POPULATION DYNAMICS OF THE GYRINID BEETLE

GYRINUS MARINUS GYLL., (COLEOPTERA, GYRINIDAE)

WITH SPECIAL REFERENCE TO ITS DISPERSAL ACTIVITIES

POPULATION DYNAMICS OF THE GYRINID BEETLE GYRINUS MARINUS GYLL.

Robbert van der Eijk

STELLINGEN

1. Het schrijvertje *Gyrinus marinus* Gyll. kan vliegen en is in tegenstelling tot wat Ochs (1969) meent in staat van het wateroppervlak op te vliegen, dus zonder vaste ondergrond.

Ochs G. (1969) The ecology and ethology of whirligig beetles. Arch. Hydrobiol. (Suppl). vol 35, 37
Dit proefschrift

2. De waarneming van onder andere Wesenberg-Lund (1943) dat schrijvertjes niet in staat zouden zijn om in een bepaalde richting te zwemmen, is onjuist.

Wesenberg-Lund C (1943). Biologie der Süsswasserinsekten. Kopenhagen.

3. De verklaring van Istock, dat het gescheiden voorkomen van de schrijvertjessoorten Dineutes nigrior en D. horni het gevolg is van concurrentie in het larvale stadium, wordt door zijn werk onvoldoende ondersteund.

Istock C (1966) Distribution, coexistence, and competition of whirligig beetles. Evolution 20:211-234
Istock C (1967) Transient competitive displacement in natural populations of whirligig beetles. Ecology 48.6.:929-937

4. Ofschoon de aanname van zowel een oorzakelijk verband tussen immigratie en extinctie als van het bestaan van een evenwichtssituatie in de eilandtheorie van MacArthur en Wilson (1967) twijfelachtig is, kan de eilandtheorie een goede leidraad zijn bij het beheren van natuurgebieden.

MacArthur, R.H. & E.O. Wilson (1967) The theory of island biogeography. Princeton University Press
Gilbert F.S. (1980) the equilibrium theory of island biogeography: fact or fiction? Journal of Biogeography 7: 209-235

5. Kwantitatieve inventarisaties in watergebieden van de zogenaamde macrofauna zijn met de gewoonlijk beschikbare tijd en financiële middelen alleen betrouwbaar uit te voeren in kleine meetgebieden; ze zijn derhalve niet bruikbaar bij studies ten behoeve van natuurbeheer.

Elliott J.M. (1977) Some methods for the statistical analysis of samples of benthic invertebrates. publ FBA (Ambleside) nr 25, 2nd ed.

6. Bij het beheren van populaties moet men zich rekenschap geven van
het Kuno-effekt.

Kuno E (1981) Dispersal and the persistence of populations in unstable habitats: a theoretical note. Oecologia 49: 123
-126.
Dit proefschrift.

7. Als   een (biologische) determineertabel is opgesteld voor   niet-
specialisten, dient de keuze van de determineereigenschappen plaats
te   vinden op grond van goed waarneembare kenmerken en niet op   grond
van de kenmerken die noodzakelijk zijn voor de systematische   inde-
ling.

Dresscher Th.G.N., H. Engel, A. Middelhoek (1960). De nederlandse bloedzuigers (Hirudinea). KNNV. 39.
Eijk R.H. van der (1977). Bloedzuigertabel. NJN

8. Economen en populatiedynamici zouden meer moeten samenwerken bij
modelontwikkeling.

9. Typelessen in het voorbereidend onderwijs vormen de beste voorbe-
reiding op het computertijdperk.

10. Het   afwijzen   van Basic als   volwaardige programmeertaal   lijkt
vaker   academische   arrogantie als grondslag   te   hebben,   dan   reële
argumenten.

11. Het   Biologisch Station te Wijster van de Landbouwuniversiteit te
Wageningen dreigt opgeheven te worden. Dit wijst op een gemeenschapp-
pelijk kenmerk van natuurlijke populaties en langlopend onderzoek:
ondanks een goede productiviteit en uitwisseling hebben zij kort-
zichtig menselijk ingrijpen van buitenaf te duchten.

12. De wijze waarop men veiligheidsgordels in motorvoertuigen kan
ontsluiten, dient uit een oogpunt·van veiligheid gestandaardiseerd te
worden.

13. Brede inzetbaarheid als promotiecriterium op de basisschool is
nadelig voor de kwaliteit van het onderwijs.

14. Wie schrijft, die blijft.

Dit proefschrift

ROBBERT HENDRIK VAN DER EIJK

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GYRINUS MARINUS GYLL, (COLEOPTERA, GYRINIDAE)
WITH SPECIAL REFERENCE TO ITS DISPERSAL ACTIVITIES

Proefschrift

ter verkrijging van de graad van

doctor in de landbouwwetenschappen,

op gezag van de rector magnificus,

dr. C.C. Oosterlee,

in het openbaar te verdedigen

op woensdag 11 maart 1987

des namiddags te vier uur in de aula

van de Landbouwuniversiteit te Wageningen

VOORWOORD

De oorspronkelijke aanleiding tot het onderzoek aan de populatiedyna-
mica van schrijvertjes ligt de zomer van 1968. Tijdens een cursus
dieroecologie in het derde studiejaar maakte ik kennis met de merk-
terugvang schattingsmethode van Jolly. Ik wilde de bruikbaarheid van
de methode testen bij het schatten van aantallen waterinsekten, maar
trof eind juni op de daarvoor uitgezochte vijver slechts schrijver-
tjes aan. Toen bleek, dat deze kevers goed als proefdieren zijn te
gebruiken bij populatiedynamisch onderzoek, omdat ze betrekkelijk
eenvoudig te vangen en met het oog te volgen en op te sporen zijn.
Dit onderzoekje is in feite het begin geweest. Twee van mijn drie
doctoraalonderwerpen heb ik aan schrijvertjes kunnen uitvoeren. Eén
ervan betrof een onderzoek naar het aantalsverloop en de bewegingen
en verdeling van individuen in een min of meer afgesloten schrijver-
tjespopulatie. In 1974 had ik de gelegenheid om een orienterend
onderzoek aan schrijvertjes te verrichten in het plassengebied in de
De Wolddelen (gelegen ten westen van Haren, onder Groningen). Met dit
onderzoek kon ik laten zien dat een uitgebreider onderzoek aan
schrijvertjes bruikbare informatie zou kunnen opleveren voor de vra-
gen, die zowel bij mij als bij de zoölogisch afdeling van het Biolo-
gisch Station Wijster leefden over de betekenis van dispersie voor de
populatiedynamica van een soort. In 1976 werd een aanvraag voor dit
promotieonderzoek, gehonoreerd door de Landbouwhogeschool Wageningen
(nu universiteit) in de vorm van een promotie-assistentschap. Zonder
deze financiële steun zou het onderzoek niet mogelijk zijn geweest.
Op het Biologisch Centrum in Haren kreeg ik de beschikking over een
oude practicumzaal. Daarvoor en voor hun hulpvaardigheid ben ik de
mensen van de administratie en van de technische afdelingen van het
oude zoölogisch lab dankbaar; het was een goede tijd.
Zeer belangrijk is de medewerking geweest van de eigenaren van de
verschillende plassen in het proefgebied, waarbij ik met name de heer
Boerema wil noemen. Zijn gastvrijheid en meelevendheid hebben we
steeds zeer gewaardeerd (gevleugeld is zijn uitroep geworden op een
eerste warme dag in het voorjaar:"Hier zit één !") . "We", dat zijn
ook de vakantiehulpen, stagiaires en studenten geweest, die hun
bijdragen aan het onderzoek hebben geleverd. Met het noemen van Jan
Kok, Jules Roholl, Ton Groothuis, Herman Grooters en Marten Zijlstra
wil ik ieder van hun bedanken. Anneke Kreulen-Jonker dank ik voor
haar medewerking aan onderzoek aan het vlieggedrag van schrijvertjes.

Veel steun heb ik gehad van de mensen van de zoölogische afdeling van
het Biologische Station in Wijster. De discussies met Piet den Boer
en Theo van Dijk heb ik altijd als nuttig ervaren. De wekelijkse
werkbesprekingen in het winterhalfjaar mis ik nog steeds.
Ook hun kritische opmerkingen bij de manuscripten van de verschillen-
de hoofdstukken en artikelen zijn van grote waarde geweest. Vooral de
inzet van Piet den Boer in het laatste jaar van het voltooien van het
proefschrift heb ik zeer op prijs gesteld.
Martien Baars en Hans Reddingius bedank ik voor de kritische opmer-
kingen die zij bij verschillende artikelen en onderwerpen hebben

CONTENTS

POPULATION DYNAMICS OF THE GYRINID BEETLE GYRINUS MARINUS GYLL.

ABSTRACT

Data concerning reproduction, survival and dispersal of the whirligig
water beetle *Gyrinus marinus Gyll.* were collected between 1974 and
1983 by observations and experiments in the laboratory and in a
field area with about 10 populations distributed over 15 pools.
The purpose of the study was to assess the importance of the disper-
sal activities for the population dynamics of the species.

The main results can be summarised as follows: In a year two new
generations emerge, one in summer and another in autumn (which subse-
quently hibernates).
The mean survival chance is rather low as is the variation in survi-
val chance. (Variation in survival during hibernation is, however,
high.)
Although there is much variation in egg production between females,
the mean egg production per population varies little between diffe-
rent populations or years. The variation in survival during larval
and pupal development is greater than that of egg production. Thus
variation in egg production can have only a minor influence on the
variation in numbers of emerging beetles.

Exchange between populations by flying is limited to a few per cent
of the specimens. It only takes place during favourable weather
conditions.
Intensive exchange of individuals occurs by swimming between (sub)po-
pulations that are connected by water. Exchange by swimming seems to
be a result of every day swimming actvity.

Key factor analyses indicate that survival during hibernation is the
most important factor in determining fluctuation in population size.
Larval development is a distant second. According to these analyses,
all other processes, activities and developmental stages seem of
minor importance for fluctuations in population size. This means that
changes in the numbers of beetles is mainly dependent on factors to
which the beetles cannot react directly. However, simulation experi-
ments with stochastic models show that stability in population size
is mainly achieved by the exchange of individuals between populations.
Even the low rate of exchange by flight appears significantly to
decrease the chance of extinction.

The importance of exchange for the survival chance of such popula-
tions has implications for the exploitations (e.g. fishing) and
control (e.g. pests) of natural populations, and the preservation of
natural habitats.

HOOFDSTUK I. INLEIDING EN SAMENVATTING

1. DE PROBLEEMSTELLING

1.1. In o.a. de publicaties van Andrewartha & Birch (1954), Southwood (1962), Wynne-Edwards (1962), MacArthur & Wilson (1967), den Boer (1968) en Johnson (1969) werd expliciet gewezen op de rol die *dispersie* [1] zou kunnen spelen in de *populatiedynamica* van een soort.
Sindsdien zijn een aantal publicaties verschenen, die bijdragen leverden aan de discussies over de oorzaken en de omstandigheden die leiden tot dispersiegedrag, de genetische achtergrond ervan, de stabiliserende invloed die dispersie zou hebben op de fluctuaties van de populatiegroottes van een soort, en de gevolgen van dispersie voor de overlevings- en vestigingskansen van populaties (bijv. Gadgil 1971, Simberloff 1974, Diamond 1975, den Boer 1977).

1.2. De grootste tegenstelling met betrekking tot dispersie betreft de vraag, wanneer een individueel dier dispersiegedrag zal vertonen. De meeste andere vragen over dispersie zijn hierop terug te voeren of stuiten mede op deze vraag.
Dit vraagstuk kan op twee manieren worden benaderd:
   (1). Gezien vanuit het gezichtspunt van de natuurlijke selektie zal dispersiegedrag alleen optreden, wanneer de kansen van een individu op een bepaalde hoeveelheid nageslacht op zijn minst niet worden verkleind als gevolg van dispersiegedrag.
In het algemeen echter wordt verondersteld dat dispersie wel een extra risico voor het dier met zich meebrengt, hetzij doordat het onderweg sterft (grotere kans op predatie), of geen geschikt woongebied vindt, dan wel doordat het geen geslachtspartner kan vinden.
Daarom wordt vaak aangenomen dat dieren alleen dispersiegedrag zullen vertonen wanneer de omstandigheden in het woongebied zo verslechteren, dat de dieren het verblijf als onaangenaam ervaren en dat in het gebied blijven slechte overlevingskansen biedt. Bij soorten die in instabiele *habitats* leven, geldt dat vanwege de slechte overlevingskansen de dieren zonder meer frekwent moeten verhuizen. Bekende voorbeelden zijn wegvliegende waterinsekten uit uitdrogende poeltjes, insekten die op fruit leven, maar in feite ook de jaarlijkse trekbewegingen zoals die door veel diersoorten worden vertoond (zie bijv. Elton 1927, Southwood 1962).
   (2). Gezien vanuit het gezichtspunt van de populatiedynamica kan vastgesteld worden dat er *populaties* uitsterven en dat er (opnieuw) populaties gevestigd worden (bijv. Simberloff 1974, Diamond 1975, den Boer 1985) en ook dat dispersie kan leiden tot een snelle kolonisatie van nieuwe woongebieden, zoals nieuwe polders of nieuw gevormde eilanden (o.a. Mook 1971, Lindroth 1971).
In 1968 formuleerde Den Boer als eerste het principe van risicospreiding (den Boer 1968, en o.a. 1977, 1981, zie ook: Andrewartha & Birch 1984). Hierbij werd nadrukkelijk het belang aangegeven van dispersie - leidend tot uitwisseling van individuen tussen verschillende gebieden, subpopulaties en populaties - voor het verhogen van de stabiliteit van het aantalsverloop in de populaties en voor het

1 de schuin gedrukte termen worden aan het eind van dit hoofdstuk verklaard.
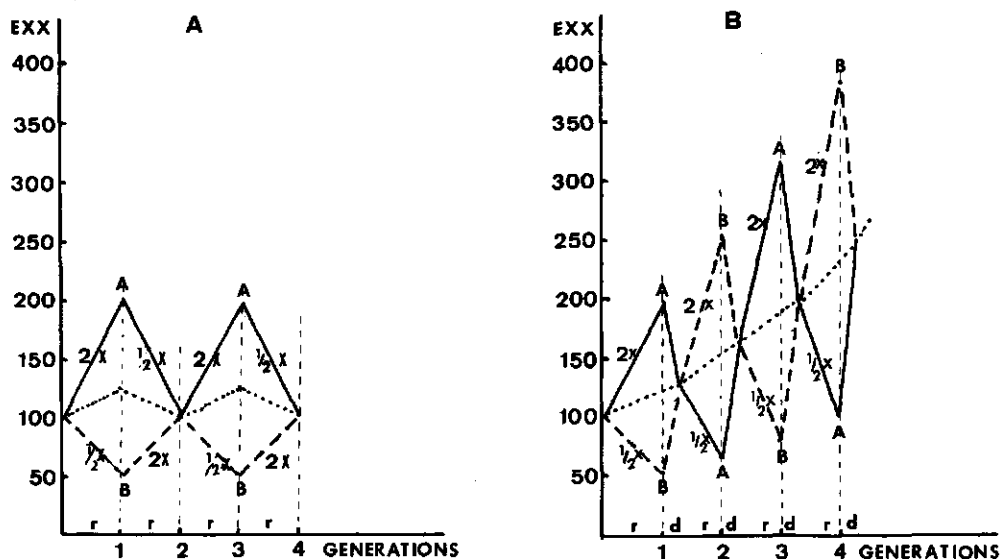
Fig. I-1. Het Kuno-effekt op het aantalsverloop in twee populaties
  a. zonder onderlinge uitwisseling
  b. met volledig uitwisseling

Stel dat er twee populaties zijn die het ene jaar in grootte verdubbelen en het daarop volgende jaar weer gehalveerd worden, zodat gemiddeld de populatiegrootte van elke populatie gelijk blijft en schommelt tussen twee waarden (fig 1A). Stel vervolgens dat als de ene populatie verdubbeld wordt, de andere op dat moment gehalveerd wordt, dan ontstaat het volgende aantalsverloop:

populatie A: 100 --- 200 --- 100 --- 200 ....
populatie B: 100 --- 50 --- 100 --- 50 ....

Stel nu dat er na elke keer dat de populaties verdubbeld, resp. gehalveerd zijn, beide populaties zich volledig mengen. In dat geval zullen beide populaties gaan groeien met een faktor 1.25 per keer (fig 1B). Immer omdat in absolute zin de halvering slechts betrekking heeft op de helft van het aantal dieren dat bij de verdubbeling aan de andere populatie is toegevoegd. Zo ontstaat een ander aantalsverloop:

populatie A	: 100 --- 200	125 ---	63	156 ---	312	195 ...
populatie B	: 100 --- 50	125 ---	250	156 ---	78	195 ...
populatie A+B	: 200 --- 250	250 ---	313	313 ---	390	390 ...
populatiegrootte						
na herverdeling	: 100 --- 125	125 ---	156	156 ---	195	390 ...

verhogen van de overlevingskansen van de soort in het areaal. Mathematisch kan worden aangetoond dat uitwisseling tussen populaties met onderling niet synchroon verlopende *netto reprodukties* van generatie op generatie een gunstig effect heeft op het aantal individuen per populatie (Kuno 1981, Metz et al 1983, Klinkhamer et al 1983). Omdat dit zogenaamde Kuno-effect in het onderhavige onderzoek op de achtergrond een belangrijke rol zal spelen, geven we in Fig. I-1 een eenvoudig getallenvoorbeeld om het principe duidelijk te maken.
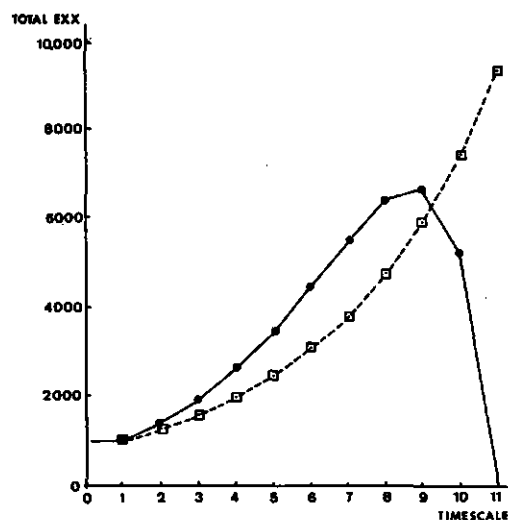
Fig. I-2. Schema van de hypothetische effecten van dispersieaktiviteiten op korte en lange termijn op het aantal individuen van een soort in een areaal met een aantal leefgebieden.
Het totale aantalsverloop in het gehele areaal:

–□– –□– = indien wel dispersie optreedt

●——● = indien geen dispersie optreedt

1.3. De verschillende benaderingen van het fenomeen dispersie, ener-
zijds vanuit de consequenties voor het individu en anderzijds vanuit
de consequenties op populatie-niveau komen samen in de volgende pro-
bleemstelling: Onder welke omstandigheden wegen de lange termijn-
voordelen op populatie-niveau van de dispersie op tegen de korte
termijn-bezwaren voor het individuele zwervende dier, waarbij voor-
en nadelen uiteindelijk worden uitgedrukt in het totale aantal nako-
melingen na een aantal generaties.

1.4. In Fig. I-2 is de probleemstelling voor een hypothetisch geval
uitgewerkt en op eenvoudige wijze grafisch weergegeven. Stel dat we
een areaal hebben waarin zich 10 leefgebieden bevinden. Op tijdstip 0
stellen we dat er 1000 individuen zijn, die gelijkelijk zijn verdeeld
over de 10 leefgebieden. Laten we een bepaalde gemiddelde overle-
vingskans voor de individuen en een bepaalde gemiddelde hoeveelheid
nageslacht veronderstellen, zodanig dat gemiddeld het aantal indivi-
duen in elk leefgebied zal toenemen. Veronderstellen we verder dat er
een bepaalde uitsterfkans is per leefgebied, onafhankelijk van de
grootte van de populatie (bijv. door milieurampen of ongunstige
winters) zodat per jaar tien procent van de populaties uitsterft.
Veronderstel tot slot ook nog dat als er dispersie optreedt, slechts
70 procent van de emigranten binnen het areaal in een van de andere
leefgebieden zal immigreren. De rest gaat op een of andere wijze
verloren. Vergelijken we nu het aantalsverloop zoals dat op grond van
deze veronderstellingen is te verwachten in twee overigens identieke
situaties, waarbij in het ene geval wel en in het andere geval geen
dispersie optreedt, dan kunnen de korte en lange termijn-effekten van
wel of geen dispersie geillustreerd worden.
Het korte termijn-effect van dispersie-aktiviteit zal zijn dat er
gemiddeld kleinere populaties per leefgebied zijn dan bij afwezigheid

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van dispersie-aktiviteit, terwijl het korte-termijn effekt van de afwezigheid van dispersie zal zijn dat het aantal populaties sterker zal afnemen dan wanneer wel dispersie plaatsvindt.
Het lange termijn-effekt van geen dispersie zal zijn dat er maar enkele, zeer grote populaties over blijven, die uiteindelijk ook zullen verdwijnen. Als er wel dispersie optreedt kan een aantal populaties van meestal gemiddelde of kleine omvang gedurende een langere tijd blijven voortbestaan. Uiteindelijk zullen die gezamen-lijk meer individuen tellen dan de enkele grote populaties die bij afwezigheid van dispersie te verwachten zijn.
Het gaat er in dit voorbeeld slechts om de bedoelde tegenstelling op korte en lange termijn duidelijk te maken. Aan de waarden en getallen in het voorbeeld moet verder geen waarde gehecht worden.

1.5. Uitgaande van de in 1.3. vermelde vraagstelling kunnen drie deel-vraagstelingen worden opgesteld:
(a). Wat is de frekwentie waarmee dispersiegedrag optreedt; welke vormen van dispersiegedrag zijn er en onder welke omstandigheden vindt dispersie plaats?
(b). Welke faktoren beïnvloeden het dispersiegedrag (weer, *reproduk-tie*, enz.)?
(c). Hoe groot is de uitwisseling tussen populaties en habitats; hoe groot is de gemiddelde overlevingskans van een emigrerend indi-vidu?

Elk van deze deel-vraagstukken kan verder opgesplitst worden in een aantal gedetailleerde vragen die via veldonderzoek en/of laboratorium experimenten beantwoord moeten kunnen worden. In het onderhavige onderzoek hebben we hiertoe een poging gedaan.
Omdat we de invloed van dispersie op de populatie-dynamica van een soort willen nagaan, moeten we ook over gegevens beschikken ten aanzien van de overige populatie-dynamische processen: de reproduktie en de overleving onder verschillende omstandigheden.

2. HET PROEFDIER EN HET PROEFGEBIED.

2.1. De mogelijkheden om gegevens in het veld te verzamelen met betrekking tot alle hierboven besproken facetten van zowel dispersie, als van reproduktie en overleving zijn zeer beperkt. Er is vrijwel geen proefdier te vinden, dat zich hiervoor op alle punten leent. Min of meer bij toeval zijn we gestuit op de waterkever het schrijvertje (*Gyrinus marinus Gyll.* (zie Fig. III-3, blz 36[1]). Deze in groepen op het wateroppervlak levende kever bleek in een vooronderzoek een geschikt proefdier te zijn. De kevergroepen houden zich meestal vlak bij de oevers op, waardoor de dieren eenvoudig zijn op te sporen en met verf gemerkte exemplaren kunnen worden teruggevonden en herkend zonder gevangen te hoeven worden.
De kevers komen na de overwintering omstreeks april aan de opper-vlakte en beginnen direkt met het leggen van eieren onder water. De larven ontwikkelen zich eveneens onder water, verpoppen zich boven

1) Fig III-3 is ook afgebeeld op de binnenzijde van de omslag

water, waarna eind juni de zomergeneratie kevers tevoorschijn komt. Deze zomergeneratie reproduceert eveneens, waarna vanaf september tot het begin van de overwintering, eind oktober de herfst-generatie ontpopt. Deze jaarcyclus is weergegeven in Fig. III-2, blz 35 . Gedurende het hele aktieve seizoen - van april tot oktober - kunnen de kevers dispersiegedrag vertonen door weg te zwemmen, dan wel weg te vliegen.

2.2. Het vinden van een geschikt proefdier is één probleem, het vinden van een geschikt proefgebied een ander. Gelukkig bleek zich nabij het Biologisch Centrum in Haren, vlak onder Groningen, het afgegrensde plassengebied 'de Wolddelen' te bevinden, bestaande uit 15 kleinere en grotere plassen, die deels onderling zijn verbonden door sloten (Fig. III-3, blz 36[1]). In het gebied bevinden zich ca 10 populaties en subpopulaties van het schrijvertje.
Door het merken en opsporen van de dieren is het mogelijk de mobiliteit van de dieren en de uitwisseling tussen de verschillende populaties en plekken te schatten. Uit dezelfde merk-terugvang gegevens kunnen de overlevingskansen en de grootte van het nageslacht geschat worden.

