functional response models.

Holling (1959, 1966) describes 3 types of functional response models derived from different types of predators.

Type 1 response: When a predator kills a constant proportion of the prey the relationship between prey density and number of prey killed is linear until a plateau is reached were the number of successful attacks remains constant.

The number of prey encountered (N_e) is linearly related to prey density (N_0) and to the searching time (T_s):

$$N_e = a' * N_0 * T_s \quad (1)$$

a' = relative rate of succesful attack , also called the searching efficiency.

When the plateau is reached N_e = constant

Type 2 response: Just as in the type 1 response a saturation level is reached but now in a gradual way. If a part of the total time available (T) is used for prey handling (T_h) the searching time equals:

$$T_s = T - T_h * N_e$$

Formula of Holling for type 2 response curve:

$$N_e = a' * T_s * N_o \quad \text{where} \quad T_s = T - T_h * N_e \text{ thus:}$$

$$N_e = a'(T - T_h * N_e) N_o$$

If N_e is brougt to the left hand side the formula becomes:

$$N_e = a' * T * N_o / (1 + a' * T_h * N_o) \text{ the 'disc equation'} \quad (2)$$

This only holds for a short observation period. It can also be said that the parasitoid searches systematicly. What we see in most experiments is that parasitoids do not avoid previous parasitized hosts thus that they encounter a host more than once. To account for this effect the approach of *Nicholson & Bailey (1935)* is used (see *Rogers, 1972*). The chance of a host being encountered is a Poisson process. The chance having no encounters (thus no parasitization) equals the zero term of the Poisson distribution:

$$P_o = \exp(-N_e/N_o)$$

The fraction that a host is encountered once ore more is thus (1-Po)

The number of prey attacked by one predator or parasitoid is:

$$N_e = N_o(1 - \exp(-N_e/N_o)) \quad (3)$$

substitution of equation (1) for N_e gives the Nicholson's 'competition curve' for a single enemy

$$N_e = N_o(1 - \exp(-a' * T_s)) \quad (4)$$

The relative rate of succesful attack $a' = (\ln(N_o/(N_o - N_e))/T_s$

Thus we can calculate a' from the results of a parasitization experiment, because we know the density N_o and count $N_{par} = N_e$ as the number of hosts parasitized in time T_s.

If it is assumed that the parasitoid searches at random, equation (2) can be built into equation (3), then we get the so called ***'Random Parasite Equation':***

$$N_{par} = N_o\{1 - \exp(-a' * T * / (1 + a' T_h * N_o))\} \quad (5)$$

Equation (5) can not be applied for most predators because they remove their prey as they find one, at the first encounter. No time is wasted in repeated encounter (re-handling) with prey, and more time is available for searching. Thus for a predator

$$T_s = T - N_{pred} * T_h$$

For the equation of Holling this leads to the same 'disc equation' if it is assumed that N*pred* = N*e* which also holds for a short period. The parameter N_e in equation (3) describes the number of

encounters that the predator would have with the prey if the predator did not consume its prey or if the prey density remained constant. Had these encounters been distributed at random, the number of prey that would have been encountered once ore more times (and therefore the number of prey eaten) was the same as in equation (4). Substituting for T_s ,equation (4) gives the ***'Random Predator Equation'***

$$N_{pred} = N_o\{1-\exp(-a'(T-N_{pred}*T_h)\} \quad (6)$$

The Random Parasite Equation can be adapted for parasites that do discriminate between parasitized and non-parisitized hosts by taking different handling times for both types of hosts (*Arditi, 1983*).

Type 3 response: If a predator reacts to an increase of prey density by increasing its proportion of prey killed over a specific range of prey density this will result in a sigmoid curve.

If is found that the relative rate of encounter a' or the searching time T_s increases with (N_o) or that T_h decreases with N_0, then a sigmoid relationship between predation or parasitation and prey density may be found. For example, the parameter a' can be assumed to increase with N_o in the following way (*Hassell, Lawton & Beddington, 1977*).

$$a' = b*N_o/(1+c*N_o) \qquad \text{(b and c are constants)} \quad (7)$$

a' rises from 0 when no hosts are present to a maximum b/c. This relationship can be substituted in (5) or (6) and gives a sigmoid functional response for a predator or a parasitoid.

CURRICULUM VITAE

Petrus, Jacobus, Maria Mols is op 14 april 1948 geboren te Tilburg als tweede van een gezin van 3 kinderen. In 1966 slaagde hij voor het HBS b diploma aan het st Odulphuslyceum te Tilburg, waarna hij starte met de studie electronica aan de TH Eindhoven. Deze studie werd anderhalf jaar later afgebroken, waarna eerst de militaire dienstplicht vervult moest worden, voordat hij in 1969 met de studie Planteziekten aan de toenmalige Landbouwhogeschool in Wageningen kon beginnen. Als hoofdvak werd de Entomologie gekozen met als bijvakken Theoretische Productie Ecologie en Natuurbeheer. De praktijktijd werd van juni 1972 tot april 1973 doorgebracht in Suriname waar onderzoek werd gedaan aan de witte rijstboorder *Rupela albinella* en zijn parasitoiden. In Wageningen werd onderzoek gedaan aan predator- prooi relaties van het roofmijt-fruitspint systeem in boomgaarden (o.l.v. Rudy Rabbinge) en een grootschalige insecteninventarisatie werd uitgevoerd van verschillende ontwikkelingstadia van Essehakhoutbossen (o.l.v. Dr. R. Cobben, en Dr. W.Bongers). Van september 1975 tot april 1976 werkte hij als student assistent bij de Plantenziektenkundige dienst aan de ontwikkeling van een methode om de witte vlieg parasitoid *Encarsia formosa* te testen op haar gevoeligheid voor pesticiden. In januari 1976 slaagde hij *cum laude* voor het ingenieurs diploma aan de Landbouwhogeschool Wageningen. Van juni 1976 tot juni 1977 werkte hij als zoöloog bij de Centrale Organisatie voor Toegepast Natuurwetenschappelijk Onderzoek (TNO) aan de invloed van gas- en aardolieboringen op het milieu.

In juni 1977 is het onderzoek begonnen naar het zoek en predatie gedrag van de loopkever *Pterostichus coerulescens* L. waaarvan de experimenten in december 1980 werden afgerond. De simulaties m.b.t. tot zoeken en predatie van de loopkever zijn voor het grootste gedeelte later uitgevoerd. In februari 1982 werd hij aangesteld bij de vakgroep Entomologie van de Landbouwuniversiteit, waar hij nog steeds werkzaam is. Zijn taak omvat onderzoek naar de rol die natuurlijke vijanden spelen bij de bestrijding van boomgaardplagen, het ontwikkelen van voorspellingsmodellen voor boomgaardplagen, het begeleiden van studenten die doctoraal onderzoek doen en het geven van colleges en praktica in het kader van het onderwijselement 'Ziekte-, plaagontwikkeling en beschadiging'.