2.3. Ter aanvulling van het onderzoek in het veld is ook een aantal experimenten in het laboratorium uitgevoerd, o.a. om de vliegaktiviteit onder verschillende omstandigheden en voor verschillende typen kevers (zoals mannetjes, vrouwtjes, oude en jonge kevers, e.d.) nader te onderzoeken.

2.4. Na een kort onderzoek als studieonderwerp in 1969 heeft het hoofdonderzoek plaatsgevonden tussen 1974 en 1983, met een onderbreking in 1975. Vanaf 1980 is de nadruk vooral gekomen op het ontwikkelen van de simulatiemodellen en het doen van aanvullende waarnemingen en experimenten en tenslotte op het uitwerken en publiceren van tot nu toe vijf artikelen.

3. DE EVALUATIE VAN DE ONDERZOEKS-GEGEVENS VIA SIMULATIE MODELLEN

3.1 Om de verzamelde gegevens te evalueren met betrekking tot de betekenis van de waargenomen dispersie-aktiviteiten is een aantal computer simulatiemodellen ontwikkeld.
Met deze modellen is het mogelijk vast te stellen welke rol de dispersie bij het schrijvertje speelt. We zullen proberen algemene uitspraken te doen over de omstandigheden waaronder de korte en de lange termijn-effekten van de dispersie-aktiviteiten elkaar in evenwicht houden. Fig. I-3 geeft nog eens een totaaloverzicht van de processen die wij in hun samenhang willen bekijken.
Het gebruiken van een uitgebreid simulatiemodel al tijdens de duur van het veldonderzoek heeft het voordeel dat het model zelf aangeeft welke gegevens beschikbaar moeten komen; het biedt daarmee een goede leidraad voor het onderzoek.

1) Fig III-3 is ook afgebeeld op de binnenzijde van de omslag
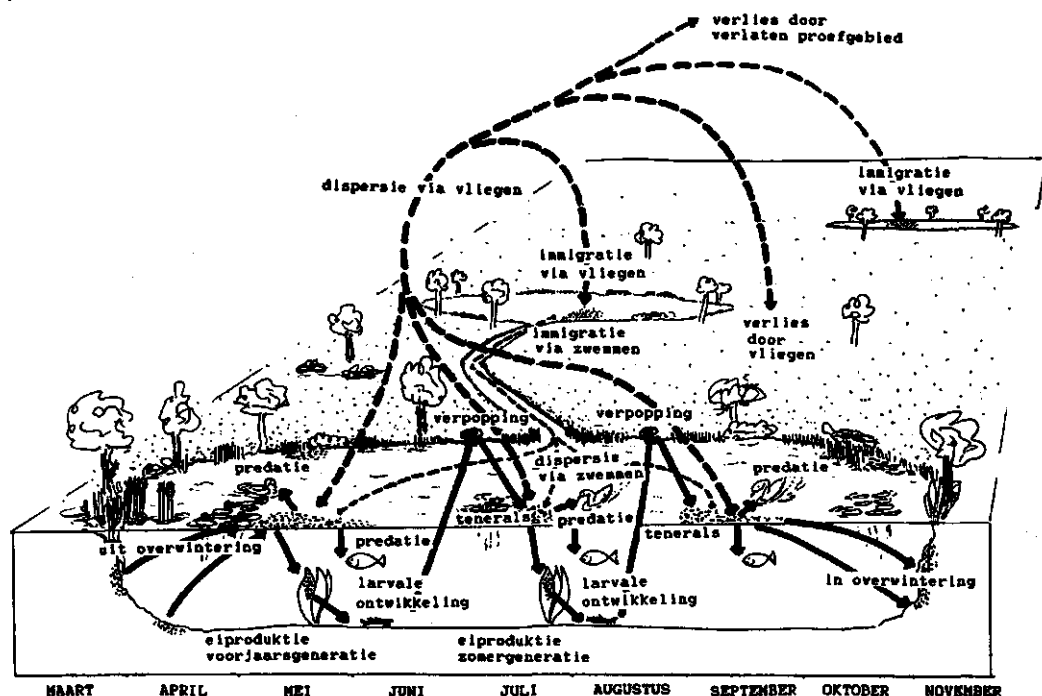
Fig. I-3. De populatie dynamische processen bij het schrijvertje in een figuratieve weergave. Enerzijds zijn de dispersieaktiviteiten van schrijvertjes ruimtelijk weergegeven, anderzijds zijn van links naar rechts de aktiviteiten aangegeven zoals die in de loop van een jaar in de verschillende maanden plaatsvinden.
----- = dispersieaktiviteiten; ———— = ontwikkeling ei->kever, overleving

4. METHODE

4.1. Alvorens een overzicht van de uitkomsten van het onderzoek te presenteren, geef ik hier eerst nog in het kort aan hoe het onderzoek is aangepakt.

4.2. De kevers zijn gemerkt door ze op de dekschilden te voorzien van een verfvlekje of door een gaatjes-patroon aan te brengen. Met een gaatjespatroon kan aan elke kever met behulp van de stippelrijen op de dekschilden een individueel code-nummer toegekend worden (Fig.VI-1, blz 72). De kevers worden daartoe gevangen, gemerkt en dan weer op dezelfde plek losgelaten. Aan de hand van terugvangsten door regelmatige bemonsteringen krijgen we informatie over de verplaatsingen van de kevers tussen twee vangsten en kunnen we tevens schat-

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tingen maken van de sterftekans (beter: 'verdwijn'kans) en van de populatiegroottes. Doordat pas uitgekomen kevers nog zacht zijn, kan door deze vangsten tevens worden geschat hoeveel jonge kevers zich in een bepaald tijdsbestek bij de populatie hebben gevoegd.

4.3. De methode van merken met gaatjes heeft nadelen: de dieren worden door het herhaaldelijk vangen verstoord en tijdelijk uit de populatie weggehaald; bovendien kan per populatie gemiddeld slechts eens per tien dagen gemonsterd worden.
Na enige jaren van experimenteren naar een goede methode konden in 1978 de kevers met verfvlekjes op de dekschilden gemerkt worden als de dekschilden eerst licht werden geschuurd. De verf bleek dan goed op de dekschilden te hechten.
Voor merken met verf is slechts een beperkt aantal kleuren beschikbaar, zodat alleen met groepsmerken kon worden gewerkt (per plas of subpopulatie een kleur). Omdat bovendien de verfmerken het vliegen onmogelijk maakte, is deze methode gebruikt om de uitwisseling tussen gebieden via zwemmen te volgen. Een voordeel van de verfmerkmethode was, dat de dieren niet meer gevangen hoefden te worden nadat ze eenmaal gemerkt waren en dat dagelijks de plaats van gemerkte dieren kon worden genoteerd. De kleuren waren met een verrekijker uitstekend te onderscheiden. Na ruim 40 dagen waren de gemerkte dieren zozeer vermengd en de aantallen zo afgenomen dat een nieuwe serie dieren kon worden uitgezet. Op die manier zijn in 1978 vier series van gemerkte dieren gevolgd. De proeven met de met verf gemerkte dieren zijn uitgevoerd in het bovenste gedeelte van het plassen gebied: het BR-complex (zie Fig. III-3, blz 36[1]), waar alle plassen met elkaar in verbinding staan.

4.4. De eiproduktie kon worden gemeten door de vrouwtjes gedurende 24 uur in petrischalen te zetten, voorzien van vochtig toiletpapier. De eieren worden dan op het papier afgezet, kunnen worden geteld en in het gebied worden uitgezet.

4.5. Om het vlieggedrag te onderzoeken, is in het laboratorium een aantal experimenten uitgevoerd, waarbij de kevers uit schalen in afgesloten bakken konden opvliegen en dan onderin de bakken konden worden verzameld (Fig. VI-2, blz 72).

5. OVERZICHT VAN DE UITKOMSTEN VAN HET ONDERZOEK

5.1. De eiproduktie en larvale ontwikkeling

5.1.1. Als in april de overwintering wordt beëindigd en de dieren weer op het water verschijnen, beginnen de vrouwtjes binnen een week met het leggen van rijen eieren op planten e.d. onder water. Dit eileggen gaat door tot halverwege augustus. Een vrouwtje zet vermoedelijks wekelijks eieren af. Na elke eiafzetting wordt een vrouwtje vermoedelijk opnieuw bevrucht.

1) Fig III-3 is ook afgebeeld op de binnenzijde van de omslag

De eieren komen na ruim 1 week uit en de larven maken hun ontwikkeling op de bodem van de sloot of plas door. Eind juni verschijnen vrij massaal de tenerals na een popstadium boven water.
Na ongeveer 10 dagen zijn de nieuwe kevers uitgehard en beginnen de vrouwtjes van deze generatie eveneens eieren af te zetten. Deze generatie van kevers komt uit in september en oktober. Er zijn per jaar dus drie min of meer van elkaar gescheiden generaties, een voorjaarsgeneratie, een zomergeneratie en een herfstgeneratie, die na overwintering de voorjaarsgeneratie in het volgende jaar vormt (zie Fig. III-2, blz 35).

5.1.2. In Tabel IV-1, blz 42, worden de eiprodukties van de voorjaarsgeneratie en de zomergeneratie met elkaar vergeleken. De eiproduktie is in de zomer lager dan in het voorjaar, omdat er dan minder vrouwtjes eieren afzetten en omdat er in de zomer per legsel minder eieren worden afgezet.

5.1.3. De ontwikkelingstijd van ei tot teneral is afhankelijk van de temperatuur. De eieren die in april tot half-mei worden afgezet, ontwikkelen zich vanwege de lage watertemperatuur langzamer dan de eieren die na half mei worden gelegd: ca 10 weken tegen 6 weken. Dit verklaart de massale ontpopping eind juni. De eieren die later gelegd zijn, halen de eerder gelegde eieren in hun ontwikkeling in.

5.2. De overleving van de kevers

5.2.1. De schattingen van de overlevingskansen van de volwassen (uitgeharde) kevers is weergegeven in Tabel V-1, blz 66. De overlevingskans neemt van het voorjaar naar de herfst af, waarbij mannetjes een betere overlevingskans hebben dan vrouwtjes: in het voorjaar heeft een mannetje een levensverwachting van 50 dagen, een vrouwtje van 42 dagen. In de herfst is deze verwachting gedaald tot respectievelijk 20 en 19 dagen.
Belangrijk is dat de variatie in de overlevingskansen tussen verschillende gebieden, maar ook tussen verschillende jaren klein is. De *variantie coefficient* (d.i. standaard deviatie/gemiddelde waarde) is minder dan 0.1. We kunnen er dus vanuit gaan dat de overlevingskansen tussen verschillende gebieden en jaren weinig verschillen en we zullen hiervan ook gebruik maken bij het schatten van andere populatiedynamische grootheden.

5.2.2 De overlevingskansen van pas ontpopte kevers (zogenaamde 'tenerals') zijn lager dan van kevers die ouder zijn dan ongeveer drie weken. Anderzijds hebben we gevonden dat bij oudere kevers de overlevingskans daalt met de leeftijd.

5.2.3. Afhankelijk van het weer gaan de dieren eind oktober in overwintering onder water. Wij vonden overwinterende dieren onder water tussen de wortels van oeverplanten. Gemiddeld 33 procent van de dieren die in oktober in overwintering gaan, overleeft de winter en

komt in april weer boven water.
In tegenstelling tot de overlevingskansen in het aktieve seizoen is er vermoedelijk een grote variatie in overlevingskansen tijdens de wintermaanden (var.coeff. tussen jaren = 0.7; var. coeff. tussen gebieden = 0.4).

5.3. De grootte van het nageslacht (tenerals)

5.3.1. Gemiddeld levert een legsel uiteindelijk 1 tot 2 tenerals op (Table IV-5, blz   ). Het gemiddelde aantal tenerals dat een vrouwtje per maand in het voorjaar voortbrengt, is ongeveer tweemaal zo groot als in de zomer (8 tegen 3 - 4). Dit verschil wordt voornamelijk veroorzaakt doordat in de zomer een kleiner aantal weken voor eiproduktie beschikbaar is.

5.3.2. De variatie in het aantal nakomelingen is groter dan bij de eiproduktie. Dit verschil in variatie tussen eiproduktie en nakomelingen geeft aan dat de ontwikkeling van ei tot teneral van meer belang is voor de populatie dynamica van het schrijvertje dan de eiproduktie. Een key-faktor analyse (zie $ 6.1.3) bevestigt deze zienswijze: de variatie in het aantal tenerals wordt het sterkst beinvloed door de variatie in de levensvatbaarheid van de eieren (percentage eieren dat uitkomt) en de variatie in overleving gedurende de larvale ontwikkeling. De variatie in eiproduktie lijkt van geen belang. Consequentie hiervan kan zijn dat de reakties van vrouwtjes op de omgeving in de vorm van meer of minder eieren van weinig invloed zullen zijn op de grootte van het nageslacht en dat de omstandigheden onder water van groter belang zijn voor de grootte van het nageslacht dan die boven water. Dit maakt een _effektieve_ dichtheidsafhankelijke reaktie via een hogere of lagere eiproduktie onwaarschijnlijk. Wij komen hier later nog op terug.

5.4. Dispersie via vliegen

5.4.1. De uitwisseling tussen populaties binnen het studiegebied is gemeten aan de hand van merk-terugvang gegevens van de met gaatjes gemerkte dieren, voorzover het populaties betreft die onderling niet via water verbonden zijn.
De mate van uitwisseling was zeer gering: in de meeste gevallen is minder dan 1 procent van de gemerkte dieren teruggevangen als vliegimmigrant elders in het gebied (Tabel II-1, blz 24). Mannetjes zijn meer dan vrouwtjes aangetroffen als vliegimmigrant. Beide sexen vliegen gedurende het hele aktieve seizoen, dus ook tijdens de periode dat er eieren worden gelegd.

5.4.2. Emigratie was alleen te constateren als deze werd gevolgd door een immigratie in een andere populatie in het gebied. Aangezien aangenomen moet worden dat een deel van de dieren die wegvliegen het proefgebied verlaat dan wel onderweg omkomt, geven de immigratiegege-

vens slechts een ondergrens aan van de omvang van de emigratie. Om een indruk te krijgen van de grootte van de emigratie via wegvliegen is in 1977 bij een populatie een deel van de kevers gekortwiekt, zodat de afname in de tijd van het aantal gekortwiekte en gevleugelde dieren met elkaar kon worden vergeleken (Fig. VI-3, blz 78). Er blijkt geen verschil tussen beide groepen dieren op te treden. Ook is er geen verschil met het afnameverloop in populaties in andere jaren (Fig. VI-4, blz 79), o.a. in 1976, toen het weer veel gunstiger was voor vliegaktiviteiten (zie onder). Dit betekent dat het aantal dieren dat wegvliegt dermate laag is, dat dit niet van invloed is op het direkte aantalsverloop. Gegeven de geschatte overlevingskansen in de populaties moet tenminste vijf procent van de kevers in een generatie wegvliegen, wil dit een meetbaar effekt hebben op de afname-snelheid van het aantal dieren in een populatie. De emigratie via vliegen bedraagt dus minder dan 5 procent per generatie.

5.4.3. Het ligt voor de hand te veronderstellen dat de vliegakti-viteit afhankelijk is van het weer. Aan de hand van een aantal expe-rimenten in het veld is vastgesteld dat er pas vlieggedrag optreedt bij luchttemperaturen van meer dan 18° C (Fig. I-4). De dieren zijn amper in staat tegen de wind in te vliegen; alleen bij lage windsnel-heden kunnen de dieren zelf hun vliegrichting bepalen (Fig. I-5). Overigens vliegen de dieren vrijwel niet als er enige wind staat, o.a. omdat het hun dan niet lukt weg te komen. Dagelijkse waarnemin-gen van kevers in een ondiep (ca 10 cm) bassin leverde slechts vlieg-waarnemingen op op zonnige dagen, zonder wind, zonder regen en met temperaturen van tenminste 19°C.

5.4.4. De afhankelijkheid van het weer verklaart ook de verschillen in de uitwisseling tussen de populaties via vliegen in 1974, 1976 en 1977. Er blijkt een verband te bestaan tussen het aantal dagen in een jaar met voor vliegen geschikte weersomstandigheden en het aantal teruggevangen vliegimmigranten (Tabel II-2, blz 25).

5.4.5. De in vergelijking met mannetjes lagere uitwisseling van vrouwtjes kan vooral worden toegeschreven aan het feit, dat het grootste deel van de gunstige dagen voor vliegaktiviteit tijdens de periode van eiproduktie valt. Na de reproduktieperiode vertonen vrouwtjes in laboratoriumexperimenten meer vliegaktiviteit dan manne-tjes, terwijl dit tijdens de periode van eileggen net andersom is (Fig. VI-6, blz 85)

5.4.6. Het verschil in vliegaktiviteit van vrouwtjes tijdens en na de reproduktieperiode kan verklaard worden uit het aantal eieren dat een vrouwtje bij zich draagt, uit het lichaamsgewicht van de vrouwtjes en uit het percentage vrouwtjes dat op een bepaald moment meedoet aan het reproduktieproces. Hoe meer eieren en hoe zwaarder een vrouwtje, hoe minder het tot vliegaktiviteit komt (Tabel II-3, blz 26).
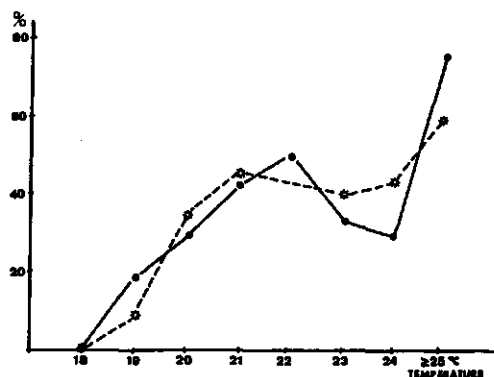
Fig. I-4. Percentage gevallen waarin kevers vlieggedrag vertoonden bij verschillende luchttemperaturen.

    – ☼ – – ☼ – = mannetjes

    ——●———●— = vrouwtjes
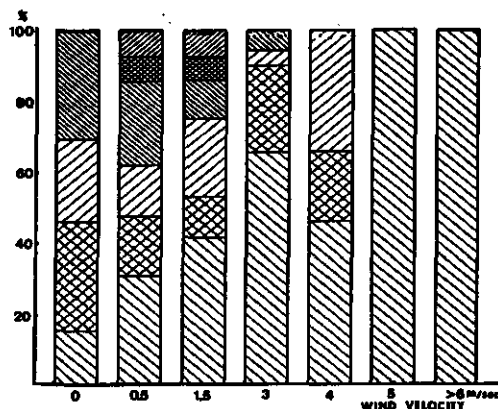
Fig. I-5. Het verband tussen de vliegrichting en de windsnelheid.
De vliegrichting van de kevers is gemeten ten opzichte van de windrichting, met een indeling in klassen van 30° naar links of naar rechts.

X-as: windsnelheid in m/sec.
Y-as: procentuele verdeling van de richtingsklassen van de vliegende kevers.
afwijking vliegrichting t.o.v. windrichting

    ◩ = 0 – 30°

    ⊠ = 31 – 60°

    ▨ = 61 – 90°

    ▩ = 91 – 120°

    ▦ = 121 – 150°

    ▨ = 151 – 180°

5.4.7. Verschillen in vliegaktiviteit zijn ook gevonden tussen tenerals en oudere kevers (Tabel VI-6, blz 85) en tevens is getest of binnen een populatie onderscheid gemaakt kan worden tussen kevers die consistent meer of minder vliegaktiviteit vertonen, door dezelfde kevers herhaalde malen aan een vliegproef te onderwerpen. Daarbij is gebleken dat kevers die in een eerdere proef een grotere vliegaktiviteit vertoonden in een latere proef ook weer de meeste vliegaktiviteit opleverden in vergelijking met de kevers die de eerste keer niet

of pas na geruime tijd vliegaktief werden (Tabel II-4, blz 26). Onder andere kon worden waargenomen dat een aantal kevers door kennelijk morphologische afwijkingen niet tot vliegen in staat was, ook al ondernamen ze daartoe wel pogingen.

5.5. Dispersie via zwemmen

5.5.1. De uitwisseling tussen populaties via zwemmen is vooral beke-ken in het noordelijke gedeelte van het proefgebied, het zogenaamde Br-complex (zie Fig. III-3, blz 36[1]). De plassen in dit complex zijn onderling door kortere of langere sloten en doorgangen verbonden. De uitwisseling is gemeten door dagelijkse notaties van de aantallen met kleur gemerkte kevers per plek in het hele complex.
Voor een goed begrip is het goed te weten dat de kevers zich overdag voornamelijk in groepen ophouden en dan weinig zwemgedrag buiten de groepen vertonen, anders dan door verstoring. Bij zonsondergang ech-ter komt er een grote aktiviteit op gang, waarbij de groepen vrijwel uiteen vallen en de kevers op hoge snelheid uitzwermen over het wateroppervlak, waarbij meestal de oevers worden aangehouden. Na enige uren ontstaat midden in de nacht een omgekeerde beweging, waarbij de kevers zich weer verzamelen op de oude groepsplekken, waar zich meestal nog een hogere concentratie kevers bevindt.

5.5.2. De uitwisseling tussen de verschillende delen van het complex is intensief: na drie tot vier weken bestaan de populaties gemiddeld voor meer dan 40 procent uit immigranten, waarbij de centraal gelezen plassen meer immigranten binnenkrijgen dan de aan de rand van het complex gelegen plassen (Tabel VII-11, blz 110).

5.5.3. De mate van emigratie (gebruikelijk aangeduid als emigra-tiesnelheid) vanuit een populatie kan worden geschat via een itera-tieve methode als de overlevingskans in de populatie en het aantal immigranten elders van deze populatie bekend zijn (zie appendix C).
Op grond van deze schattingen komen we tot een emigratiesnelheid per week van 0.36 in het voorjaar (d.w.z. gemiddeld 36 procent van de dieren zwemt gemiddeld per week weg). In de loop van het jaar neemt de emigratiesnelheid af tot 0.20 in de herfst (E-waarden in Tabel VII-4, blz 102).

5.5.4. Door het aantal dieren dat elders als immigrant wordt waar-genomen te vergelijken met het geschatte aantal dieren dat is geëmi-greerd, is een schatting te maken van de overlevingskans onderweg (Q -waarden in Tabel VII-4, blz 102). Gemiddeld schatten we dat 72 procent van de dieren die emigreren elders als immigrant terugkomt, waarbij geen verschillen zijn gebleken tussen gebieden of tussen verschillende periodes van het jaar. Een populatie verliest aan emigranten ongeveer evenveel individuen als door sterfte.

1) Fig III-3 is ook afgebeeld op de binnenzijde van de omslag

5.5.5. De verhouding tussen de emigratie en de immigratie vanuit en in een populatie wordt weergegeven door het dispersie-ratio, $Db = $ immigranten/emigranten. In de meeste gevallen is $Db<1$, dat wil zeggen dat in het algemeen een populatie meer verliest aan emigranten dan het terugkrijgt aan immigranten. Echter, in 8 van de 24 gevallen (1 op de 3 dus) krijgen we een schatting van $Db>1$. Deze populaties hadden dus direkt getalsmatig voordeel van de dispersie via zwemmen (Db-waarden in Tabel VII-4, blz 102).

5.5.6. Bij de met verf gemerkte dieren kon geen onderscheid gemaakt worden tussen mannetjes en vrouwtjes, maar uit de terugvanggegevens van met gaatjes gemerkte dieren blijkt dat mannetjes meer als immi- grant via zwemmen worden gevangen dan vrouwtjes, zodat we mogen aannemen dat mannetjes ook meer wegzwemmen uit een populatie dan vrouwtjes (Tabel VII-1, blz 98).

5.5.7. Zoals te verwachten was, is er een omgekeerd evenredig verband tussen de uitwisseling via zwemmen en de afstand tussen twee plassen, waarbij we de afstand weergeven in het aantal tussenliggende plassen (Tabel II-5, blz 27). Er zijn echter uitzonderingen. Kennelijk moeten we aannemen dat ook andere faktoren dan de afstand van belang zijn, zoals het aantal alternatieve routes tussen twee plassen, de bereik- baarheid van een plas (plantengroei, ruw water) en de verdeling van de groepen kevers over het Br-complex.

5.5.8. Indien er vanuit wordt gegaan dat wegzwemmen vooral optreedt als reaktie op ongunstige of onaangename omstandigheden zou verwacht mogen worden dat met een toenemende populatiegrootte ook de rela- tieve emigratiesnelheid zou toenemen. We vinden echter een omgekeerd verband. De emigratie uit grotere populaties is relatief lager dan die uit kleinere populaties, terwijl bovendien de immigratie in grotere populaties groter is dan die in kleinere populaties (Tabel II-6, blz 28). Er is dus kennelijk een tendens om naar grotere popu- laties te trekken en daar te blijven, mogelijk mede veroorzaakt door de aantrekkingskracht die de kevers op elkaar uitoefenen.

5.5.9. We hebben de gegevens betreffende de uitwisseling tussen delen van het Br-complex gerelateerd aan verschillende weersgegevens (Tabel VII-13, blz 115) en vinden een significant lagere uitwisseling als de nachttemperatuur lager is dan 8° C. Mogelijk is er een hogere uitwis- seling tijdens regen dan wanneer het droog is. De verklaring van deze relaties kan gezocht worden in het feit dat de uitwisseling voorname- lijk 's nachts plaatsvindt en dat de oriëntatie van de kevers is verstoord tijdens regen waardoor de dieren verdwalen. Er zijn aanwij- zingen dat de kevers bij hun oriëntatie gebruikmaken van teruggekaat- ste trillingen en golven op het wateroppervlak (Eggers 1927, van der Eijk 1973).

6. DE COMPUTER SIMULATIES

6.1.Key-factor analyse

6.1.1. De verzamelde veldgegevens zijn gebruikt in computer-simula-
tiemodellen. Zo konden de gegevens geëvalueerd worden met betrekking
tot de invloed van de geringe dispersie via vliegen en de sterke
uitwisseling via zwemmen op het aantalsverloop per populatie.
Hierbij hebben we gebruik gemaakt van verschillende typen simulatie-
modellen.

6.1.2. In een eerste simulatiemodel is het aantalsverloop gesimuleerd
uitgaande van de gemiddelde waarden en variatiecoëfficienten, zoals
we die hebben geschat voor de overlevingskansen per ontwikkelings-
stadium van ei tot reproducerende volwassen kever en voor de overle-
vingskansen tijdens dispersie-aktiviteiten.
Met het model wordt *stochastisch* het aantalsverloop per ontwikke-
lingsstadium in een jaar per week gesimuleerd, beginnend met het
aantal gelegde eieren, via het aantal larven en poppen, het aantal
tenerals naar het aantal volwassen kevers dat uiteindelijk na de
winter nog over is. We hebben dit 100 keer herhaald, iedere keer
startend met 1000 vrouwtjes in april, waarbij voor de overlevingskan-
sen per stadium telkens volgens toeval waarden zijn getrokken uit de
log-normale verdeling die volgt uit het opgegeven gemiddelde en de
variatiecoëfficient.
Het gemiddelde verloop, weergegeven in Fig. VIII-2, blz 124, laat
zien dat de combinatie van de tijdens het veldonderzoek geschatte
waarden van de overlevingskansen tijdens de verschillende stadia een
aantalsverloop genereert, dat niet tot uitsterven van de populatie
leidt. Na de winter zijn de aantallen kevers gemiddeld wat hoger dan
bij de start een jaar eerder. We moeten bedenken dat in deze simula-
tie de veldsituatie zeer versimpeld is weergegeven. Naar onze erva-
ring zal het aantal kevers aan het eind van een simulatie lager
uitvallen, naarmate het simulatiemodel gedetailleerder van opzet
wordt.

6.1.3. De verliezen aan individuen tijdens elk ontwikkelingsstadium
zijn tegen elkaar afgewogen met de methode voor een key-factor ana-
lyse van Varley & Gradwell (1960) en Morris (1963). De methode geeft
aan welke bijdrage elk stadium levert aan de variatie in het aantals-
verloop in het eindstadium, in ons geval de variatie in het aantal
kevers na de winter. De gemiddelde uitkomsten zijn samengevat in
Tabel VIII-3, blz 126. Hoe hoger de k-waarde, hoe groter het verlies
aan individuen in dat stadium. Een stadium met een hoge k-waarde,
maar met een lage variatie in die k-waarde zal toch een slechts
geringe invloed hebben op de variatie in het aantal kevers na de
winter. Daarom kijken we naar het produkt k*st.dev. van elk ontwikke-
lingsstadium (waarbij st.dev. = standaard deviatie een maat is voor
de mate van variatie in k-waarden). Dan blijkt dat voor de variatie
in het aantal kevers na de winter de overleving tijdens de winter de
belangrijkste faktor is, gevolgd door de ontwikkelingsstadia van ei

tot teneral van de zomer- en de herfstgeneraties. Een correlatietest geeft aan dat er een sterk verband is tussen de overleving tijdens de winter en het aantal kevers na de winter.

6.1.4. Het feit dat de overwintering de belangrijkste faktor in de variatie van het aantalsverloop (van de kevers) blijkt te zijn – de zogeheten key-faktor – betekent dat er een belangrijke instabiliteit in de populatie dynamica van de schrijvertjes blijkt op te treden. Het ligt immers voor de hand te veronderstellen dat de kevers, als ze eenmaal hun plek voor de overwintering hebben opgezocht, nauwelijks in staat zullen zijn te reageren op verslechterende omstandigheden tijdens de winter.
Er zijn twee manieren waarop de kevers de effekten van de onzekere overwintering kunnen beperken. Een mogelijkheid is een dichtheidsafhankelijke reaktie, een andere is dat de risico's over een zo groot mogelijk aantal gebieden wordt gespreid via dispersieaktiviteiten.
Uit het veldonderzoek zijn geen aanwijzingen verkregen dat dichtheidsafhankelijke processen een belangrijke rol (kunnen) spelen.

6.2. Simulatiemodellen met uitwisseling tussen populaties

6.2.1. We hebben gezien dat dispersie kan plaatsvinden via zwemmen en via vliegen. Om de betekenis van deze dispersieaktiviteiten voor het aantalsverloop na te gaan zijn uiteindelijk gecompliceerde simulatiemodellen gebruikt, die de veldsituatie zo gedetailleerd mogelijk nabootsen, zowel met betrekking tot de dispersie als met betrekking tot de overleving en de reproduktie.

6.2.2. Uitleg van het simulatiemodel voert op deze plek veel te ver. We beperken ons hier tot enige globale informatie.
Overleving, reproduktie en dispersie worden als afzonderlijke processen gesimuleerd. Het model rekent met individuen, niet met groepen van individuen. Dit betekent bijvoorbeeld dat bij de verdeling van de emigranten uit een populatie voor elk individu expliciet wordt gekozen waar deze zal immigreren en of hij wel zal immigreren. Er vindt dus geen verdeling van de emigranten over de leefgebieden plaats volgens een bepaalde verdeelsleutel.
Iedere keer dat het nodig is, wordt voor elke variabele (zoals het aantal dieren dat emigreert of het aantal eieren dat een vrouwtje zal leggen) volgens toeval een waarde getrokken uit de log-normaal verdeling die is gedefiniëerd door de opgegeven gemiddelde waarde en variatiecoëfficiënt, zoals die zijn geschat in het veldonderzoek. In het model wordt gewerkt met 10 of 20 leefgebieden, met elk 500 individuen aan de start, dan wel met een volgens toeval bepaald startaantal. In Fig. VIII-3, blz 129, wordt een vereenvoudigd schematisch overzicht van het model gegeven.
Van het model zijn versies met een verschillende graad van gedetailleerdheid gebruikt, afhankelijk van het te onderzoeken probleem.

6.2.3 Allereerst onderzoeken we de gevolgen van het waargenomen dispersiegedrag op het aantalsverloop. Daartoe wordt er in het model een tweede soort B geïntroduceerd, die identiek is aan de eerste soort A, doch geen dispersie vertoont. Op die manier zijn we in staat de situatie met dispersie te vergelijken met die zonder dispersie. Om de invloed van de variabiliteit (instabiliteit) van het milieu op de populatiedynamica na te gaan, zijn simulaties uitgevoerd met verschillende variatiecoëfficienten (0.3, 0.5 en 0.7). De uitkomsten van de simulaties na 20 jaar worden weergegeven door de gemiddelde netto reproduktiesnelheid $R = (P_{20}/P_0)^{0.05}$ (P_j = populatiegrootte in jaar j) en het aantal populaties N. De dispersie kan laag (5 %) of hoog (50 % van de kevers emigreert) zijn. De overlevingskans tijdens dispersie en dus de kans om in een ander leefgebied te immigreren is 0.5 (Tabel II-7, blz 31).

6.2.4. De simulaties geven aan dat met een toenemende variabiliteit de vooruitzichten voor soort B slechter worden; R wordt kleiner dan 1 en het aantal populaties neemt af in 20 jaar. Bij lage variabiliteit heeft soort A een lagere R-waarde en minder populaties na 20 jaar dan soort B. In dat geval werkt de dispersie in het nadeel van soort A in vergelijking met soort B. Maar als de variabiliteit groter wordt, krijgen de populaties van soort A dankzij de dispersie betere overlevingskansen dan die van soort B.
Zelfs een laag dispersieniveau van vijf procent, waarvan dan bovendien de helft verloren gaat, verlaagt de kans op uitsterven aanmerkelijk. Onder de gegeven omstandigheden geeft een laag dispersieniveau zelfs betere resultaten dan een intensieve graad van dispersie.
Als gevolg van de dispersie-aktiviteiten worden de fluctuaties in populatiegrootte gereduceerd (Fig. VIII-5, blz 145). Op korte termijn zijn de voordelen van geen dispersie nog wel groter dan die van wel dispersie, maar op langere termijn (ca 70 jaar) sterft soort B uit en trekt soort A aan het langste eind. Hoewel soort A kleinere populaties heeft, overleeft deze op termijn beter dan soort B.

6.2.5. Om de genetische konsekwenties van dispersie na te gaan, is in het model de mogelijkheid ingebouwd dat het dispersiegedrag onderworpen is aan genetische selektie. Aangenomen is dat er twee *genotypen* M en B zijn in plaats van twee soorten A en B. Het ene genotype kan emigreren, laten we zeggen door te vliegen, de andere kan dat niet. Bij veel keversoorten komt deze situatie voor in de vorm van kortvleugelige (brachiptere) en langvleugelige (macroptere) exemplaren binnen een populatie. In ons model kan, in overeenstemming met de meeste literatuurgegevens op dit punt, alleen de homozygoot MM ook werkelijk vliegen.
Fig. VIII-6, blz 148, geeft een representatief voorbeeld van een dergelijke simulatie weer. Als we een simulatie doen zonder dat er feitelijk dispersie optreedt (het is als het ware steeds te slecht weer om te kunnen vliegen) worden de genotypes verdeeld volgens de wetten van Mendel in de verhouding MM:BB:MB = 1:1:2. Maar als er wel dispersie optreedt, ontstaat een situatie waarbij genotype BB een groter aandeel in de populaties gaat vormen dan genotype MM. Genotype

MM wordt echter niet geheel weggeselekteerd. Een belangrijke rol
lijkt hierin het heterozygote genotype MB te spelen, dat wel de
eigenschap M met zich meedraagt, maar deze niet tot uiting kan laten
komen door weg te vliegen. Binnen het genotype MB is de eigenschap M
daardoor niet als zodanig onderhevig aan selektie en daarmee niet uit
de populatie te verwijderen.
Het aantalsverloop is binnen het genotype MM veel stabieler dan bin-
nen de genotypen MB en BB, waardoor het deel MM-dieren in de popula-
tie toe- resp. afneemt als de populatie groter, dan wel kleiner wordt
(Fig. VIII-7, blz 149).

6.2.6. Deze simulaties lijken de hypothese en veldwaarnemingen te
bevestigen dat dispersie kan optreden, enkel en alleen omdat de
omstandigheden daarvoor gunstig zijn, en dat het optreden van disper-
sie niet afhankelijk hoeft te zijn van verslechterende omstandigheden
in het leefgebied.
Omdat er echter een samenhang is tussen enerzijds de overlevings-
kansen van het individu in een populatie, de variabiliteit in de
populatiedynamische processen, zoals overleving en reproduktie, en
het aantal leefgebieden en anderzijds de mate van dispersie en de
overlevingskansen tijdens dispersie, is er voor elke situatie een
optimaal dispersieniveau op te geven. Daarbij wordt het maximale
lange termijn-effekt van dispersie voor het voortbestaan van een
soort in een bepaald gebied verwezenlijkt, gegeven de genoemde res-
trikties op korte termijn.

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VERKLARING VAN ENIGE TERMEN

dispersie: Hiermee worden in dit proefschrift alle aktiviteiten van een dier bedoeld, die tot gevolg hebben dat het zijn leefgebied verlaat. Het omvat het hele proces van emigratie, immigratie en van wat er onderweg gebeurt.

genotype: Het genotype van een bepaald organisme is zijn samenstelling van genetische eigenschappen, terwijl het fenotype de vorm is waarop die genetische eigenschappen tot uiting komen. Wanneer een genetische eigenschap recessief is, zal deze alleen tot uiting komen in het fenotype, als deze niet wordt weggedrukt door de dominante versie van de eigenschap. In de situatie die wij zullen toepassen: dieren zullen alleen langvleugelig zijn als de dominante eigenschap van kortvleugeligheid geheel afwezig is.

Gyrinus marinus Gyll.: Dit is de Latijnse benaming van het schrijvertje. Het schrijvertje behoort tot de familie van de Gyrinidae, die weer enigszins verwant zijn aan de grote familie van de waterroofkevers de Dytiscidae. Gyrinidae worden in alle werelddelen aangetroffen en de meeste soorten hebben een levenswijze die vergelijkbaar is met die van Gyrinus marinus. In Nederland komen ongeveer vijf soorten voor, waarvan we de soorten G. paykulli Ochs, G. minutus F. en G. colymbus Er. af en toe in onze vangsten tussen de G. marinus exemplaren hebben aangetroffen.

habitat: In dit proefschrift wordt habitat gebruikt in de betekenis van leefgebied. Het duidt een gebied aan dat in principe voor bewoning door een bepaalde soort geschikt is. Binnen een leefgebied kunnen meer of minder geschikte stukken voorkomen. Aangezien 'habitat' vaak ook in engere zin wordt gebruikt, zullen we in de Nederlandse tekst verder het woord leefgebied gebruiken.

netto reproduktie: Gewoonlijk aangeduid met de letter R. Hiermee wordt de vermenigvuldigingsfaktor bedoeld, waarmee het aantal dieren in een bepaald leefgebied per tijdseenheid (meestal per generatie of per jaar) verandert. R is de resultante van alle populatie-dynamische processen en als zodanig een louter statistische grootheid.

populatiedynamica: Dit is het totaal aan processen die een rol spelen bij het verloop van het aantal dieren in een bepaald gebied, waarvan de voortplanting, de mortaliteit en de dispersie de belangrijkste zijn. Maar bijv. de processen, die de verdeling van individuen over het leefgebied bepalen, kunnen ook tot de populatiedynamica gerekend worden.

reproduktie: Onder reproduktie wordt het totale proces van de voortplanting begrepen: de paring, het eileggen en de ontwikkeling van jongen (larven) tot aan de geslachtsrijpe volwassen dieren.

stochastisch: Bij een stochastisch simulatiemodel wordt niet gewerkt met vaste waarden voor de verschillende grootheden om processen mee na te bootsen, maar worden de waarden per keer dat er een nodig is volgens een bepaalde toevalstrekking gekozen uit een bepaalde verdeling van mogelijke waarden.

(sub)populatie: De dieren van één soort die gezamenlijk in een leefgebied voorkomen, vormen een populatie. In feite is een populatie een statistische grootheid om een omschreven aantal individuen aan te duiden. Een populatie-bioloog zal meestal proberen een populatie als een eenheid te beschrijven door de populatie te beperken tot bijvoorbeeld die dieren die in een leefgebied de mogelijkheid hebben tot interaktie, op welke wijze dan ook. Bijvoorbeeld, de dieren van een soort die in een geisoleerde plas voorkomen, kun je beschouwen als een populatie. Als er binnen een populatie kleinere groepen dieren zijn te onderscheiden met een hogere kans op interaktie dan tussen de dieren van verschillende groepen, dan kan elk zo'n kleinere groep als een subeenheid van de populatie worden aangeduid met de term 'subpopulatie'.

variatie-coëfficiënt: Dit is de grootheid waarmee we de mate van variatie rondom een geschatte gemiddelde waarde voor een variabele (emigratiesnelheid, sterftekans, aantal nakomelingen, e.d.) opgeven. De standaard-deviatie doet dat ook, maar die is absoluut en heeft alleen betekenis in combinatie met de gemiddelde waarde. Door de standaard-deviatie te delen door het gemiddelde wordt de variatie-coëfficiënt als maat voor de variatie verkregen, die onafhankelijk is

van de waarde van het gemiddelde, waardoor variatie-coëfficienten voor verschillende situaties direkt met elkaar vergeleken kunnen worden.

POPULATION DYNAMICS OF THE GYRINID BEETLE GYRINUS MARINUS GYLL.

CHAPTER II SUMMARY

1. INTRODUCTION

1.1. The central purpose of this study is to test different views
concerning the biological significance of dispersal activity between
populations. There are important controversies both about the causes
of dispersal and about its role in population dynamics.

1.2. One traditional approach starts from the supposition that emi-
gration should only occur due to adverse conditions in the present
habitat. Risks connected with staying in the population should have
become at least as high as the risks during dispersal before emigra-
tion is expected to occur. Otherwise, dispersal would be accompanied
by increased mortality, which would lead to reduction or elimination
of the dispersal behaviour by natural selection.

1.3. An alternative approach was introduced by Den Boer. He supposes
that exchange of individuals between populations will decrease the
chance of extinction of a species by 'spreading the risk'. In his
view it is not necessary to assume bad conditions to understand the
occurrence of emigration. It seems more probable that animals – at
least insects such as carabid beetles – emigrate when the conditions
for emigration are favourable.

1.4. The first view approach focuses on the mortality risk to the
emigrating and not-emigrating individuals, Den Boer's approach on the
possible · advantages of the exchange of individuals between popula-
tions for the species as a whole. Supporters of the first approach
object that advantages of dispersal, which only occur at the popula-
tion level, are not individual characteristics of the sort which are
the subject of natural selection.

1.5. Population biology is an empirical science, or should be, and a
case study could throw light on this problem. I therefore looked for
a species in a situation that would give the opportunity to investi-
gate the problem satisfactorily.
The waterbeetle *Gyrinus marinus Gyll.* (whirligig beetle) appeared to
be a favourable species. The adult beetles live in groups on the
water surface near the banks of pools and ditches. The beetles can
easily be captured and recaptured, and can be observed by eye. They
disperse both by swimming and by flight. Egg production, size of
offspring and the chance of survival can be estimated by simple
methods. I concentrated upon an area of about 15 pools with *Gyrinus*-
populations (Fig III-3, pag 36[1]). Some pools are connected by dit-
ches, others are isolated and whirligig beetles could only reach
these by flight.

1.6. From 1974 to 1983 field data were collected with the help of
experiments and by capture-recapture studies of marked beetles. Next,
computer simulation models were developed to investigate the conse-

1) Fig III-3 is also printed inside the frontcover

quences of the field data for the population dynamics of *Gyrinus marinus* in particular, and for other species in general, by changing the values for reproduction, survival, dispersal, etc.

2. FIELD DATA

2.1. Methods

2.1.1. Beetles were captured, marked with pin-pricks on the elytra and released again at the place where they were caught. The pattern of the pricks over the rows of dots on the elytra giving an individual number (Fig VI-1, pag 72). By the captures/recaptures we got information about the exchange of beetles between different populations, the size of offspring, the chance of survival and the number of beetles (population size).

2.1.2. The technique of marking with pin-pricks gives too few data to permit following exchange by swimming. Therefore, in 1978 the beetles were marked with paint-spots, so that they could be observed without the necessity of recapture. The marks could be recorded while the beetles were on the water surface. Beetles of the same population were marked with the same color, and each day all over the study area we could note the numbers of beetles with different colors. After about 40 - 50 days there were too few marked beetles left and they were too mixed together to give data on exchange. A new set of beetles was then marked and released, and in this way in four periods throughout the year new beetles are released. The experiments were carried out in the upper part of the study area with pools that are interconnected by ditches (Br-complex).

2.1.3. Egg production can be studied by putting females for 24 hours in a tube or petri-dish with moist paper. Eggs are laid on the paper, and if kept moist they will develop and hatch after about one week.

2.2. Reproduction

2.2.1. In April, when hibernation ends, females start laying eggs. Egg laying is continued until mid-August. The eggs are laid in rows under water on water plants. The larvae live on the bottom of the pools and they pupate in a cocoon outside the water on water plants or in the soil.

2.2.2. A female oviposites at least once a week and is probably fertilized after each oviposition. At the end of June the first tenerals emerge. These beetles start reproduction about 10 days after emerging. The recruitment of this summer generation emerges from mid-September onwards. Because of the low survival chances there occur three more or less separate generations in a year: a reproducing spring generation (i.e. the hibernated autumn generation), a re-

producing summer generation, and a hibernating autumn generation (Fig III-2, pag 35).

2.2.3. In Table IV-1 (pag 44) the egg production of the spring and summer generations are compared. Egg production in summer is lower than in spring because fewer females oviposit and because each female lays fewer eggs per oviposition in summer.

2.3.4. Development from egg to teneral depends on temperature. Therefore, eggs laid from April to mid-May develop slower than eggs laid from mid-May onwards (about 10 weeks and 6 weeks, respectively).

2.3.5. On the average 1 or 2 tenerals emerge per oviposition, in summer somewhat fewer than in spring (Table IV-5, pag 52). The mean number of tenerals per female/per month in spring is about twice that in summer (8 as compared with 3 or 4). This difference is mainly due to the smaller number of weeks for oviposition in summer than in spring.

2.3.6. The variation in recruitment is greater than we found for egg production. This difference in variation between egg production and recruitment indicates that the development from egg to teneral is more important for the dynamics of *Gyrinus* populations than egg production, so that factors such as the reactions of females concerning the places to lay eggs should have only a limited effect on recruitment size.
A key-factor analysis gives as a result that variation in recruitment is most influenced by variation in the viability of the eggs, and by variation during larval and pupal development. Variation in egg production seems not to be important. Thus, conditions below the water surface (eggs and larvae) are of more importance for the rate of reproduction than the conditions at the water surface (adult beetles).

2.3 Survival of adults

2.3.1. The survival chances of adult beetles per week and per month in isolated pools are shown in Table V-1, pag 64.
The survival rate decreases from spring to autumn and males have a better chance of survival than females; in spring a male on average has a life expectancy of 50 days, a female of 42 days. In autumn this expectancy is decreased to 20 and 19 days, respectively. Fortunately, variation coefficients were very low (less than 0.1). Thus, the chance of survival of different populations was about equal.

2.3.2. The survival chance of freshly emerged beetles (tenerals) is lower than that of beetles older than about three weeks, but we also found a decreasing survival chance with age.

2.3.3. At the end of October the beetles start hibernating below the
water surface.   On the average 33 per cent of the beetles survived
the winter and appeared again in April.   This corresponds with a mean
chance of survival per week of 0.95. Variation in   survival   during
hibernation   is   higher between different years (v.c = 0.7) than   be-
tween populations (v.c. = 0.4)

2.4. dispersal by flight

2.4.1. Exchange of   individuals by flight between   populations   was
recorded   within the study area by the recapture of marked beetles in
pools that did not have water connections with the pool in which   the
marked beetles were released.

2.4.2.   Such   exchange   is observed when emigration is   followed   by
immigration within the study area. But some proportion of the emigra-
ted   beetles   will have left the study area or will have   died.   Thus
immigration data give only minimum estimates of emigration.
The intensity of this exchange is very low: in most cases fewer than
1 per cent of the marked beetles were recaptured after flight activi-
ties   (Table II-1).   Males were more frequently recaptured as   flying
immigrants than females.
Flight   occurs from April to October,   thus also during the reproduc-
tion period.

Table II-1. Exchange between pools by flight.   The percentage of mar-
            ked beetles recaptured after flight.

        N = number of individuals released

	N		APRIL		MAY		JUNE		JULY		AUGUST	
	MALES	FEM.	MALES	FEM.	MALES	FEM.	MALES	FEM.	MALES	FEM.	MALES	FEM.
1974	5928	3601	0.48	0.13	0.09	0.00	0.22	0.00	0.22	0.00	0.11	0.22
1976	5638	4200	1.37	0.00	1.12	0.36	1.74	0.00	2.06	0.99	1.48	0.12
1977	2353	1994	1.77	1.01	0.39	0.49	0.42	0.79	0.31	0.12	0.13	0.17

2.4.3. To   get   a better impression of the emigration rate   from   an
isolated population we clip the wings of some of the beetles.   In the
weekly   recaptures   the decrease in numbers of both   clip-winged   and
full-winged beetles was followed.   No differences in rate of decrease
were found between clip-winged and full-winged beetles (Fig VI-3, pag
78).
But   this   experiment was carried out in 1977 when   the   weather   was

rather cold. However, when we compare the decrease rate of the clip-
winged beetles in 1977 with that of full-winged populations in 1976
(a year with many warm days) no differences can be found (Fig VI-4,
pag 79).   Thus, emigration by flight has no measurable influence on
the decrease in numbers of a population. Given the estimated decrease
rates of population size we can estimate that at least 5 per cent of
the beetles have to emigrate before we would be able to detect this
in the decrease of population size.

2.4.4.   It is obvious that flight activities depend on weather condi-
tions, and some experiments confirm this relationship. Fig I-4, pag
11 (or Table VI-2, pag 80) shows that no flight occurs below 18° C.
The beetles have no power to fly against the wind: only at low wind
velocities can they choose their own direction of flight (Fig I-5,
pag 11,   Table VI-4,   pag 82). They only exceptionally fly at all if
there is wind, because their efforts to take off usually fail then.
Daily observations of beetles at an artificial, small, shallow pool
only recorded flight on sunny days without wind, without rain and
with temperatures above 19° C.
This dependence on weather conditions may be the cause of the diffe-
rences in exchange by flight we found in 1974, 1976 and 1977.   There
appeared to be a relationship between the number of days with favour-
able weather for flight in a year and the exchange of individuals we
recorded (Table II-2).

Table II-2. The number of days favourable for flight and exchange by
             flight

YEAR	FAVOURABLE DAYS			% EXCHANGED	
	TOTAL	DURING REPRODUCTION	PER MONTH	MALES	FEMALES
		n %			
1974	30	21 (70.0)	5.0	0.22	0.11
1976	64	56 (87.5)	10.7	1.60	0.40
1977	22	19 (86.4)	4.4	0.34	0.30

2.4.5.   The lower exchange by females may be due to the many favour-
able days that occur during reproduction, when the flight ability of
females is lower than after the reproduction period, as we found in
laboratory experiments.
In these experiments we compared the flight of males and females. Fig
VI-6 (pag 85) shows that in spring when all females reproduce the
flight activity of males is higher than that of females, but after
reproduction was finished more females than males flew away. During
the summer generation this phenomenon recurs. The different flight

activity of females during and after reproduction can be explained by the relations we found between the flight activities of females and the number of eggs per female, the proportion of reproducing females and body weight (Table II-3). Experiments also show that recently emerged beetles (tenerals) show less flight activity than older beetles (Table VI-6, pag 87).

Table II-3. Flight activity of females, eggs per female, bodyweight and the proportion of females that oviposit.

FEMALES	WITH FLIGHT	WITHOUT FLIGHT
EGGS PER FEMALE	19.7	23.4
BODY-WEIGHT	17.7 mg	19.8 mg
% FEMALES OVIPOSITING	52.2	65.8

2.4.6. Differences in individual flight ability were tested in repeated experiments with the same individuals. Beetles that showed flight activity in the first test showed in later tests a greater willingness to fly than beetles that had not flown the first time. Thus, we may assume that there are differences in flight ability between individual beetles (Table II-4).

Table II-4. Flight activity and individual ability in repeated tests.

IN THE FIRST TEST:	WITH FLIGHT		WITHOUT FLIGHT	
	MALES	FEMALES	MALES	FEMALES
IN FIRST TEST	287	226	189	199
IN SECOND TEST WITH FLIGHT	217	169	116	71
% WITH FLIGHT	75.6	74.8	61.4	35.7

2.5. dispersal by swimming

2.5.1. At the Br-complex (cf. Fig III-3, pag 361) there is extensive exchange by swimming between (sub)populations. On the average after 3 - 4 weeks most of the populations consist for more than 40 per cent of immigrants (Table VII-11, pag 110).
The pools in the centre of the complex get more immigrants than the

1) Fig III-3 is also printed inside the frontcover   - 26 -

pools situated at the outer edges.

2.5.2. The emigration rate from a population can be estimated when both the chance of survival in the population and of the emigrants, and the number of these emigrants that have immigrated elsewhere, are known.
There is some decrease of the mean emigration rate per week from 0.36 in the first period (spring) to 0.20 in the fourth period (autumn), see E-values in Table VII-4, pag 102. The centre populations on the average have a higher emigration rate than the border populations.

2.5.3. Survival during dispersal can be estimated by comparing the number of beetles that has emigrated and the number that is found as immigrant elsewhere. On the average we found a survival rate of about 72 per cent (see Q_e-values in Table VII-4, pag 102), without signifi-cant differences between pools or periods. The loss to a population by emigration is about equal to the loss by mortality.

2.5.4. The relationship between emigration from and immigration into a population can be expressed as the dispersal-ratio Db = immigrants/ emigrants. In most cases Db<1, so, generally a population lost more beetles by emigration than it got by immigration. But, in eight out of the 24 cases Db>1 so that these populations is directly benefitted by dispersal (Db-values in Table VII-4).

2.5.5. With the paint-marked beetles no difference could be made be-tween males and females, but with the pinprick-marked beetles we could compare the proportion of males and of females recaptured after immigration by swimming. Males were recaptured more frequently than females, so that we may assume that males emigrate more frequently than females (Table VII-1, pag 98).

2.5.6. As might have been be expected, a reverse relationship is found between the distance between two pools and the exchange between these pools (Table II-5). However, there are exceptions. Apparently factors other than distance can also be important. We found, that the number of alternative routes, the route along which a pool can be reached, and the distribution of aggregations of beetles over the area can influence the degree of immigration into a population.

Table II-5. The relation between the distribution of the immigrating emigrants from one pool over the other pools and the distance between that and the other pools (distance ex-pressed as the number of intermediate pools).

NUMBER OF INTER-MEDIATE POOLS	0	1	2	3	TOTAL
MEAN	64.2	19.7	12.0	4.1	100.0 %

2.5.7. If emigration were a reaction to adverse conditions we could
expect a relationship between emigration and population size. But if
emigration occurs by accident, or because the conditions for emigra-
tion are favourable, no relationship between emigration and popula-
tion size should be expected.
In our case, however, we found a reverse relationship; emigration
from larger populations is smaller than from smaller populations.
Moreover, immigration is probably greater into larger populations
(Table II-6). Thus, there seems to be a tendency to stay in and to go
to larger populations, possibly due to the attraction that groups of
beetles exert on individuals that pass by.

Table II-6. Emigration and immigration in relation to population size

POPULATION SIZE	1-4	5-35	36-74	75-129	>129 ind.	TOTAL
EMIGRATION RATE	0.00	0.41	0.40	0.16	0.27	
PERCENTAGE IMMIGRANTS	1.3	14.5	21.1	20.6	42.6	100 %

2.5.8. We further looked at the influence of weather conditions on
exchange between populations. The numbers of beetles that exchange
during various weather conditions are compared in Table VII-13, pag
115.
We found that exchange between pools is significantly lower if the
minimum temperature at night is below 8° C. There may be more exchan-
ge in rainy than in dry weather. These results may be explained by
the fact that the majority of swimming-activities occur at night and
that the orientation of the beetles is disturbed by rain, so that a
beetle may loose its way and arrive somewhere else.

3. COMPUTER SIMULATIONS

3.1. Key-factor analysis

3.1.1. The field data were used to feed computer simulation-models by
which we could evaluate the results of the field study in regard to
the consequences for *Gyrinus* populations both of the small rate of
dispersal by flight and of the high dispersal rate by swimming.
Different models were constructed.

3.1.2. A first model uses the mean values and variation coefficients,
as these were found for the chances of survival per developmental
stage, for dispersal activities, and for the number of offspring per

- 28 -

female. Stochastically throughout the year, we simulate the changes
in numbers of individuals per stage, starting from the numbers of
eggs laid, via the numbers of larvae and pupae, the numbers of tene-
rals, to the numbers of beetles that survive hibernation.
This was repeated 100 times, each time starting with 1000 males and
1000 females in April. The numbers were computed per week. The mean
course of these numbers is shown in Fig VIII-2, pag 124. After hiber-
nation the number of beetles is generally somewhat higher than at the
start of the year before. However, in this computation the real si-
tuation was highly simplified.

3.1.3. The losses of individuals in each stage were treated according
to the method of key-factor analysis. In this way we could test which
stages may be especially responsible for the variation in population
size over the years. The average results of this exercise are given
in Table VIII-2, pag 125 and VIII-3, pag 126.
The higher the k-value the greater the decrease in numbers during
that stage. A stage with a high k-value, but a low standard devia-
tion, nevertheless has little influence on the variation in the
number of beetles in spring over the years.
We therefore calculated the product of k×st.dev. to find the stages
that may contribute most to the variation in population size. Most
important for population size seems to be the survival from hiberna-
tion, followed by the development from egg to teneral in both genera-
tions.

3.1.4. The fact that hibernation may be the key-factor (which is
corroborated by a high correlation between survival during hiber-
nation and population size after hibernation) introduces an permanent
factor of instability in the population dynamics of these beetles. It
is obvious that the beetles can not "protect" themselves against bad
winter conditions once the winter has started.
There are two possibilities to minimize the effects of the highly
variable chance of survival during hibernation in spring by behaviour
of the beetles: (1) density-dependent reaction in egg production, (2)
spreading the risk over as many habitats as possible by dispersal
activities.
The field study does not give any indication that density-dependent
reactions would play an important part. The role of dispersal is
traced by simulation models, of which the results are given below.

3.2. Simulation models with dispersal

3.2.1. Dispersal occurs both by flight and by swimming. The influence
of the dispersal activities as found in the field on population size,
and on the chance of population survival, must be investigated by
complicated models that simulate not only the process of dispersal
as well as possible, but also the processes of reproduction and sur-
vival.

3.2.2. It would take too much space to explain the model fully here,
so I restrict myself to some general remarks.
Survival, reproduction and dispersal are simulated as separate pro-
cesses.   The model considers individuals, not groups of individuals.
Each time a value is needed it is randomly chosen from the log-normal
distribution that was fitted to the mean value and variation coeffi-
cient of the field data.
There are 10 or 20 "habitats" at the start with 500 individuals or
with a randomly chosen number. The beetles can exchange between the
habitats.
A diagram of the model is given in Fig VIII-3, pag 129.
We made different versions of the model, depending on the problem we
wanted to investigate.

3.2.3. First, we analysed the consequences of dispersal activities.
In this model a second species (species B) is introduced, which is
identical to the first one (species A), except that it lacks the
ability to exchange between the habitats. In this way the situation
with dispersal activities can be compared with the same situation
without dispersal.
The simulation was run with variation coefficients 0.3, 0.5 and 0.7.
In this way the influence of variability (instability) could be
estimated.   The results after 20 "years" are given by the mean net
reproductive rate $R = (P_{20}/P_0)^{0.05}$ (P_x = population size in year x),
as well as the number of populations (N) that survived.
Dispersal can be low (5 %), or high (50 %). The survival chance per
individual during dispersal (i.e. the chance to immigrate into an-
other habitat) is 0.5 (Table II-7).

3.2.4. If the variability is low species A has a lower R and a lower
N than species B: dispersal activities are disadvantageous in that
case. But with increasing variability the situation for species B
becomes worse: both R and N decrease.
Even a low dispersal intensity decreases the chances of extinction. A
low dispersal rate appears even to be better in this regard than a
high one.
The fluctuations in population size of the A-species are importantly
reduced by its dispersal activities (Fig VIII-5, pag 145). On the
short term the advantages of staying seem greater than those of dis-
persal, but on the long term the not-dispersing species risks extinc-
tion. Although the dispersing A-species lives in smaller populations
it will survive the B-species (Table II-7).

3.2.5. To test the genetic consequences of dispersal we built in the

no clear evidence is found for such selection, but we imagined there
are two genotypes M and B: M can fly, and B cannot fly (for example
macropterous and brachypterous, respectively). In our model only the
homozygotic macropterous genotype (MM) is actually capable of flight.
Fig VIII-6 (pag 148) gives an example of the results of such simula-
tions. Without dispersal the genotypes are distributed according to a

Mendelean distribution, but when dispersal occurs the BB-type makes up an increasing part of the population. The MM-type, however, is not selected away. The course of numbers of the MM-type is much more stable than that of the MB- and the BB-types (Fig VIII-7, pag 148).

Table II-7. Simulation of different situations with (A) and without (B) dispersal over 10 habitats.

SURV. = survival chance, LOW=0.12, HIGH=0.5 per generation
DISP = dispersal chance per individual
VAR   = variation coefficient in all processes (heterogenity of the habitat)
R   = net reproductive rate R = (P_1/P_0)
POP   = number of populations after 20 years

SURV.	VAR	DISP	R		X POP	
			A	B	A	B
LOW	0.3	5 %	0.99	1.00	10	10
		50 %	0.79	1.00	10	10
	0.5	5 %	0.94	0.80	10	3
		50 %	0.79	0.80	10	3
	0.7	5 %	0.87	0.64	10	0
		50 %	0.74	0.64	8	0
HIGH	0.3	5 %	1.01	1.03	10	10
		50 %	0.81	1.03	10	10
	0.5	5 %	0.97	0.86	10	4
		50 %	0.81	0.86	10	4
	0.7	5 %	0.95	0.65	10	0
		50 %	0.79	0.65	10	0

3.2.6. These simulations seem to confirm the field observations, which suggest that dispersal occurs when the circumstances are favourable for dispersal activities. However, because of dependence on both variability, and on survival chances in the population as well as during dispersal, the intensity of dispersal is not neutral. The best "strategy" seems to be to show a low but non-zero dispersal intensity.
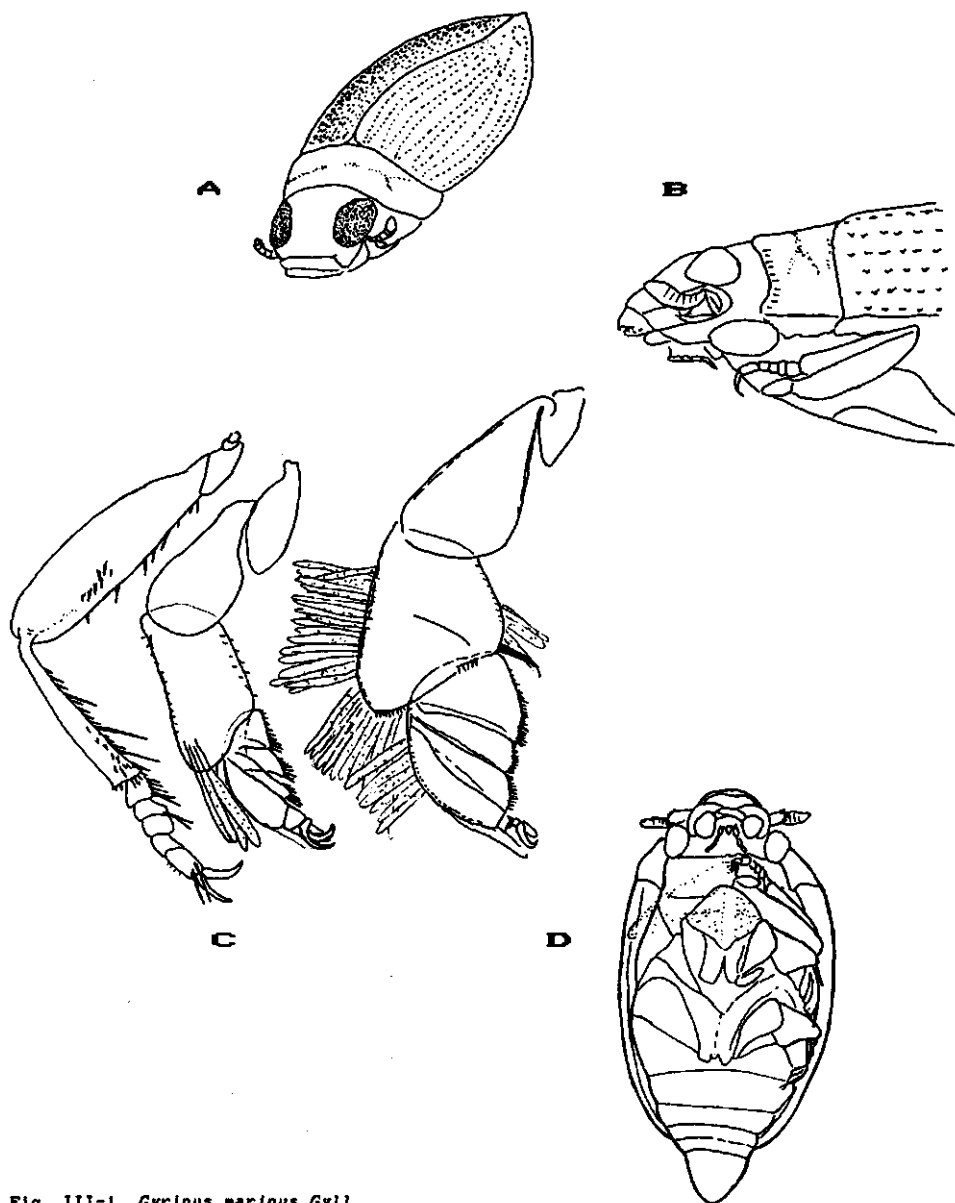
Fig. III-1. *Gyrinus marinus Gyll.*
        A. beetle in dorsal view.
        B. side view, showing the divided eyes.
        C. The legs in detail.
        D. Ventral view.

CHAPTER III   INTRODUCTION

1. STATING THE PROBLEM

1.1.   Starting with the publications of Andrewartha and Birch (1954),
Southwood   (1962),   MacArthur and Wilson (1967) Wynne-Edwards (1962),
den Boer (1968), and Johnson (1969) serious attention was paid to the
role of dispersal in population dynamics. Since then a growing number
of   publications   contribute to discussions about   the   factors   that
introduce   dispersal   behaviour,   about the genetic   consequences   of
dispersal,   and   about the influence of dispersal on the variation of
population size and thus on the chances of survival and   (re)founding
of populations (e.g.   Gadgil 1971, Simberloff 1974, Diamond 1975, den
Boer 1977).

1.2.   Most   contradictions   concern the question why some   individual
should show dispersal activity.   Other problems around dispersal   may
be converted to this central question. The fenomenon of dispersal can
be approached from two sides.
(1).   From the point of view of natural selection dispersal behaviour
should   only be shown when the chance to get progeny should at   least
not   be reduced by the dispersal activities.   As it is generally   as-
sumed   that dispersal will introduce an extra risk not to encounter a
mate,   many authors suppose that dispersal behaviour will only   occur
when   the risk not to reproduce in the present habitat has   increased
(e.g. Elton 1927, Southwood 1962).
(2).   From the point of view of population dynamics there is evidence
that   populations of a number of different species become extinct and
are refounded rather frequently (e.g.   Simberloff 1974, Diamond 1975,
den   Boer   1985),   as well as evidence that dispersal may lead   to   a
rapid colonization of new habitats (e.g.   Mook 1971,   Lindroth 1971).
The principal of 'spreading of risk',   formulated by den Boer   (1968,
and e.g. 1977, 1981; Andrewartha and Birch 1984), emphasizes the con-
tribution   of exchange of individuals between (sub)populations to the
survival of (sub)populations concerned.   Moreover,   such an   exchange
between   populations   with   asynchronous changes of numbers   may   in-
crease, just for mathematical reasons, net reproduction and thus mean
population size (Kuno 1981, Metz et al 1983, Klinkhamer et al 1983).

1.3.   This difference in the evaluation of dispersal, (1) in relation
to the progeny of the dispersing individuals,   and (2) in relation to
the variation in population size and survival of populations, lead to
differences   in opinion about the causes of dispersal   behaviour.   We
may   bring   these different appoaches under the same   denominator   by
trying to answer the question: Under what conditions do the long-term
advantages of exchange between populations counterbalance the   short-
term risk of dying without progeny of the dispersing individuals ?
This   principal question can be divided in a number   of   subquestions
that   each   can be answered by studies and experiments in   field   and
laboratory:
(a). What   is the frequency of dispersal activity,   what kind of dis-

persal activity is shown, under what circumstances does dis-
persal occur?
(b). Which factors do influence the dispersal behaviour (weather,
hunger, lack of reproduction, etc.)?
(c). What is the exchange rate of individuals between populations,
what is the chance to survive dispersal activities?

1.4. Because the effects of dispersal on population dynamics will
have to be traced, not only data on dispersal have to be collected,
but also data on reproduction and survival.

2. FIELD STUDY

2.1. The possibilities to collect in the field data about dispersal,
about exchange of individuals between (sub)populations and about
reproduction and survival, are limited. However, we found a suitable
object in the water beetle *Gyrinus marinus Gyll.* (whirligig beetles;
Fig. III-1). These beetles live on the water surface of ditches and
pools, mostly in groups at traditional places near the banks. The
beetles hibernate until about mid-April below the water surface.
Reproduction follows promptly hibernation. Until about mid-August fe-
males are frequently laying eggs under water. The larvae grow up
below the water surface, pupate outside the water, and beetles of the
new generation emerge from the end of June onwards. This summer
generation also reproduces, resulting in an autumn generation that
emerges in September and October. End of October the beetles of this
generation start hibernation. During the whole active period between
April and November the beetles can show dispersal activities, either
by flight or by swimming. The year cycle of *Gyrinus marinus* is summa-
rized in Fig III-2.

2.2. A suitable study area was found in the northern part of the
Netherlands near Groningen. It consists of 15 pools, which are partly
interconnected by ditches (Fig. III-3). In this area about 10 (sub)-
populations of *Gyrinus marinus* can be distinguised.

2.3. By marking the beetles their mobility as well as the contribu-
tion to exchange between different pools and ditches, could be esti-
mated by regularly recapturing the beetles. From the same capture-
recapture data the numbers of beetles, the survival rates and the
sizes of progeny could be estimated.

2.4. In addition to the field study a number of laboratory experi-
ments were carried out, for example to induce flight activity under
different conditions and for different kinds of beetles (females,
males, etc.).
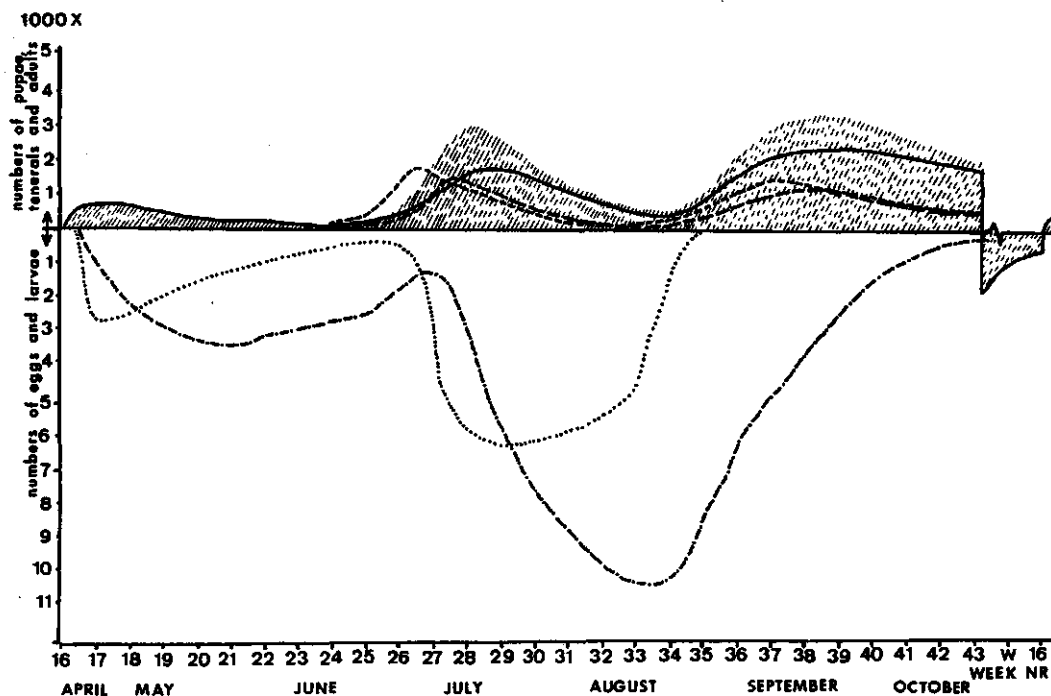
Fig. III-2. An outline of the course in numbers in different delopmental stages during the year. The numbers of the stages on the water surface (pupae, tenerals and adult beetles) are set out upwards; those of the stages below the water surface are set out downwards.

```
........  = number of eggs
—·—·    = number of larvae
------    = number of pupae
— — —    = number of tenerals
————    = number of adult beetles
//////////////  = number of tenerals + adult beetles
```

3. EVALUATION OF THE DATA BY SIMULATION MODELS

3.1. The evaluation of the collected data occurred by developing simulation models, which made it possible to investigate the role of dispersal in the population dynamics of *Gyrinus marinus*, and to ascertain under what conditions the advantages of exchange between populations at the population level may counterbalance the risk of dispersal at the individual level. As the model is feeded with field data, it gives information about the data that have still to be collected, i.e. what kind of experiments have to be done to complete the study.

Fig. III-3. The study area. Wn - Sz = location symbols
- = water area
● = sites about permanently occupied by groups of beetles
○ = sites occasionally occupied by groups of beetles.
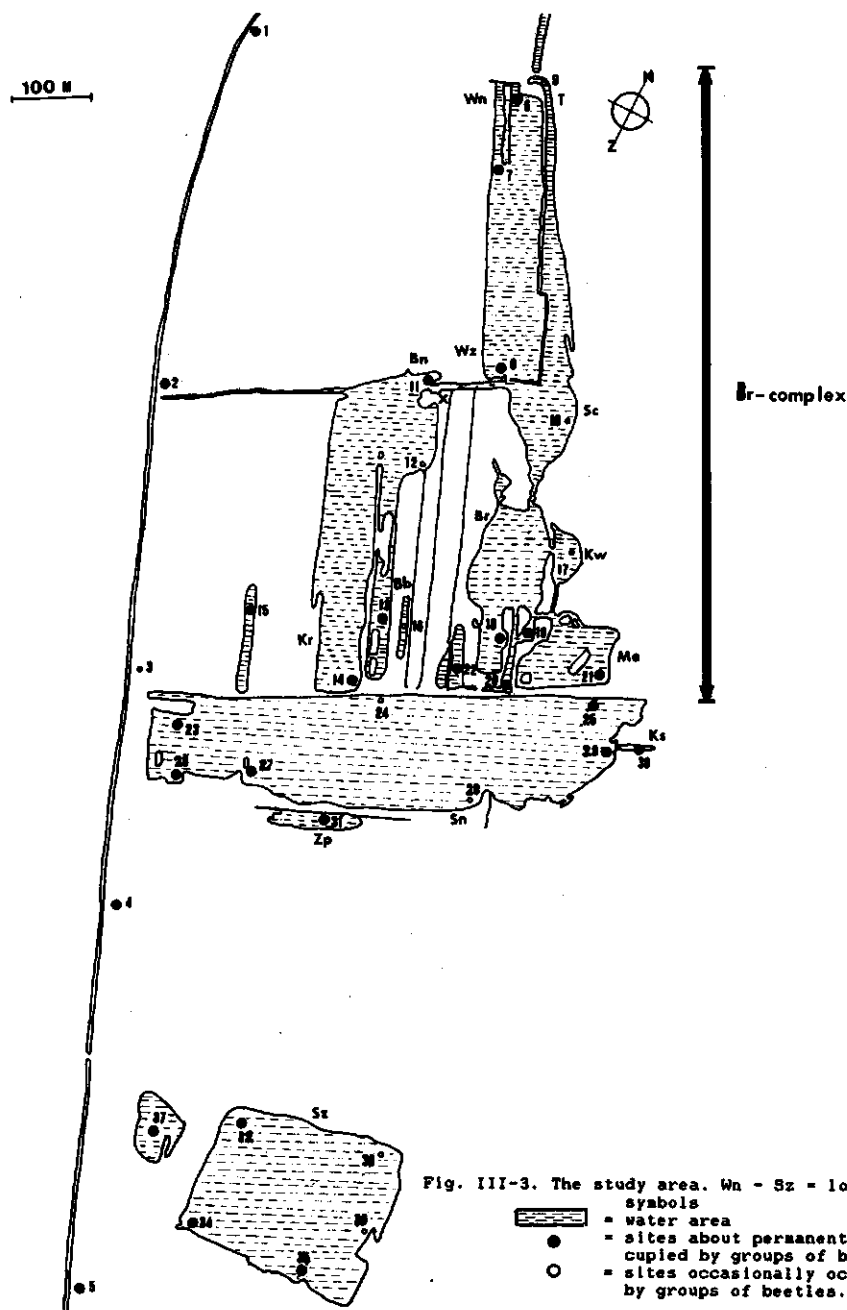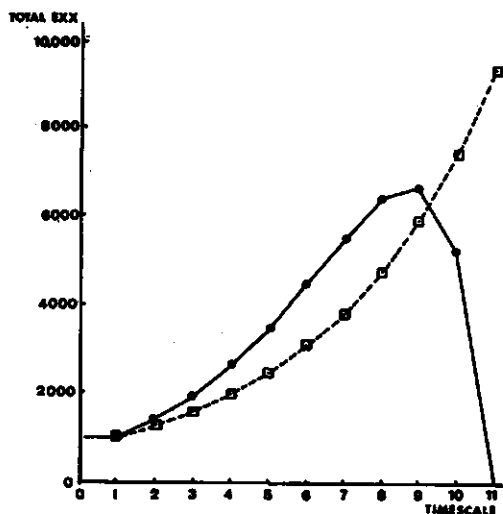
Fig. III-4. A hypothetical scheme of the possible long term and short term effects of the occurence of dispersal activity on the number of individuals of a species in a certain area.

☐---☐ = number of individuals in all habitats in the area when dispersal occurs.
●——● = number of individuals in all habitats in the area if no dispersal occurs.

3.2. The difference between long term and short term effects of dispersal is schematically pictured in Fig III-4. Suppose there are X habitats in an area with at the start 1000 individuals in total, distributed over all habitats.
Suppose further, such a survival rate and such a reproduction rate that on the average the total population size increases.
Suppose, such a chance of extinction, that in each time period (e.g. a year) a number of populations (e.g. 10 %) become extinct.
In case dispersal occurs, suppose finally, that there is some chance to survive emigration (i.e. the chance to immigrate into another habitat, e.g. 70 %)
The short term effect of dispersal activity will be: on the average less individuals per habitat in comparison with the situation without dispersal activity, whereas the short term effect of no dispersal will be: a more steep decrease of the number of populations in the area than in case dispersal occurs.
The long term effect of no dispersal will be: a few populations with very high numbers, finally leading, however, to complete extinction of all populations in the area, whereas with dispersal a number of populations of moderate sizes will continue to exist.

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CHAPTER IV   REPRODUCTION[1]

SUMMARY

Between 1974 and 1983 data concerning egg production and recruitment
were obtained by sampling populations of the whirligig water beetle
Gyrinus marinus Gyll. All females reproduce, but they differ in the
number of eggs laid per oviposition and in the frequency of oviposi-
tion.   There are two reproducing generations a year, one in spring
(April-June) and one in summer (July-August). Females emerging in
July and August reproduce immediately after emergence, but at a lower
level than the females of the spring generation.   In June the egg
production of spring females also decreases. No significant differen-
ces in egg production occur between populations in different sites or
in different years.   Individual properties and circumstances of the
females probably have a distinct influence on variation in egg pro-
duction. A female probably oviposites and is fertilized at least once
a week. Without fertilization egg production and the viability of the
eggs decrease after two weeks.   On the average, 60 per cent of the
eggs hatch.

Development from egg to teneral takes about 10 weeks in spring and
autumn and about six weeks in summer. The hatching and development of
eggs laid in April is probably retarded until the half of May. Varia-
tion in the length of the developmental period will cause variation
in recruitment and in the number of hibernating beetles. Variation in
egg-viability and in larval and/or pupal development are probably of
equal importance to the variation in the numbers of tenerals emerg-
ing. The variation in egg production is of no importance.
Recruitment (number of tenerals/female) of the generations repro-
ducing in spring and in summer are independent of each other. Between
years the rate of recruitment differs significantly, and probably de-
pends more on environmental conditions such as weather than egg
production seems to do.

1. INTRODUCTION

1.1.   Reproduction   consists   of (a) the reproductive   activities   of
females and males (fertilization, egg production and egg laying), and
(b) development of the eggs until the emergence of tenerals (recruit-
ment). It is frequently supposed that a population reacts to changing
circumstances (such as food shortage) by adjusting its egg produc-
tion, particularly if density-dependent processes have been assumed,
which are usually thought to have a regulating effect on population
size (e.g. Baars and van Dijk 1984). By means of key factor analyses
(Varley and Gradwell 1960, Podoler and Rogers 1975) a number of case
studies have shown that the mortality of a stage in the development
between egg production and the emergence of adults is a key factor in
the population dynamics of the species (e.g. review in Podoler and
Rogers 1975).

1 This chapter is also published with minor changes in text in Oecologia (1986) 69:31-40

1.2. We have carried out measurements and experiments on the re-pro-
duction of whirligig beetles (*Gyrinus marinus Gyll.*),to obtain esti-
mates of the relationships between egg production, development and
final recruitment. These measurements and experiments are part of a
comprehensive study of the population dynamics of whirligig beetles
which also includes survival and dispersal.

1.3. Reproduction of whirligig beetles starts with the laying of eggs
under water. After hatching, the larvae grow up under water and
pupate outside the water. Each stage in the development from ovocyt
to mature adult beetle has its specific growth rate and its own
survival chance. The influence of each stage upon the ultimate varia-
tion in recruitment is of special interest. For example, if egg
production has the greatest influence, the living conditions of the
females will probably have a significant influence upon the size of
recruitment. But if the conditions for the larvae under water provide
the most important factor for the variation in recruitment it may be
fairly unimportant to recruitment what happens to the females. We
therefore give special attention to variation in egg production and
to that in the emergence of tenerals. A full description of reproduc-
tion will embrace (a) information about reproductive activities both
of females (number of females reproducing, number of ovipositions,
number of eggs per oviposition, individual differences) and of males
(frequency of fertilizations, influence of fertilization upon egg
viability), and (b) information about development from egg to adult
(proportion of eggs which hatch, time of development, variation in
survival) and about recruitment (number of tenerals per female, per
generation, and per month).

2. METHODS

2.1. As gyrinid beetles live on the water surface of small water
bodies they are convenient subjects for poppulation dynamic field
studies. Most of the data were collected from ten populations in the
main study-area in the northern part of the Netherlands near Gronin-
gen. These were supplemented with data from other populations within
a radius of about 20 km around Groningen. The populations will be
indicated by location-symbols and year: for example, Zp-76 and Wn-83
concern populations Zp in 1976 and Wn in 1983 (for the meaning of the
location-symbols see Fig III-3, pag 36).

2.2. In the field the eggs are laid on submersed water plants, but
the number of eggs produced per female can easily be measured by
putting single females in tubes or petri-dishes with moistened toilet
paper for 24 hours. The ripe eggs will then be laid in rows on the
paper. When the paper on which the eggs are laid is kept moist, the
eyes of the embryos become visible through the thin egg scale and it
is possible to ascertain the number of viable eggs after five days at
room temperature.
Young females start oviposition about 10 days after emergence. Unless

otherwise stated we used only females with hardened elytra (females
older than two weeks) in the experiments.
From population Zp-76 10 to 20 females of each sample taken in April
until June were kept in formalin and later dissected to count the
number of eggs in the ovaries.
By repeatedly measuring the egg production of the same individually-
marked females from populations Zp-76 and Mp-83 the egg production of
individual females was estimated during the reproduction season. (The
technique of individual marking is described in chapter VI). In this
way it was possible to estimate the rate of egg production in the
ovaries, the frequency of ovipositions and the frequency of fertili-
zations per female.

2.3. If a female was fertilized before she was captured a sperma-
tophore was also left on the paper. After 20 June 1983 all males were
removed from population Mp-83 to trace the influence of both the
frequency of copulations and of the duration of the effect of a
single fertilization on egg production and on the viability of the
eggs laid.

2.4. Recruitment is estimated by the percentage of 'very soft' beet-
les (tenerals) in the samples. After a beetle has emerged, it takes
one to several weeks before the hardening of the cuticula, especially
of the elytra, is completed. Until five to seven days after emergence
the beetles can be distinguished from previously emerged tenerals.

2.5. Time will be indicated by numbered weeks. In each year the same
seven days bear the same number. In this way data of different years
are directly comparable (i.e. 1 April always is the last day of week
13, etc.).

2.6. Variation in the data is expressed as the variation coefficient
(v.c.=standard deviation/ mean value). Variation coeffecients in time
sequences (data of the same population in different years) will be
indicated as $v.c._t$, and in space sequences (data of different popula-
tions in the same period) by $v.c._p$.

2.7. Statistical tests used are all reffered to Sachs 1983. Unfor-
tunitely different authors use different symbols in the same tests.
The tests and the symbols used in this paper are as follows: t-test,
parameter t; Mann-Whitney U-test: U, for large samples normally
distributed parameter z; Kruskall-Wallis H-test: H, z; correlation
test: r or z; Spearman correlationtest: r, z; Chi-square test: X^2 ;
Anovar: F; Wilcoxon paired signed-rank test: R, z; Fisher-test: z. If
possible the normally distributed parameter z is used, because of the
comparability of different tests and its independence of the size of
the samples.
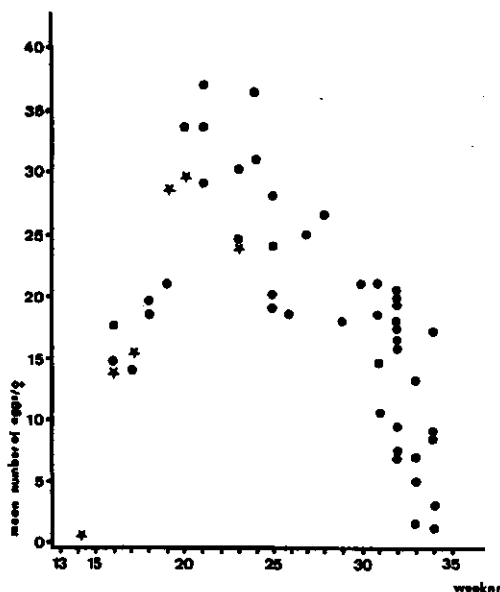
Fig. IV-1. Mean number of eggs per female per
week

✱ = mean number of eggs found in
the ovaries of a female
● = mean number of eggs laid in
one oviposition

3. RESULTS

3.A. *Egg production*

Egg production will first be considered at population level and then
at individual level (per female). Finally the influence of fertiliza-
tion upon egg production will be discussed.

A.1. Egg production per generation.

A.1.1. Egg production starts after hibernation in April and conti-
nues until mid-August. About the end of June the first young beetles
emerge. These beetles start to reproduce within two weeks. The off-
spring of this generation emerges from early September until hiberna-
tion at the end of October. The successive reproducing generations
only partly overlap (about 25 per cent in summer and about 2 per cent
in spring).
As long as a female is alive she produces eggs, until about the last
week of August (week 35). Females caught on the first day of activity
already have many developing ovocytes. It takes several weeks before
all females are reproducing, and the number of ripe eggs in the
overies increases until the second half of May (weeks 19 - 22, see

~42~

Fig. IV-1).
During the period for which both measurements are available the
number of eggs laid per female is correlated with the number of eggs
in the ovaries (1976, weeks 16 - 24, comparing the regression coeffi-
cients of the time sequences of eggs laid and eggs in ovaries:
t=0.84, df=404, P > 0.05). But the number of eggs laid per week is
significantly higher than the weekly number of eggs in the ovaries
(Mann-Whitney U-tests per week: all tests P<0.02). After week 22
(early June) the number of eggs laid decreases significantly with
time (Spearman test r = -0.819, n=41, P<0.001). Females of the summer
generation start oviposition about ten days after emergence, but
their egg production is lower than that of females of the spring
generation. (Mann-Whitney U-tests: see Table IV-1). It is striking
that the decrease in egg production of the spring generation begins
as early as the second week of June (week 23), i.e. about six weeks
before the first oviposition of the summer generation (Spearman test
on mean numbers of eggs laid per female: weeks 22 - 27, n=13, r=-
0.698, P<0.02).
The decrease of egg production of the spring generation is due both
to a decrease in the number of eggs laid per oviposition and to a
decrease in the fraction of females that ovipositates (Table IV-1;
Spearman tests: weeks 22 -27, eggs/ovip.: n=347, z=3.017, P<0.005; %
fem/ovip.: n=12, r=0.612, P<0.05).

A.1.2. The differences in egg production between the generations in
spring and in summer may be the result of a greater heterogeneity in
the ages of the individuals of the summer generation. We have seen
above that in springtime it takes some weeks before the females come
fully to reproduction. The same may be true for the young females of
the summer generation. Young beetles can be roughly divided into five
age classes depending on the degree of hardening of the elytra. A
number of experiments were carried out to relate egg production to
age (Table IV-2). A significant correlation is found between hardness
of the elytra and the proportion of reproducing females (Spearman
test: n=23, r=-0.50, P<0.01), but between hardness and the amount of
egg production per female no correlation can be stated (n=23,r=-0.18,
P>0.10).
Another reason for the decreasing egg production from June to the end
of the egg production period is probably to be found in the decreas-
ing fraction of females that has been fertilized (i.e. fraction of
females with spermatophores, see Fig. IV-2 and S A.3).

A.1.3. The variation in numbers of eggs laid in summer is signifi-
cantly higher than in springtime (U-test on v.c.-values in Table IV-
1: z=3.58, P<0.002), due to the decreasing mean number of eggs laid
per oviposition from June onwards. Comparing different populations in
the same week of the same year (variation in space) gives a mean
v.c., = 0.17 (st.dev. = 0.08, n=6), comparing populations in the same
week of different years gives a mean v.c., = 0.14 (st.dev. = 0.08,
n=12). Analyses of variance show no significant influence of time or
space on the variation in egg production (Anovar tests: 10 x P>0.10,

Table IV-1. Variability in egg production per week.
           Frequency distributions of egg production on moist paper.

           % O   : percentage of females with oviposition
           m (st.dev) : mean number of eggs laid per ovipositing
                        female (+ standard deviation)
           v.c.   : coefficient of variation (v.c. = st.dev./m)

SPRING GENERATION						SUMMER GENERATION					
pop.	week	% O	m	(st.dev)	v.c.	pop.	week	% O	m	(st.dev)	v.c.
Hk 79	16:	56.2	28.89	6.01	0.21	Sn 74	28:	-	23.70	12.63	0.53
Mp 83	16:	76.6	18.37	5.04	0.27	Zp 76	28:	92.0	27.55	9.41	0.34
Mp 83	17:	68.7	20.00	7.81	0.39	Mp 83	28:	89.1	23.83	8.18	0.34
Mp 83	18:	69.2	25.37	7.06	0.28	On 78	29:	59.6	28.24	10.22	0.36
Hk 79	19:	64.0	27.81	5.15	0.19	Sl 78	30:	-	19.56	13.15	0.67
Hk 79	20:	71.8	27.68	7.76	0.28	Rv 79	30:	60.5	19.00	9.49	0.50
Zp 76	20:	84.2	38.75	11.18	0.29	Sn 79	30:	38.1	25.63	7.76	0.30
Sn 74	22:	-	27.50	2.64	0.10	Hk 79	31:	63.2	25.86	12.39	0.48
Mp 83	22:	93.7	38.33	11.99	0.31	Ro 79	31:	69.2	29.00	8.69	0.30
Mp 83	23:	81.5	35.23	6.26	0.18	On 79	32:	57.1	23.96	6.08	0.25
Zp 76	23:	82.0	28.85	7.56	0.26	Da 79	32:	42.4	22.29	12.24	0.55
Zp 76	24:	92.3	38.33	10.18	0.27	Hk 79	32:	62.5	28.09	11.80	0.42
Mp 83	24:	92.0	33.48	8.18	0.24	Wh 79	32:	36.8	22.86	6.36	0.28
Mp 83	25:	68.2	32.67	3.72	0.11	As 78	32:	61.5	31.56	10.76	0.34
On 79	25:	63.8	29.86	9.62	0.32	On 78	32:	68.5	20.48	13.36	0.65
On 79	25:	61.1	28.94	5.83	0.20	On 78	32:	32.6	19.00	10.08	0.53
Zp 76	25:	78.6	35.00	14.14	0.40	Zp 76	33:	75.9	22.59	7.92	0.35
Zp 76	26:	58.8	29.80	9.50	0.32	As 78	33:	3.1			
Mp 83	26:	83.3	28.50	4.12	0.14	Dk 78	33:	33.3	18.33	8.76	0.48
Mp 83	27:	72.2	29.62	8.77	0.30	On 79	33:	51.1	23.70	8.29	0.35
						Br 79	33:	11.4	21.25	8.54	0.40
						On 79	34:	64.7	24.55	5.68	0.23
wk 16 - 21:		71.2	25.62	8.89	0.35						
wk 22 - 27:		78.4	31.30	9.82	0.31	wk 28 - 34:		59.7	24.91	10.51	0.42
wk 16 - 34:		75.0	26.88	10.45	0.39						

U-tests on differences between week 22-27 (gen. 1 = n_1) and week 28 - 34 (gen. 2 = n_2):

variable	n_1	n_2	U	Z	significance = *
% females ovipositing (%O) (< week 32	12	15	39.5	2.46	P<0.01 *
number of eggs laid per female (m)	13	21	14.0	4.34	P<0.001 *
st.dev. of m	13	21	95.5	1.45	P>0.05
coefficient of variation (v.c.)	13	21	35.5	3.58	P<0.002 *
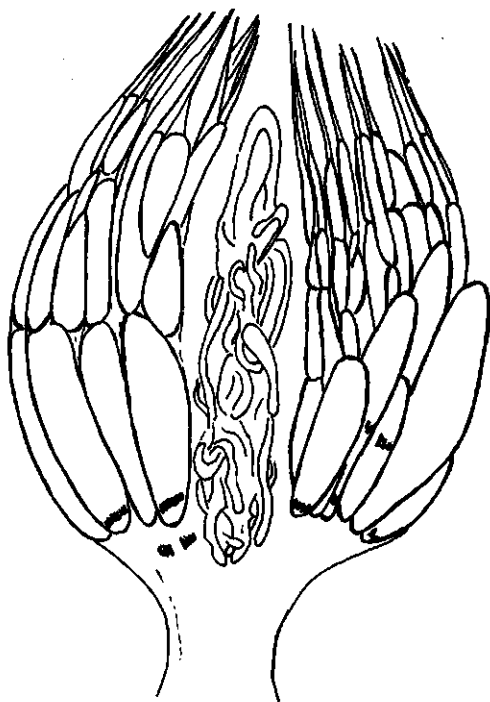
Fig. IV-2. Example of the ovaries of a female dissected after she has laid 32 eggs.
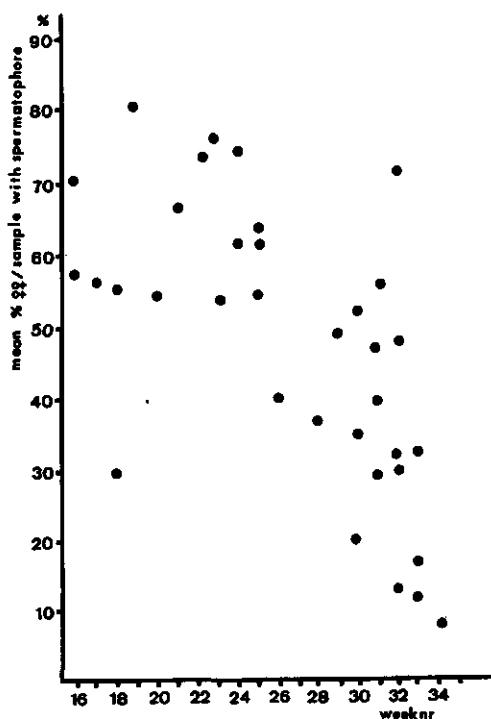
Fig. IV-3. Mean percentage of females per week with a spermatophore deposited before oviposition.

Table IV-2. Egg production in relation to age.
Proportion of ovipositing females and the mean number of eggs laid per oviposition by females with differently hardened elytra.

	degree of hardening of elytra				
	very soft	soft	rather soft	rather hard	hard
indication of age (days)	<7	5	-14	>14	>14
number of females	71	144	296	177	127
% females ovipositing	5.63	20.14	43.24	55.93	62.20
eggs laid (mean)	21.75	21.34	23.23	23.14	26.54

2 x P<0.02), except a significant influence of time between week 16 and week 25, when egg production is building up (Anovar: 4 x P<0.002, 1 x P<0.05, 1 x P>0.10). Apparently the number of eggs laid per female is less dependent on circumstances that differ specifically from place to place or from year to year (such as the availability of food) than on factors connected with the individual beetles. Alternatively, such circumstances may not have fluctuated in space or time in a way that significantly influences egg production in a population. A logical next step is therefore to consider the egg production inside the generation i.e. per individual female.

A.2. Egg production per individual female.

A.2.1. The egg production of individual females in the course of time under field conditions can be studied by frequently recapturing individually marked females and testing oviposition capability and egg production on moist paper (see Methods). The tests were carried out in 1983 with females of the Mp-83 population.

A.2.2. There were no females that did not reproduce at all. If tested in two successive weeks every female laid eggs at least once, except during the first two tests in April. If tested in four consecutive weeks 16 out of 17 females laid eggs three or four times. About 80 per cent of the females in a sample laid eggs, so a female seems to

Table III-3. Egg production of individually-marked females in population Mp-83 during the reproduction season.

    x : number of catches per female
    n : number of females
    o : mean number of tests (out of x trials) with oviposition
    %o : percentage of tests with oviposition
    e : mean number of eggs per oviposition (v.c. = var.coef.)
    t : mean number of weeks between first and last capture
    f : number of ovipositions with a spermatofore

x	n	o	%o	e	v.c.	t	t/x	f	%f/(x.n)
1	47	0.81	80.9	19.3	0.29	-		32	68.1
2	27	1.74	87.0	25.8	0.45	3.3	1.65	33	61.1
3	16	2.25	75.0	29.1	0.37	4.7	1.57	23	47.9
4	13	2.92	73.0	31.3	0.38	6.2	1.55	29	55.8
5	8	4.25	85.0	31.5	0.30	7.2	1.44	24	60.0
6	2	4.50	75.0	36.5	0.39	7.5	1.25	5	41.7
7	3	5.30	75.7	32.5	0.33	8.3	1.19	11	52.3
8	1	5.00	62.5	28.4	0.24	9.0	1.13	3	37.5

have ripe eggs most of the time (Table III-3). The successive tests on 8 and 13 June show that development of a new set of ripe eggs in the ovaries can be accomplished in five days. This indicates that oviposition in the field may occur more frequently than our sampling, i.e. more frequently than weekly. Indeed many developing ovocytes and nearly ripe eggs were found in females that were dissected immediately after egg laying (Fig. IV-2).
From recaptures of newly hatched females it appears that 9 out of 10 females can lay eggs within 10 days after emerging (cf A.3.4.)

A.2.3. Individual females show significant differences in egg production, i.e. some females lay more eggs per oviposition than others (Anovar: df=48,55; F=2.22; P=0.01). From the Anovar test it appears that about 80 per cent of the total variation in egg production is due to variation-in-time of individuals.
In A.1 it was shown that egg production in spring is higher than in summer, but also that from June onwards egg production decreases. One possible reason for this (cf. A.1) could be the increasing age of the females. Females that are not recaptured again can be considered to have died, either from old age or from an accident (e.g. predation). Generally, the last time a female was recaptured she laid less eggs than she did at previous captures (captures 2 May to 20 June; Wilcoxon test: n=17, T=21, P<0.01). Significantly more females did not lay eggs at their last capture than at their previous captures (X^2 test: df=1, X^2 = 5.31, P<0.025). In Table III-3 some results concerning repeated oviposition of individual females are reviewed.

A.3. Effects of fertilization on egg production and on viability of eggs.

A.3.1. In June and July 1983 in several populations a mean viability of eggs was found of 59.5 per cent (st.dev. 35.54, v.c. = 0.60).

A.3.2. In 67.3 per cent (152 out of 226) of the oviposition tests a spermatophore was left with the eggs on the paper; it was less frequently found without eggs (12 out of 161 spermatophore records: 7.5 %). A female is apparently fertilized several times during the reproduction period at about the same frequency as she is laying eggs. But since the percentage of females captured with a spermatophore decreased from week 22 onwards (Spearman test: r=-0.585, n=10, P(<=0.05, see Fig IV-3), the fraction of fertilized females is lower in the summer generation than in the spring generation (U-test: n_i=n_2=15, U=26.5, z=3.568, P<0.001). The situation is comparable with that of the numbers of eggs laid per oviposition (Fig IV-1). The decrease in the percentage of spermatophores starts before the first individuals of the new generation emerge. Probably the capacity for spermatophore production decreases with increasing age of the males, similar to the decreasing egg production of females at old age. Newly emerged males may have to spend some time to built up their spermatophore production (cf A.3.4).

Frequent fertilization may be important for egg production. In experiments with pairs of carabid beetles in petri dishes the females were fertilized several times a week. In the absence of fertilization the egg production and the viability of the eggs decrease (van Dijk pers.comm.). The same probably applies to gyrinid beetles.

A.3.3. To test the role of fertilization all males were removed on 20 June from the Mp-83 population and in the following weeks the reproduction of the females was recorded. Newly emerged males were removed, but we could not prevent a number of females from being fertilized in the second week of July (the somewhat better results at 18 July may be due to that, see Table IV-4). During the first two weeks the removal of the males influenced neither egg production nor the viability of the eggs (Table IV-4). After three weeks the percentage of reproducing females had not yet changed, but the number of eggs laid per female decreased significantly (t-test: df=136, t=2.335, P<0.025), as did the viability of the eggs (Table IV-4: % of females with viable eggs: X^2-test df = 3, X^2 = 30.21, P<0.001; Table IV-3: % viable eggs: X^2-test df=3, X^2 = 106.1, P<0.001). A second indication

Table IV-4. Influence of removal of males from Mp-83 population on the egg production and on the percentage of viable eggs.
+ sp / - sp : with / without a spermatofore
C % : percentage from total number of captured females
D % : percentage from number of egg-laying females

Date		20-6	27-6	4-7	11-7	18-7
A						
number of females		26	12	18	52	78
captured	+ sp	16	0	1	11	1
captured	- sp	10	12	17	41	77
B						
mean number of eggs						
laid per female		33	29	30	24	27
C						
number (%) of females						
with eggs	+ sp	16 (62)	-	1 (6)	11 (21)	1 (1)
with eggs	- sp	2 (8)	10 (83)	12 (67)	36 (69)	65 (83)
D						
number (%) of females						
with viable eggs	+ sp	13 (81)	-	1 (100)	5 (45)	0 (0)
with viable eggs	- sp	?	10 (100)	10 (83)	6 (17)	13 (20)
E						
% viable eggs from						
females	+ sp	57	-	20	32	0
females	- sp	?	42	41	15	13

for the importance of fertilization for egg production and develop-
ment is found in the significant difference in viability between eggs
of females with and those without a spermatophore (Fisher test (a) on
% of females with viable eggs: n=126, z=6.416, P(0.001; (b) on % of
viable eggs: n=43, z=1.87, P(0.05).

A.3.4. In this experiment it also appeared that the egg production of
young females starts irrespective of fertilization. But to maintain
egg production as well as a high fraction of viable eggs frequent
fertilizations are necessary.
On 11 July we captured eleven females with a spermatophore. These
females must have been fertilized by newly emerged males. From our
sampling we know that first males emerged about 1 July. Hence, within
about ten days after emerging males are capable of producing a sper-
matophore. (The increase of the number of reproducing males is possi-
bly also indicated by the - not significant - temporary increase of
fertilized females between week 26-31 in Fig. IV-3.)
Moreover, among the egg-laying females there were also young females
that had emerged about 1 July, i.e. females are also able to start
reproduction within about 10 days after emerging.

3.B. *The recruitment*

The development from egg to teneral (recently emerged beetles) takes
several weeks and can be divided into several stages, each with its
own survival rate, time of development and variation. We were not
able to collect data about larval development under water or about
pupation. But from the egg production and the number of beetles that
have emerged weekly, some estimates can be made about survival rates
during development.
First, the proportion of tenerals in the total population, and the
time required for development from egg to adult will be considered.
Then we will be in a position to estimate the numbers of emerging
beetles per week. From these analyses it is possible to estimate both
the development rate during the whole season, the recruitment per
generation, per female and per oviposition, and the survival rate
from egg until emergence.

B.1. The proportion of tenerals in the samples

B.1.1. Recently emerged beetles (tenerals) are easy to recognize by
their very soft cuticula. The process of hardening takes about ten or
more days; tenerals in a sample can be considered as not older than
about one week. By measuring the proportion of tenerals in the sam-
ples the weekly emergence of new beetles can be followed. Emergence
begins in all years in the 25th week (about 20 June), reaching a
maximum in week 27 (first week of July). The different times at which
egg production begins from year to year have little influence on the
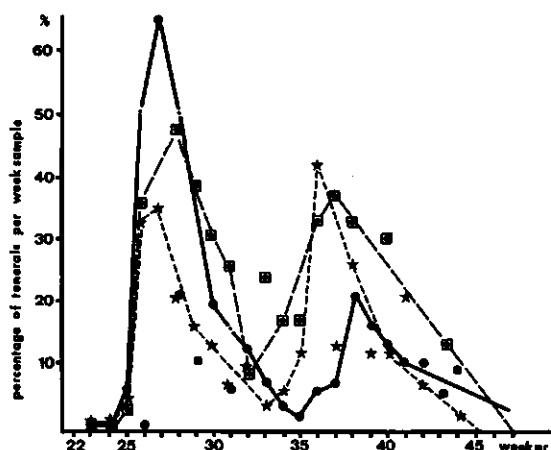
Fig. IV-4. Percentage of tenerals per week sample. week sample = all samples from different populations in one week together

■ : samples 1974
★ : samples 1976
● : samples 1977

first date that tenerals start emerging (Fig IV-4). Females and males emerge in equal percentages. Until about week 33 (mid-August) the proportion of emerged tenerals decreases, and then increases again due to the emergence of the autumn generation. A second maximum is reached in weeks 36 - 38 (early September). Emergence then decreases again until it is terminated by hibernation at the end of October (about week 43). No tenerals are found at the begining of the next spring. The time of emergence of the summer generation is more stable from year to year then that of the autumn generation (Fig IV-4).

B.2. The rate of development from egg to teneral

B.2.1. In order to relate the number of tenerals emerged in a given period to the number of parent-females in a previous period of egg laying, the time required for development from egg to teneral must be known.

B.2.2. Each year the first eggs are laid in weeks 15 - 17 and the first tenerals in great numbers are captured in week 26. The time required for development is thus nine to eleven weeks. However, in summer development is more rapid. Egg production of the summer generation starts at about week 28 and the first tenerals are found in week 33 - 35 (Fig IV-4), that is, development is completed in five to seven weeks.

B.2.3. It is well known that the time required for the development of insects depends on temperature. Blunck (1914, 1924), studying the rate of development of eggs and larvae of *Dytiscus marginalis L.* (a waterbeetle living in the same waters as *Gyrinus marinus*), found that the hatching of eggs and the growth of larvae takes much more time when the temperature is below 15° C than when it is higher than this. The rate of development does not change with variation in temperature above 15° C. Van Dijk (1979b) found threshold temperatures of about 10° C for egg-laying of the carabid beetle *Pterostichus versicolor Sturm*, and a strong delay in hatching and the growth of larvae at low temperatures (van Dijk, pers. comm.). Ringelberg (1976) described the temperature during the year for different Dutch pools. As the pools in our study area are not deeper than 1 to 2 meters we may assume from Ringelberg's data that water temperatures at the bottom (where *Gyrinus* larvae live) exceed 15° C by the middle of May and are below 15° C again by the beginning of October.

B.2.4. If the temperature regime for *Gyrinus* development is comparable with that of *Dytiscus*, the hatching of eggs laid in April and at the beginning of May would be retarded for several weeks whereas in summer eggs would hatch within one week. First instar larvae would have a low rate of development until the temperature rises above the threshold value. If the threshold temperature is exceeded about mid-May, the time required for development in springtime would be about 5 or 6 weeks, like in summer. As a consequence of retarded hatching and of the different rates of development, both the tenerals from eggs laid in April and those from eggs in May should emerge from the end of June through the first half of July (weeks 26 - 29). Egg production ends at week 35 (last week of August) and the number of tenerals decreases after about week 40 (when water temperature is below 15°C).

B.3. The number of emerging tenerals

B.3.1. The number of emerged tenerals per week (Y_i) can be estimated from the percentage of tenerals per sample (z_i) when the total number of beetles (A_i is known. However, direct estimates of the total numbers of beetles are not reliable enough to give reliable values for Y_i. The total number of beetles and the number of emerged beetles per week are estimated by an iterative method, in combination with weekly estimates of the survival chance and of the population size by capture-recapture methods (Chapter V, van der Eijk, in prep.). The results are estimated for 1000 beetles in week 14 at the beginning of the season.

B.3.2. Recruitment is usually estimated per generation as the mean number of tenerals per female, by dividing the total number of tenerals by the total number of females. This may be valid for reproduction in spring, although mortality is ignored: when the last tenerals

Table 5. Mean values (and variation coefficients) of the recruitment per generation, per female and per oviposition starting from 1000 individuals in week 14 (start April). n = number of populations; m = mean number of eggs laid per oviposition; fn = number of females oviposited at least once in a month; Sf = number of week-ovipositions per month; Sy = number of tenerals emerged each month; Sy/Sf = mean number of tenerals per week-oviposition; Sy/nf = mean number of tenerals per female; (Sy/Sf)/m = proportion of tenerals per week and eggs per oviposition.

a. Sy

	n	April	May	June	July	August
1974	4	896 (0.56)	2780 (0.54)	2022 (0.52)	2604 (0.46)	8582 (0.57)
1976	5	432 (0.24)	1222 (0.22)	959 (0.20)	1754 (0.36)	1675 (0.48)
1977	5	1221 (0.64)	3484 (0.64)	2760 (0.64)	1923 (0.72)	2501 (0.76)
mean		850 (0.47)	2495 (0.46)	1914 (0.47)	2093 (0.23)	4252 (0.89)

b. Sy/Sf

	n	April	May	June	July	August
1974	4	1.27 (0.90)	1.97 (0.86)	1.97 (0.80)	1.66 (0.86)	1.76 (0.75)
1976	5	0.54 (0.64)	0.86 (0.63)	0.84 (0.62)	1.72 (0.65)	2.00 (0.95)
1977	5	1.80 (0.78)	2.91 (0.77)	2.88 (0.77)	0.92 (0.65)	1.00 (0.84)
mean ‡		1.20 (0.53)	1.91 (0.54)	1.90 (0.54)	1.43 (0.31)	1.59 (0.33)

c. $\frac{Sy/Sf}{m}$

	n	April	May	June	July	August
1974	4	0.08 (0.55)	0.08 (0.55)	0.08 (0.55)	0.08 (0.36)	0.08 (0.36)
1976	5	0.07 (0.27)	0.07 (0.27)	0.07 (0.27)	0.04 (0.25)	0.04 (0.25)
1977	5	0.10 (0.66)	0.10 (0.66)	0.10 (0.66)	0.04 (0.43)	0.04 (0.43)
mean		0.08 (0.18)	0.08 (0.18)	0.08 (0.18)	0.05 (0.43)	0.05 (0.43)

d. Sy/nf

	n	April	May	June	July	August
1974	4	3.25 (0.90)	8.47 (0.86)	8.00 (0.81)	3.14 (0.83)	4.82 (0.90)
1976	5	1.53 (0.64)	3.67 (0.63)	3.40 (0.62)	3.14 (0.67)	3.81 (1.07)
1977	5	5.11 (0.78)	12.42 (0.77)	11.78 (0.77)	1.39 (0.64)	1.90 (0.84)
mean ‡		3.30 (0.54)	8.19 (0.54)	7.73 (0.54)	2.56 (0.40)	3.51 (0.42)

‡ average values calculated from year means

are emerging many of the first ones are already dead. Information about possible differences in reproduction succes in different months is also lost. But for reproduction in summer the total number of tenerals cannot be related to the total number of females, because the number of reproducing females during summer increases by newly emerged tenerals. It therefore seems better to relate recruitment and the number of reproducing females seperately for each month for both generations, since the same procedure must be followed to permit comparison between the generations.

B.3.3. Because of the changing development rates it is not possible to relate the number of reproducing females in one period (week or month) directly to the number of beetles emerging after a given number of weeks. We may assume, however, that there is a relation between the number of eggs laid in a given month and the number of tenerals that originates from that month of egg-laying. On this assumption, the number of tenerals of one generation per month of egg production is proportional to the number of eggs laid in the corresponding month. The number of eggs laid in a month depends on the number of eggs per oviposition (m, cf. Table IV-1) and on the number of females (F_i) that oviposit each week in the relevant month, i.e. it depends on the sum (Sf) of that number of females: $Sf = \Sigma(F_i)$. A measure for the number of eggs laid in a month is found by $Se = m{\times}Sf$. The total number of eggs laid per generation (SSe) is found by adding the Se-values of the months: $SSe = \Sigma(Se)$. The total number of tenerals per generation is found by $Y = \Sigma(Y_i)$. The number of tenerals per month is estimated then as $Sy = Y{\times}(Se/SSe)$.

B.4. Recruitment per oviposition, per female and per generation

B.4.1. On the average half (47 %) of the recruitment of the spring generation originates from egg production in May, about 37 per cent from that in June and only 16 per cent can be attributed to egg production in April. Egg production in July accounts for 35 per cent of the recruitment in the autumn generation; 65 % derives from egg production in August. (All differences appear signigicant with Wilcoxon tests on n=14 populations, P<0.025; Table IV-5a.)

B.4.2. Recruitment of different populations, of different generations, or in different years can be compared at three levels: in relation to the numbers of females, of ovipositions, or of eggs.
The monthly sum (Sf) of the numbers of egg-laying females per week is a measure for the mean number of week-ovipositions in that month. Sy/Sf then gives the mean number of tenerals that result from one week of egg laying of a female (Table IV-5b). Because the monthly Sy-values are estimated proportionally with the mean monthly egg production, the proportion of the Sy/Sf values for the different months within the same generation mainly varies due to variation in survival and is hardly affected by variation in reproduction. Variation coefficients for the different months within the spring generation there-

fore show little variation (cf. Table IV-5b). In summer the variable influx of newly emerged females also has an effect on the variation of Sy/Sf.
On the average the egg production of a female during one week results in spring in 1.8, and in summer in 1.5 tenerals (i.e. per oviposition in case of one single oviposition per female per week). Differences between months are not significant (H-test, df=4, H=4.3, P>0.30).
If X is the number of ovipositions per female in one week (X=1 or X>1, see A.2.), then an average estimate of survival during the development from egg te teneral (i.e. of reproduction success can be found by relating Sy/Sf to the number of eggs laid per oviposition (m). A reproductive success of 0.08/X for the spring and of 0.05/X for the summer generation is thus found (Table IV-5c), i.e. at best (if X=1, one oviposition /female/week) one of every 12.5 eggs in spring and one of every 20 eggs in summer develops into a teneral.

B.4.3. The number of females that oviposites in a month fluctuates depending on survival and in summer also on the influx of new females. Therefore, when recruitment is related to the number of egg-laying females in a given month, it must be related to the number of females that has oviposited at least once in the month concerned (nf, see B.3.1). The average estimated Sy/nf-values are given in Table IV-5d. In April, in July and in August on the average 3 tenerals emerge from the total monthly egg production per female; in May and June this is 8 tenerals per female (Wilcoxon test: significant difference between May or June and one of the other months, n=14, T=4, P<0.01).
Although recruitment from spring- and from summer generation are about equal per oviposition, females reproducing in May and June produce more tenerals per month than females of the summer generation. This is due to the higher number of weeks during which a female will lay eggs in May and June than in summer (on the average 4.16 and 1.91 weeks respectively) as well as to the lower proportion of eggs that will develop into a teneral in summer than in spring.

B.4.4. There are significant differences between the years in regard to the recruitment of the summer generation (both tenerals per oviposition and tenerals per female), but not of the spring generation (Anovar: df_1 = 3, df_2 = 11; spring: F = 2.58, P>0.10; summer: F=6.93, P< 0.05).
No relation is found between the recruitment (either per female, per oviposition or per generation) of the spring generation and that of the summer generation (n=14, r=0.12, P>0.05), i.e. the recruitments of each reproducing generation in a year apparently varies independently of the other.

4. DISCUSSION

1. Variation in egg production

1.1 After egg production has reached its maximum in mid-May it de-
creases again in June both in terms of the number of eggs laid per
oviposition and in terms of the proportion of females that ovipo-
sites. This decrease continues during the reproduction of the summer
generation in July and August.

1.2. There are some indications that this decreasing reproductive
effort is due to some factor connected with the beetles themselves,
apart from possible external factors such as food shortage. A prob-
able negative relation was found between the number of eggs laid per
oviposition and the increasing age of the female (cf. 3.A.2). The
reproduction of young females, that are just starting, is also low.
Furthermore egg-production appeares dependent on the frequency of
fertilization. As the frequency with which a spermatophore is depo-
sited decreases from May to August, it may be that a decrease in the
frequency of copulations causes the decrease in egg-production.

1.3. An Anovar-test on the sequences of ovipositions of individual
females indicates that most variation in egg production is due to
variation in time per female, i.e. to the temporary circumstances of
life of each female (luck in getting food, males or shelter, influen-
ces of weather and water quality, etc.).

1.4. Another indication of the importance of the life histories of
individual females may be that the standard deviations of egg produc-
tion per oviposition do not decrease when the mean number of eggs
laid decreases (Table 1). If we suppose that the upper limit of the
number of eggs laid per oviposition depends on the number of ova-
rioles of a female, then, when the mean number of eggs laid per
oviposition decreases, due to accidental factors, the upper limit
will not change, leading to an unchanged standard deviation. The
variation in egg production between populations and between genera-
tions is smaller than between the females in a population (coeffi-
cient of variation v.c.=0.17 and v.c.=0.14 versus v.c.=0.39). If some
external factor, like food supply, quality of food and temperature
were important for variation in egg production per population, a
greater variation in time and place should be expected than was
actually found. Apparently, the different habitats are rather similar
concerning these kinds of features. But, although great numbers of
insects may be drowned daily at the water surface (Norlin 1964, 1967)
- potential food for whirligig beetles - great differences between
individuals may occur in the quantity and quality of the food taken.
Some studies support the hypothesis that predators (at least insects)
may struggle with food-shortage in spite of plenty of preys being
available (van Dijk 1986, White 1978, Dempster and Pollard 1981).
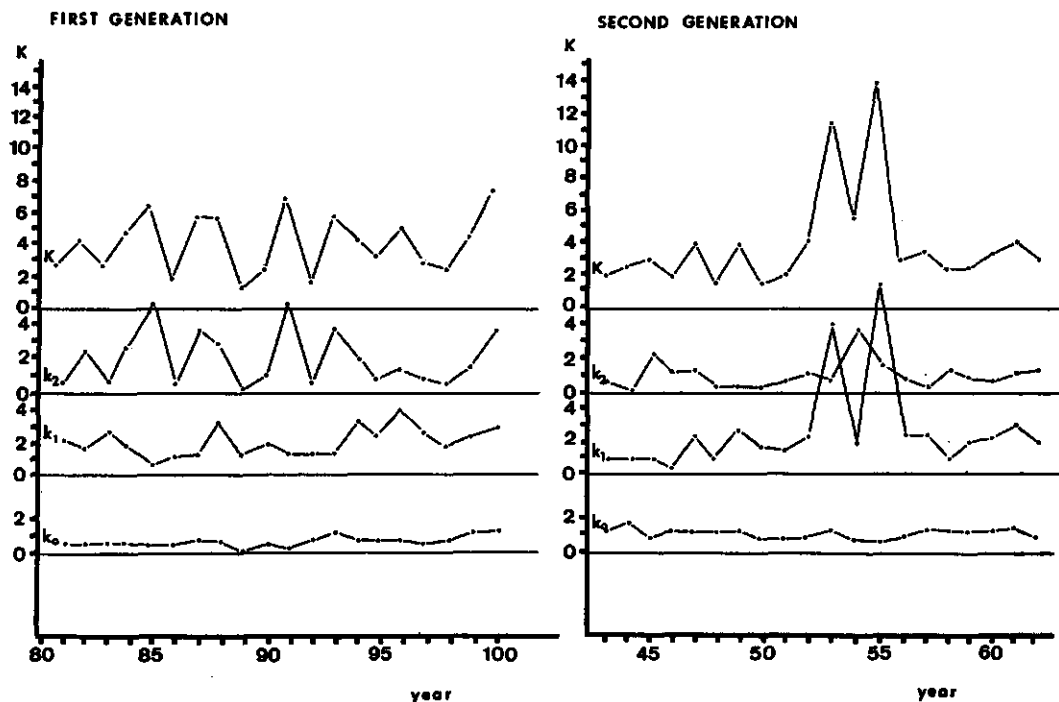
Fig. IV-5. Key-factor analysis of a simulated reproduction process over 100 generations. The picture shows as an example the output of k-values during 20 years from both reproducing generations separately.

k_0 = egg production
k_1 = viability of eggs
k_2 = larval + pupal development

SCHEME OF THE MODEL

STAGE	MEAN VALUES (VAR.COEF.)			MEAN K-VALUES	(VAR.COEF.)	REGR. COEF.	
	FIRST GEN.	SECOND GEN.					
FEMALES (optimal eggprod./oviposition)	38	32					
egg production			k_0	0.59 (0.56)	0.73 (0.50)	0.04	0.01
EGGS LAID (mean egg-number per oviposition)	32 (0.14)	25 (0.14)					
viability of eggs			k_1	1.89 (0.74)	1.89 (0.77)	0.30	0.64
FIRST LARVAL INSTAR (part of eggs hatched)	0.55 (0.34)	0.55 (0.34)					
larval and pupal development			k_2	1.69 (1.18)	1.34 (1.24)	0.66	0.35
TENERALS (number of tenerals emerged)	1.8 (0.54)	1.5 (0.32)					
			K	4.17 (0.59)	3.95 (0.56)		

2. Variation in recruitment

2.1. Variation between estimates can be due both to the process studied and to errors of estimation. Egg production was measured directly from ovipositions, but recruitment was estimated indirectly from other estimates like survival chance, number of females, number of ovipositions, etc. The values given for variation in recruitment are therefore less reliable than those concerning egg production.

2.2. Each of the developmental stages from egg to emerged tenerals has its own variation. The importance of each stage for the variation in final recruitment can be analysed in a manner analogous to the key-factor analysis of Varley and Gradwell (Varley and Gradwell 1960, Southwood 1978). The first stage is that of egg-development and oviposition (k_0). A maximum potential natality of about 38 eggs per oviposition was found in spring and of about 32 eggs per oviposition in summer. On the average 32 eggs are laid per oviposition in spring and 25 in summer (cf. Table IV-1, variation coefficient between populations: $v.c._1 = 0.14$). About 55 per cent of the eggs hatch, with a variation coefficient of $v.c = 0.34$ (k_1). No estimates are available for the larval and pupal stages, but it was estimated that 1.8 tenerals emerge from the egg-production in one week in spring $(v.c. = 0.54)$ and 1.5 in summer $(v.c = 0.32)$ (k_2).

2.3. A simple stochastic simulation model was constructed to trace the influence of the variation in survival in each stage upon ultimate recruitment. In this model the stages concerned are described by normal frequency distributions defined by the estimated mean and standard deviation of their survival rates. For each generation values for the survival rates of the concerned stages are drawn at random from their normal distributions. The model was run for 100 spring generations and for 100 summer generations separately (Fig IV-5).   There is no single distinct key-factor. Variation in egg production does not play any part. A regression analysis on the k-values (cf. Podoler and Rogers 1975) confirms the impression from Fig IV-5 that variation in k_2 (i.e. in larval and pupal development) contributes most to the changes in K in spring and variation in k_1 (viability of eggs) does so in summer.

3. Variation in egg production and in recruitment compared

3.1. We have suggested that egg production is possibly more dependent on the capacities and vicissitudes of individual females than on conditions at the population and/or habitat level. Variation in egg production between populations is small; all our field data can be considered as samples from one statistical population.

3.2. In contrast, recruitment appeares to be significantly dependent on conditions at population or habitat level. If density-dependent processes do occur, they probably work during the development between

oviposition and the emergence of tenerals more than during egg pro-
duction and egg laying. The same is suggested by Heessen and Brun-
sting (1981) for carabid beetles, and by Istock (1966) for *Dineutus*
beetles (American gyrinids). The absence of any correlation between
the recruitments of the spring and summer generations gives no indi-
cation of any density-dependent process that influences the amount of
recruitment.

4. Influence of the time required for development

4.1. Reproduction is generally seen as a numerical process in which a
given number of females lays a given number of eggs, which provides a
given number of young adults as recruitment. In theoretical analysis,
especially in computer simulation models, the role of the time taken
for development from egg to adult is often disregarded. But when
population dynamics are described in separate processes for reproduc-
tion, survival and dispersal, taking account of the time occupied by
each process, it becomes clear that time can be an essential parame-
ter. For example, the longer the development of the larvae, the later
the number of reproducing females in the second generation will
increase, the smaller the number of tenerals that emerge in autumn,
and so the smaller the number of adults that hibernate. The total
recruitment in a whole year will decrease with 65 to 80 per cent if
the time required for development is increased only two weeks, res-
pectively from 6 to 8 and from 8 to 10 weeks. Furthermore, survival
during development is probably lower when development takes more
time.
Given that hibernation begins at the end of October, the end of the
period of reproduction and the time required for development are
about optimal.

4.2. A maximum in emergence occurs shortly before hibernation, provi-
ding a large number of beetles to enter hibernation. Egg production
in September would be too late for larval and pupal development to be
completed before winter. A shorter developmental period (which is
probably not possible anyway) would lead to too early emergence and
thus to a smaller number of beetles in hibernation.

5. Influence of the frequency of fertilization

5.1. When fertilization fails for several weeks, egg production de-
creases and most of the eggs laid are not viable. Apart from its
influence within the population, the frequency of fertilization may
also have important consequences for the egg production of females
that emigrate by flight. Dispersal by flight occurs in low numbers,
also during the reproduction period, but more by males than by fe-
males (Chapter VI). Since the influence of a single fertilization
ceases after about two weeks, it may be functional that males show a
greater flight activity than females; especially in newly founded

populations, females must be soon accompanied by males.

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CHAPTER V. SURVIVAL OF ADULTS

SUMMARY. Survival chances have been estimated for populations of the waterbeetle *Gyrinus marinus Gyll.* from capture-recapture sequences in 1974 - 1978. The average weekly survival chance is estimated as about 0.9247 in spring, decreasing to 0.7701 in autumn; males survive longer than females. Survival shows little variation in time or space (variation coefficient v.c.< 0.1). Survival chance possibly decreases with age. Freshly emerged tenerals apparently have a lower survival chance than older beetles. The survival chance from hibernation (October - April) is about 0.33, with a greater variation between years (coefficient of variation v.c.= 0.7) than between populations (v.c.= 0.4).

1. INTRODUCTION

1.1. Loss of individuals in a population can be due to mortality or emigration. Losses by flight from *Gyrinus marinus* populations are small (chapter VI). The study of *Gyrinus* populations in isolated pools therefore gives estimates of real survival rates, while the study of open populations affords estimates of 'survival' rates that are the result both of mortality and of emigration by swimming. A comparison of open and closed populations thus permits an estimate of population loss due to emigration.

1.2. The survival chance of individuals may be dependent on their age. Recently emerged tenerals have only small food reserves (small fat bodies) and empty stomachs. This may entail a lower survival chance for tenerals than for older beetles. Succeeding in finding food shortly after emerging may be essential to survival in the first weeks after emerging.

1.3. Survival chance may decrease as a beetle gets older. In spring all beetles are of about the same age (having emerged the previous autumn) and if survival depends on age than the average survival chance for the population as a whole will decrease during spring. In summer, however, the population is composed of beetles of different ages, since new beetles emerge every week. The average survival chance for the population as a whole should therefore be rather constant in summer. The same will be the case if survival depends mainly on predation or food supply.

2. METHODS

2.1. This study has been carried out since 1974 in an area of pools and brooks in the Northern part of the Netherlands (Fig. III-3, pag

36). Some pools are closed, others are connected with each other by ditches.
The population size in the closed pools is mainly affected by death and recruitment; in the open pools it is also influenced by immigration and emigration. Real survival chance - due to the death of individuals - can therefore only be estimated in the closed pools. Throughout this paper closed and open populations are considered separately.

2.2. During daytime *Gyrinus* (whirligig) beetles live in groups on the surface of the water along particular parts of the banks of a pool, where they are easy to see and to catch. After sunset the beetles swarm around for several hours.
Three generations are present: in spring the generation of the hibernated beetles reproduces, in summer (July, August) there is a reproducing summer generation and in autumn (September, October) the hibernating generation emerges. (For more features of the natural history of *Gyrinus marinus* see Chapter IV).

2.3. The beetles were marked individually by means of pin-pricks (see Chapter VI for more details). The beetles have to be caught, carried to the laboratory and the marks have to be read off with a binocular. When some hundred beetles are caught in a single sample it takes one to three days before they can be released again. In general, a population can thus be sampled at intervals of about 10 days.

2.4. When frequent recaptures of marked individuals are available several methods can be used to estimate the survival chance and/or population size during the period of sampling. In some methods survival chance is assumed to be constant (Lack 1943, Fisher and Ford 1947, Bailey 1951). The identical methods of Jolly (1965) and Seber (1965) only assume equal capture chances of all individuals throughout the sample period. For the method of Manly and Parr (1968) it is sufficient when individuals have an equal capture chance per sample. Because of the rather high capture chances (see below) we are able to use a method which is based on estimating the average period that a beetle has been present in the population (TS method). This mean time of presence corresponds with a mean survival chance per individual of 0.5 over that period. This is the most direct method of estimation and also the most detailed, because the survival chances are given per date of release. A disadvantage is that the method gives a minimum estimate since an individual will usually survive for some time after the last recapture. This method gives more reliable - for higher - estimates of the survival chance than the methods of Jolly, of Fisher and Ford or of Manly and Parr (Van der Eijk, in prep., Appendix B).

3. RESULTS

3.1. The reliability of the samples

3.1.1. The reliability of the estimates of survival depends on the reliability of the samples and the recapture chance per individual. The chance (estimated according to Manly and Parr 1968) that a beetle was captured in a sample varied between 0.2 in open and large pools and more than 0.4 in small closed pools and in ditches. Males have a greater capture chance than females (Wilcoxon test: n=90, z=2.41, P<0.02).

3.1.2. In small, closed pools and ditches the average chance of recapture of marked beetles is more than 0.7. In some cases beetles are recaptured on the average more than once. In most other situations 10 - 30 % of the beetles is recaptured. There is no significant difference in this recapture chance between males and females (Wilcoxon test: n=18, T=62, P>0.05).

3.2. Survival chances of males and females in open and isolated populations

3.2.1. The survival chances of males and females can be compared per population and for each generation with the Wilcoxon matched pair signed-rank test (Table V-1). The average survival chance per week varies in isolated populations between 0.9247 for males in spring and 0.7701 for females in autumn; on the average 8 of each 100 male beetles is lost per week in spring and about 23 female beetles per week in autumn. This corresponds to a monthly survival chance of 0.7123 in spring and of 0.3224 in autumn. Except in the spring, the survival chance of males and females does not differ in open populations. But in isolated populations males have a better survival per generation than females. The Friedman test indicates that the survival chance in isolated populations decreases from the spring generation to the autumn generation. However, the Wilcoxon and Wilcox test (providing multiple comparisons of samples, cf. Sachs 1982) shows that in general there are no significant differences between the spring and the summer generations. In open populations a significant decrease in survival is found only for males. The lower survival chances in autumn may be due to a lower capture chance as hibernation approaches.

3.2.2. Note the low variation coefficients v.c. (=st.dev/mean), which in most cases are far below 0.1. The different habitats show hardly any overall differences in the conditions that determine survival chance. The same low v.c.-values are found when the survival chances of the same population in different years are compared: mean v.c. = 0.02 - 0.08 (for sexes, generations and open or isolated populations seperately). No differences appear between the variation coefficients of open and of isolated populations.

Table V-1. Survival chances of males and females in isolated and
open populations, estimated with the TS method.
Survival chances of males and females are compared with
the Wilcoxon test, that from generations/population with
the Friedman test, that of open and isolated populations
with the Mann-Whitney U-test.
The Friedman-test is used on k=3 and n=6 or 7, see table,
giving test statistic Xr(cf SACHS 1983, p 550)
N = number of populations, Q = survival chance per week,
v.c. = variation coefficient, P = 2-tailed level of signi-
ficance of R (= parameter in Wilcoxon-test), Z = parameter
in normal distribution (Z = 1.96 -> P = 0.05; Z = 3.10 ->
P = 0.002)

		ISOLATED POPULATIONS (I)				WILCOXON	
		MALES		FEMALES		TEST	
	N	Q	v.c.	Q	v.c.	R	P
TOTAL PERIOD	16	0.9247	(0.017)	0.9216	(0.028)	58	>0.05
SPRING	12	0.9076	(0.035)	0.8912	(0.045)	5	(0.02
SUMMER	15	0.8780	(0.048)	0.8613	(0.057)	20	(0.025
AUTUMN	7	0.7836	(0.094)	0.7701	(0.072)	(13	>0.05)

	N	Xr^2		N	Xr^2
FRIEDMAN TEST	7	14.00		7	12.29
BETWEEN GEN.		P<0.001			P<0.001

		OPEN POPULATIONS (0)				WILCOXON		U-TEST OPEN - ISOLATED POP.	
		MALES		FEMALES		TEST		males	females
	N	Q	v.c.	Q	v.c.	R	P	Z	Z
TOTAL PERIOD	13	0.9002	(0.042)	0.8923	(0.030)	30	>0.05	4.28	3.95
SPRING	10	0.8894	(0.062)	0.8508	(0.055)	2	(0.002	0.75	1.94
SUMMER	9	0.8687	(0.041)	0.8539	(0.074)	22	>0.05	4.90	3.09
AUTUMN	5	0.7801	(0.069)	0.7937	(0.050)	(5	>0.05)	2.81	(1.03)

	N	Xr^2		N	Xr^2
FRIEDMAN TEST	7	12.29		6	6.33
BETWEEN GEN.		P<0.001			0.10>P>0.05

3.2.3. As could be expected, in most cases the survival in isolated
populations is significantly greater than that in open populations,
with the exception of males in the spring (Mann-Whitney U-test Table
V-1). The difference between the survival chance in open and in
isolated populations gives some indication of the rate of loss in
open populations due to swim-emigration (Table V-2). This emigration
is highest in spring (16 resp. 27 % of the loss due to emigration),
but decreases to 5 - 7 % in summer, and is very small in autumn (0 -

1.6 %). Swim-emigration will be treated more extensively in Chapter VII.

Table V-2. Number of beetles per 1000 lost per week in open and in isolated populations, and the fraction of beetles lost in open populations by emigration, estimated from the mean values of Table V-1.

O = number per 1000 beetles lost in open populations
I = number per 1000 beetles lost in isolated populations
E = number per 1000 beetles lost in open populations due to emigration
%E = percentage of loss in open populations due to emigration

	MALES				FEMALES			
PERIOD	O	I	E	%E	O	I	E	%E
TOTAL PERIOD	99.8	- 75.2	= 24.5	24.5	107.7	- 78.4	= 29.3	27.2
SPRING	110.6	92.4	18.2	16.5	149.2	108.8	40.4	27.1
SUMMER	131.3	122.0	9.3	7.1	146.1	138.7	7.4	5.1
AUTUMN	219.9	216.4	3.5	1.6	206.3	229.9	-	-

3.3. Survival chance in relation to age

3.3.1. The supposition that freshly emerged tenerals should have a lower survival chance than older beetles is tested in four popula- tions by comparing the frequency of recapturing of tenerals released with a very soft elytra (probably younger than 1 week) with that of beetles with harder elytra at release (Table V-3). If the recaptures are tested per release date per pool a signigicant difference was found for males but not for females (U-test on sample data: n_1 = 17, n_2 = 51; males: U = 315.5, z = 1.72, P<0.05; females: U = 410.5, z = 0.33, P>0.05). However, if testing the total results the beetles ap- peared to be better recaptured as they were growing older (X^2 -test: males X^2 = 92.97, P<0.001; females: X^2 = 30.30, P<0.001). The fact that these results are not, of barely, significant may indicate that the assumed lower survival chance for tenerals only applies to the first days after emerging and that by the time of first capture most young tenerals had already found some food.

3.3.2. All beetles present in the spring did emerged the previous autumn, and thus grew older together. If their survival chance is age-dependent the time spent (TS) in the population will decrease with age until week 25 (third week of June = last week before the tenerals of the next generation will appear) the age-composition of the population is rather homogeneous. We have seen (Table V-1) that a
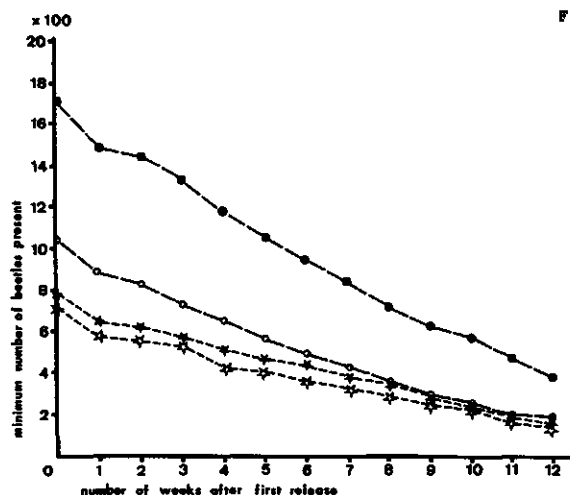
Fig. V-1. Course over 12 weeks of the number of beetles at least present per week in isolated populations.
Beetles released in spring (1974 - 1977).

For example of the total number of males (P_0 = 1726) released at different dates in spring 1974 - 1977 at least 1495 (P_1) are still present after 1 week, 1448 (P_2) after 2 weeks, etc.

● = males released in spring

★ = females released in spring

○ = males released in summer

☆ = females released in summer

Table V-3. The mean percentage of beetles recaptured in relation to the hardness of the elytra when released.
r = total number released
c = total number recaptured
%c = percentage recaptured: (c/r * 100%)

HARDNESS	VERY SOFT			SOFT			RATHER SOFT			RATHER HARD/HARD		
POPULATION	r	c	%c	r	c	%c	r	c	%c	r	c	%c
MALES												
Ks-74	20	13	65.0	24	15	62.5	26	14	53.9	91	53	58.2
Ks-76	9	4	44.4	10	7	70.0	7	6	85.7	47	33	70.2
Sn-74	172	31	18.0	99	17	17.2	101	18	17.8	431	66	15.3
Zp-76	77	32	41.6	46	25	54.4	34	18	52.9	350	160	45.7
TOTAL	278	80	28.8	179	64	35.8	169	56	33.3	519	312	60.1
FEMALES												
Ks-74	14	8	57.1	27	12	44.4	24	13	54.2	44	19	43.2
Ks-74	13	5	38.5	10	5	50.0	10	7	70.0	39	27	69.3
Sn-74	184	19	10.3	102	9	8.8	80	14	17.5	136	16	11.8
Zp-76	62	21	33.9	34	11	32.4	30	10	33.3	279	119	42.7
TOTAL	273	53	19.4	173	37	21.4	144	44	30.6	498	181	36.4

decrease in survival rate occurs from April to June, which seems to indicate an age-dependent survival chance, but the decrease continues in summer and autumn, indicating that there is probably some relation with the time of year. We therefore analyse changes in the rate of survival during a period of 12 weeks after release, irrespective of the date of release. All records of such 12-week periods from isolated populations are used in a cumulative frequency distribution of the times spent in the population (see Fig V-1). A period of 12 weeks is chosen because this approximately coincides with a single generation and gives an optimal combination of the period and the number of records. The survival chance can be expressed as (a) the survival chance from week $w-1$ to week w (e.g. for males in spring, for $w=3 \rightarrow 4$, Q_4 = 1164/1326 = 0.8778), or (b) a mean survival chance per week from the period $w = 0 - t$: $Q = Q_t^{(1/t)}$ (e.g. for males in spring Q_4 = $(1164/1726)^{(1/4)}$ = $0.6744^{(1/4)}$ = 0.9062). Spearman tests on the decrease of the weekly Q-values of both males and females from 1 to 12 weeks after the first release in spring do not give significant r-values, i.e. survival chances in spring do not decrease significantly with age. In summer no decrease in survival chance is found with the increasing number of weeks after release (Table V-4).

Table V-4. Course of survival chances of males and females until 12 weeks after release (cf. Fig. V-1).
$Qw-(w-1)$: survival chance from week $w-1$ to week w
$Qmean$: mean survival chance per week from week 0 to week w (Q_{mean} = $(P_w/P_o)^{(1/w)}$.
P_w : number of beetles in week w
Spearman : $r > 0.587 \rightarrow P < 0.05$

NUMBER OF WEEKS AFTER RELEASE	$Q_{w-(w-1)}$				Q_{mean}			
	SPRING		SUMMER/AUTUMN		SPRING		SUMMER/AUTUMN	
	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES	FEMALE
1	0.8662	0.8191	0.8239	0.7953	0.8662	0.8191	0.8239	0.7953
2	0.9686	0.9658	0.9717	0.9655	0.9159	0.8894	0.8947	0.8763
3	0.9157	0.9275	0.8673	0.9177	0.9159	0.9020	0.8855	0.8999
4	0.8778	0.9010	0.8805	0.8285	0.9062	0.9017	0.8843	0.8741
5	0.9107	0.8882	0.8796	0.9459	0.9071	0.8990	0.8833	0.8880
6	0.9009	0.9458	0.8666	0.8955	0.9061	0.9066	0.8805	0.8893
7	0.8733	0.8578	0.8660	0.9139	0.9013	0.8995	0.8784	0.8927
8	0.8525	0.9171	0.8176	0.8632	0.8951	0.9017	0.8706	0.8890
9	0.8678	0.8076	0.8418	0.8451	0.8920	0.8907	0.8673	0.8840
10	0.9173	0.8159	0.8456	0.9167	0.8945	0.8829	0.8651	0.8872
11	0.8410	0.8717	0.7897	0.6909	0.8895	0.8819	0.8580	0.8673
12	0.7857	0.7970	0.9246	0.9211	0.8803	0.8745	0.8633	0.8716
SPEARMAN TEST r	-0.5105	-0.5804	0.0315	-0.1049	-0.5219	-0.2452	-0.5315	-0.0629

Table V-5. Survival chance during hibernation.

Winter	Population	Percentage that survived hibernation				
		males	females	mean	st.dev.	v.c.
1965/1976	Ks	14.3	20.3	17.3	4.3	0.25
	Sn	10.0	15.4	12.7	3.8	0.30
	mean	12.2	17.8	15.1	4.4	0.29
1976/1977	S1	23.8	20.7	22.3	2.2	0.10
1981/1982	Mp	44.6	31.6	38.1	9.2	0.24
	Wh	64.7	84.4.	74.6	13.9	0.19
	mean	54.7	58.0	56.3	23.2	0.41
	mean	31.5	34.6	33.0	24.4	0.74
	st.dev.	22.9	28.5	24.4		
	v.c.	0.73	0.82	0.74		

3.4. Survival during hibernation

3.4.1. Survival during hibernation can be considered as an indepen-
dent factor in the population dynamics of this species. Beetles
hibernate under water at the bottom of a pool and between roots of
waterplants at the banks. The beginning and end of the hibernation
period depend on the weather but this runs about from end-October to
mid-April.

3.4.2. Survival during hibernation is estimated in three winters and
for five populations by means of recaptures in spring of beetles that
had been released in autumn. The number of hibernated beetles in
spring is estimated with the methods of Craig (Southwood 1978; the
method is based on the number of individuals recaptured once, twice,
etc.). By comparing this number with the number of marked beetles
released in autumn, the surviaval chance during hibernation can be
estimated (Table V-5). This method gives a mean survival chance of
0.33, but there is some indication that there is a high variation
from year to year (v.c.=0.7), and a smaller variation between popula-
tions in the same year (mean v.c.=0.4). On the average, survival
rates in winter seem to be higher than during the active season: per
month the mean survival in winter is 0.80 (per week 0.95, compare
with Table V-1). Furthermore, we may have underestimated survival in
winter, since the Craig methods suppose a survival chance $Q=1$ during
the sample period.

3.5. Causes of death

3.5.1. No systematic study has been made of predation or food supply as causes of death, but the estimates of survival rates and some available observations do give some indication of the importance of each of these factors.

3.5.2. Predation by fishes or ducks was occasionally observed, but many times we saw fishes or ducks swimming nearby or even through a group of whirligig beetles without paying any attention to them. We preformed a small experiment with two ducklings in a shallow bath. In addition to whirligig beetles, many small watersnails and larvae and pupae of mosquitoes were present. At first the ducks hunted the beetles, but as soon as they detected the other prey under water they ignored the fast-swimming beetles and ate the other animals that were much easier to catch.

3.5.3. The beetles are probably not favoured as food, as they seem to have a bad taste (Ochs 1969). This may be the reason why they usually stay in groups during the day. Apart from the lower chance per individual to be caught if one is in a group (Cushing and Jones 1968), potential predators may more easily recognize a group of beetles as unfavourable than a single beetle. Fish in an aquarium at first try to eat beetles released into the aquarium, but usually the beetles are spit out again. After some time the fish ignore the beetles. In experiments in pools with fish without experience with whirligig beetles, the beetles were eaten, but possibly also spit out most of the time. We have the impression that beetles are more frequently attacked in such experiments than in pools where they have been present for a longer time. Another indication that in natural populations predation is not very important quantitatively, is that no consistent differences were found between the populations in ditches (with few or no fishes and/or ducks) and populations in pools (with both fishes and ducks).

3.5.4. We have no data about food. However, the frequent ovipositions during the reproduction period (Chapter IV) can be an indication that in general food is not in short supply. In carabid beetles it has been shown that egg production decreases with a shortage of food (Baars and van Dijk 1984, van Dijk 1983). Death by starvation probably occurs infrequently.

3.5.5. Little is known about diseases and parasites of whirligig beetles. The population in a fishpool in our area was strongly infected by *Laboulbeniales* moulds (*Ascomycetes*). Nearly every beetle had mould fruit-bodies along its sides. But there is no indication that the survival chance of the beetles is influenced by this parasite (Scheloske 1969, Meijer 1975). In other populations beetles were rarely found with these parasites.

3.5.6. An indication of the proportion of beetles with maladjustments congenital or resulting from developmental failures may be the frequency of abnormalities of the elytra we recorded while marking the beetles. Of 15051 males from 13 different years and/or populations on the average 2.34 per cent (st.dev. 0.40) had abnormalities in shape or punctation of the elytra; among 10878 females 3.14 per cent (st.dev. 1.11) had abnormalities. The difference between males and females is significant (t-test: df=24, t=2.43, P<0.05), which may be one of the causes for the lower survival chance of females.

4. DISCUSSION

4.1. Several causes of mortality have been indicated. There seems to be no key factor for mortality such as a specific predator. The chance to survive may be lower outside a group than inside one. We have suggested that a single beetle may be less recognizable than a group as bad-tasting prey. The risk of death seems to be connected with the activities of the individual beetle itself and with generally unfavourable circumstances like cold weather over a longer period or a dusty water-surface where a beetle can get stuck by accident. There is probably a decrease in the chance of survival from spring to autumn. This should not be caused by age (cf Table V-4). The risk of death could increase during the year if there should be an increase in predation by young ducks and fishes that have no experience with whirligig beetles and still have to learn that the beetles are unfavourable prey.

4.2. A number of factors may account for the lower survival chance of females than of males. For ovipositing a female has to be under water, where the eggs are laid in rows on waterplants, and are highly visible for predators (fish) and not able to escape as quickly as on the surface. Secondly, we found a significant higher frequency of physical maladjustments among females than males. The frequency of fatal maladjustments or of abnormalities that hinder the ability to swim, for example, is possible also higher for females.

4.3. The low variation in survival chance during the season, both between different populations and between different years indicates that survival chance is either determined by many and/or rather constant environmental factors, which do not vary much over space and time, or are mainly connected with features of the beetles themselves.

4.4. The variation in winter-mortality is much greater than that in mortality during the active season. Mortality during hibernation therefore generally contributes more to the variation in population size than mortality during the rest of the year. The variation from year to year is about twice that between populations in the same year. This may indicate that winter mortality depends more on general weather conditions (severe winters) than on local conditions.

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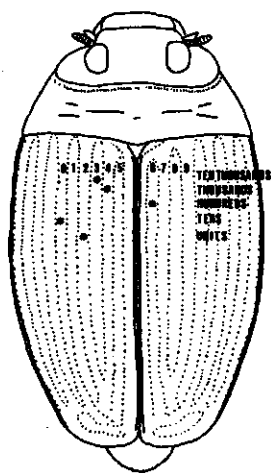
Fig. VI-1. The number code for pin prick marks
on the elytra.
Shown is number code 34602.
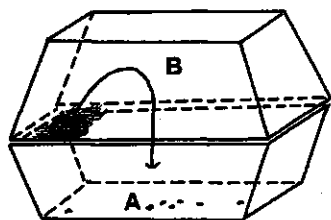
Fig. VI-2. Arrangement of cases in laboratory
experiments for flight activity.
See text for further explanation.

CHAPTER VI   DISPERSAL BY FLIGHT

SUMMARY
As part of a comprehensive study of the population dynamics of the whirligig beetle *Gyrinus marinus Gyll.* experiments were performed concerning flight activity. From capture-recapture experiments it appears that only a small percentage of the beetles move from one pond to another by flight. Flight activity only occurs if the weather is favourable, i.e. if the air temperature is more than about 17° C and the wind is feeble, and probably only if the sun is shining. In the Netherlands the opportunity to fly is therefore very limited by weather conditions. Flight activity of males and females occurs from April till the middle of October, thus including the period of reproduction. During reproduction females fly, but to a lesser extent than males. The different degree of dispersal during and after reproduction corresponds with the different degree of dispersal of mothers (and their eggs) and offspring. The hypothesis that flight occurred simply because the weather was favourable for flight cannot be rejected. The possibility of randomly occuring flight dispersal and the significance of a small dispersal activity for population dynamics is analysed in a separate paper with the help of simulations (Chapter VIII).

1. INTRODUCTION

1.1 Many studies have been published concerning dispersal, based on experimental or on field data or treating the question from a theoretical point of view, but the number of field studies that give information about the dispersal activity of insects from natural populations or about exchange between insect populations is rather small, especially if dispersal occurs by flight (Clark 1962; Macleod and Donnelly 1963; Fletcher 1974; Inoue et al. 1973; Botterweg 1978). Many studies concern the colonization of new habitats or islands, and lack field information about the populations from which the colonizing individuals originate (Diamond 1969; Haeck 1971; Meijer 1980).

1.2. In 1976 a study was begun concerning the dispersal activities of a whirligig beetle, *Gyrinus marinus Gyll* . Data were collected on reproduction, birth and death rates, and the general life history of these beetles. The study initially focused on exchange between populations by swimming. When a small number of individually-marked beetles were recaptured after flight, the study was expanded to include some experiments on flight activity in order to investigate the significance of flight for population dynamics. In this chapter the results concerning flight activity will be presented.

2 METHODS

2.0.1. Since whirligig beetles live in groups on the surface and near the edges of fresh water bodies they ar easily caught. After being marked and released, they are easily recaptured. Moreover direct observation in the field is possible without causing any disturbance. These beetles are therefore wellsuited for a study of population dynamics, in particular of dispersal. This field study was carried out in an area of about 800 x 2,300 m, with 13 large and small pools and some ditches, situated near Groningen in the northern Netherlands. Some pools were interconnected by ditches or narrow passages, others were isolated from other pools (Fig.III-3, pag 36).
The data to be discussed in this paper derive from field observations of exchanges between populations, field experiments, and laboratory experiments. The data are of four sorts:

2.1 Exchange by flight between ponds

2.1.1. Exchanges by flight between the ponds were estimated with capture-recapture techniques using marked beetles. We marked the beetles individually by means of a number code using pinpricks in the interstrial spaces on the elytra (Fig VI-1). This well-known method (Southwood 1978) does not harm the beetles and does not obstruct flight. The beetles were captured with a long net. The sample sites were noted exactly. After marking the newly captured beetles and noting the recaptures, all the animals were released again at their respective capture sites. The beetles were kept in glass tubes with moist filter paper at 4° C in a refrigerator until marked and released. We used no beetles released after August since the mean period between the last capture of an individual beetle before exchange and the first recapture after exchange was 48 days (st.dev. 32). For beetles released after August both the opportunity to fly away and the chance of being recaptured after immigration decrease, so that inclusion of such beetles would give an underestimate of amount of exchange.

2.2 Emigration by flight from a population

2.2.1. The wings of part of the population in an isolated ditch (SnS in Fig III-3, pag 36) were clipped by tearing off the wingtips with a pair of tweezers. After clipping the beetles were kept under observation for 24 hours (to avoid losses in the field caused by the clipping) and then released. All beetles in the ditch were individually marked, and we sampled and released almost every week during 1977. With the help of recaptures (average recapture chance per week = 0.7) we could follow the decreasing numbers of both groups in the population very closely. As the clip-winged beetles could not leave the population and the unclipped ones could only do so by flight, differences between the decrease rates of the two groups reflect the flight activity of unclipped beetles.

2.3 The relation between weather and flight activity

2.3.1.   The influence of temperature,   sunshine, and wind velocity on
flight   activity was studied by field experiments and by observations
of flight activity on a small shallow artificial pool.

2.3.1.   In   the   field experiments 5-10 beetles were   placed   in   dry
dishes   on meadowland between pools Bh and Br in the study area (site
x   in Fig III-3).   Flight activity of individual beetles was recorded
continuously. Each flying beetle was followed as long as possible, by
eye or with binoculars,   noting direction and altitude of flight   and
whether   the   beetle   plunged down into a pool.   After 5-10   min   the
remaining   beetles were replaced by new ones.   Temperature   near   the
dishes,   radiation   from the sky,   and wind velocity at 1 m above the
soil were measured every 5 min.

2.3.2.   An artificial pool was built on the flat roof of a shed   near
my   house.   The beetles on this pool could be observed all the   times
from my window,   while disturbance by men,   ducks,   or fishes was ex-
cluded. As the pool was very shallow (maximum depth 10 cm), the water
temperature   could   vary considerably during the day and form day   to
day, much more so than in the pools an itches in the field. A thermo-
meter was placed in the pool,   just at the surface of the water.   The
temperature could be read with binoculars from the window.

2.4. Flight activity of different types of individuals

2.4.1.   The flight activity of different individuals was compared   in
laboratory experiments. Two transparant plastic cases of 35 x 20 x 15
cm   were   placed on top of one another,   as shown in Fig VI-2   .   The
beetles were placed in dry dishes (about 40 individuals per dish)   on
a strip of gauze between the cases. Beetles which flew away fell down
into   case   A and could be collected and counted.   An experiment   was
considered   finished when for 10 min no more beetles had made   flight
attempts. Beetles that had been kept in the refrigerator were brought
up to air temperature before the experiment.

3 RESULTS

3.1 Exchange by flight between ponds in the study area

3.1.1. Exchange between pools in the study area can occur by swimming
or by flight. The latter can only be measured between pools which are
not   connected   by water,   by counting recaptures of   marked   beetles
originating from another pool. Table VI-1 gives the numbers of marked
beetles released in 1974, 1976, and 1977, and the numbers and percen-
tages of beetles recaptured elsewhere in the study area after flight.
Flight   activity   occured during the whole season but   especially   in
summer. In contrast to many other species of beetles for which flight

a) MALES

MONTH	April rel	rec	May rel	rec	June rel	rec	July rel	rec	August rel	rec	Total rel	rec	Total %rec
Pools 1974													
Sn	625	4	352	0	283	1	526	0	447	2	2,233	7	0.31
Br-complex	378	1	522	0	128	0	572	2	1,082	0	2,682	3	0.11
Zpl	33	0	10	0	-	-	-	-	-	-	43	0	0.00
Sz	203	1	231	1	48	0	262	1	226	0	970	3	0.22
Total	1,239	6	1,115	1	459	1	1,360	3	1,755	2	5,928	13	0.22
Pools 1976													
Sn	457	11	208	3	464	10	233	2	31	0	1,393	26	1.87
Br-complex	404	3	569	5	283	4	955	27	612	12	2,823	51	1.81
Zpl	322	3	43	0	11	0	98	0	295	3	769	6	0.78
Zb	-	-	-	-	-	-	100	3	16	1	116	4	3.44
Sz	61	0	74	2	46	0	166	0	190	1	537	3	0.56
Total	1,244	17	894	10	804	14	1,552	32	1,144	17	5,638	90	1.60
Pools 1977													
Sn	-	-	124	1	117	1	146	0	35	0	422	2	0.47
Br-complex	10	1	107	0	103	0	696	2	534	1	1,450	4	0.28
Zpl	93	1	12	0	12	0	109	1	101	0	327	2	0.61
Sz	10	0	15	0	5	0	27	0	97	0	154	0	0.00
Total	113	2	258	1	237	1	978	3	767	1	2,353	8	0.34

b) FEMALES

MONTH	April rel	rec	May rel	rec	June rel	rec	July rel	rec	August rel	rec	Total rel	rec	Total %rec
Pools 1974													
Sn	394	1	184	0	179	0	298	0	244	2	1,299	3	0.23
Br-complex	255	0	355	0	92	0	431	0	432	0	1,473	0	0.00
Zpl	16	0	6	0	-	-	-	-	-	-	22	0	0.00
Sz	107	0	121	0	36	0	235	0	216	1	499	1	0.20
Total	772	1	666	0	307	0	964	0	892	2	3,601	4	0.11
Pools 1976													
Sn	342	0	124	1	322	0	182	0	22	0	992	1	0.10
Br-complex	296	0	351	1	161	0	781	11	430	1	2,046	13	0.64
Zpl	229	0	40	0	5	0	192	1	254	0	720	1	0.14
Zb	-	-	-	-	-	-	100	2	9	0	102	2	1.96
Sz	50	0	37	0	11	0	165	0	97	0	360	0	0.00
Total	917	0	552	2	499	0	1,420	14	812	1	4,200	17	0.40
Pools 1977													
Sn	-	-	74	0	101	0	114	0	49	0	338	0	0.00
Br-complex	25	1	103	1	125	1	622	0	409	1	1,284	4	0.31
Zpl	71	0	14	0	24	1	78	1	75	0	262	2	0.76
Sz	3	0	13	0	3	0	29	0	62	0	110	0	0.00
Total	99	1	204	1	253	2	843	1	595	1	1,994	6	0.30

Table VI-1. Recapture after flight. Number of marked beetles released in pools SN, Br-complex, Zpl, SZ and Zb
          from April through August in 1974, 1976 and 1977, and the number of recaptures after flight.
          Br-complex = pools BR+K+M+S+W1+W2+Bh+Kr (cf Fig III-3, pag 36)
          rel   = number released
          rec   = number recaptured after exchange by flight
          %rec   = percentage recaptured after exchange by flight

is not a common means of displacement (Johnson 1969; Thiele 1977; van
Huizen 1979), gyrinid beetles show flight activity even during the
period of reproduction (from April till about 20 August: cf Chapter
IV)

3.1.2. Very little exchange by flight was recorded. In general less
than 1% of the beetles released were recaptured in another isolated
pond. On the average we recaptured 2.8 times more exchanged males
(0.79%) than females (0.28%). Of course, these data underestimate
exchange within the study area, because not all emigrants will be
recaptured. The chance of recapturing a marked beetle over the season
varied for different pools between 0.2 and 0.6. But even if it were
two or three times more frequent than we observed, the rate of ex-
change by flight would still be small, probably not exceding an
emigration rate of 5%. Exchange by flight of males seems to have
occurred more often in 1976 than in the other two years (Mann-Whitney
U-test: $U=1$, $p<0.01$, $n_1=5$, $n_2=8$). For females no significant diffe-
rence was measured ($U=15$, $p>0.05$, $n_1=5$, $n_2=8$).

3.1.3. Because the chance of recapture is fairly low, this experiment
cannot fully answer the question whether it is the rate of emigration
by flight which is low, or whether only a small proportion of the
flying emigrants arrived in pools within the study area and were then
recaptured. To address this question we carried out experiments with
clip-winged and full-winged beetles.

3.2 Loss from a population by flight emigration

3.2.1. In 1977 we measured the extent of emigration by flight by
comparing the rates at which clip-winged and full-winged individuals
are lost to or survive in a population. The experiment was executed
three times, in spring (release date 28 April), summer (release date
5 July) and autumn (release date 14 September, females only). The
results of these experiments are shown in Fig VI-3. There were no
differences between the survival rates of males and females or of
clip-winged and full-winged individuals; nor were there differences
between the results of the different experiments. The curves of the
clip-winged parts of the populations do lie below those of the full-
winged parts of the population, but this is due to a faster decrease
of the clip-winged individuals in the first part of the experiment
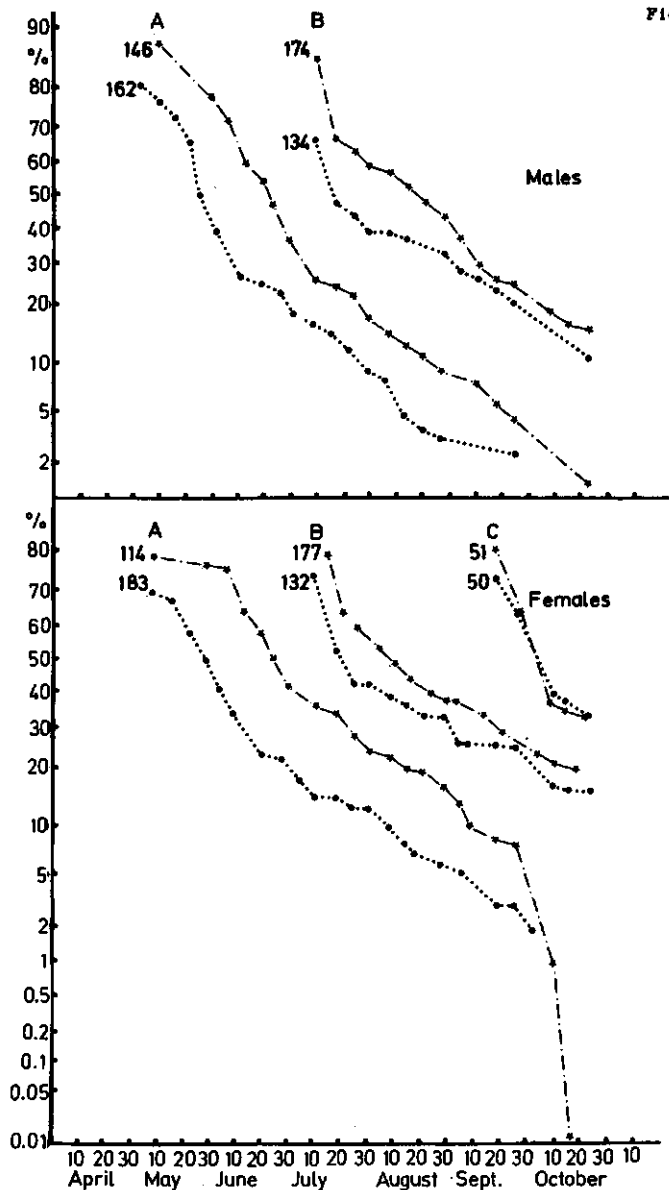
Fig. VI-3. The influence of emigration by flight on population decrease rates.

Decrease rates of a clip-winged part (...●......●), and of a full-winged part (-★·—·★) of an isolated marked population in 1977. The marked beetles were released for the first time on 28 April (A), 5 July (B) and 14 September (C, females only).
Y-axis: minimum percentage of beetles present in the population at the sample date (probit scale, see Southwood 1978)
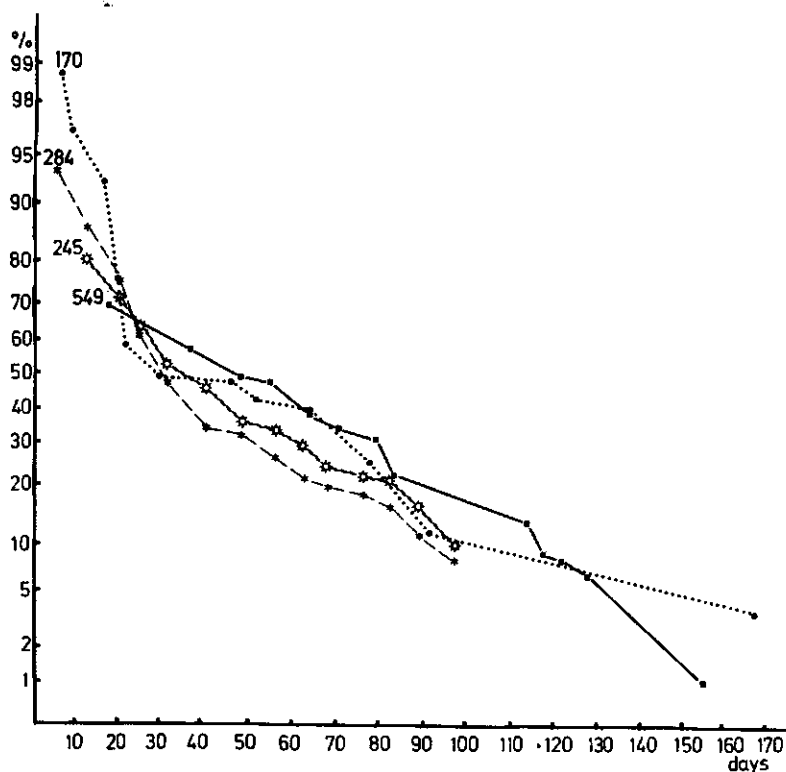
Fig. VI-4. Decrease rates of three isolated populations in
          different years. Y-axis: minimum percentage of beetles
          present in the population x days after first release
          (probit scale). X-axis: number of days after first
          release.
          ··•·····•· SpG, pool outside the study area (1969)
          —■——■ Zp, isolated pool in the study area (1976)
          —☆——☆ SnS isolated ditch, clip-winged part of the
                     population (1977)
          —✦——✦ SnS, full-winged part of the population (1977)

winged parts of the population, but this is due to a faster decrease
of the clip-winged individuals in the first part of the experiment
(U-test: U=2, $n_1 = n_2 = 5$, P=0.05, decrease to 50%). The survival rates
of clip-winged and full-winged beetles did not differ in the second
and third parts of the experiments (U-test: U=24, $n_1 = n_2 = 7$, p>>0.05,
decrease to 25%, and to 12.5%). The lower initial survival rate is
probably a side-effect of the clipping itself, leading to an in-
creased death rate in the first weeks after clipping despite the 24 h

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the beetles were kept before release. Since after that initial period there is no apparent difference between clip-winged and full-winged beetles, it seems probable that emigration by flight to an extent that could noticeably influence the numbers of individuals in the population did not occur. It should be noted that survival rates in the first and second experiments did not decrease towards the end of the season. Apparently the chance of death is independent of age or sex. Because the mean survival rate is 0.55-0.60 each month, most beetles must die from causes other than old age (see also Chapter V).

3.2.2. It is unfortunate that we did the experiments in 1977, a year with rather bad weather conditions for flight (see below). However, if we compare the survival rates of this population with those of other isolated populations in other years (1976, for example, was very warm), we find no difference (Fig VI-4). Apparently emigration by flight is in general very limited, even if weather conditions are favourable. In the field we have never observed an exodus like that found at the artificial pool (see below), or as described for Corixidae (Pajunen 1970). At the same time it is important to emphasize that we did observe some flight emigration in our capture-recapture program in populations of different size, during the whole season and in different years (Table VI-1).

Table VI-2. Flight activity of beetles in field experiments at different air temperatures. See text for further explanation.
n   = number of experiments within the given temperature range
fl = number of experiments with flight activity
%fl = percentage of experiments with flight activity

TEMPERATURE RANGE	MALES												FEMALES											
	Lowest temperature			Highest temperature			Lowest temperature			Highest temperature		
	n	fl	%fl	n	fl	%fl	n	fl	%fl	n	fl	%fl
17-17.9 C	8	0	0.0	0	-	-	8	0	0.0	0	-	-
18-18.9 C	14	2	14.3	10	0	0.0	11	0	0.0	10	0	0.0
19-19.9 C	13	8	61.5	11	2	18.2	16	9	56.3	12	1	8.3
20.20.9 C	20	4	20.0	21	6	28.6	20	5	25.0	23	8	34.8
21-21.9 C	19	7	36.8	11	5	45.5	20	10	50.0	12	5	41.7
22-22.9 C	4	1	25.0	12	6	50.0	7	4	57.1	10	5	50.0
23-23.9 C	3	1	33.3	9	3	33.3	2	0	0.0	10	4	40.0
24-24.9 C	4	2	50.0	7	2	28.6	3	1	33.3	7	3	42.9
>24.9 C	5	3	60.0	8	6	75.0	6	3	50.0	10	6	60.0

3.3 The influence of weather upon flight activity

3.3.1. For insects with feeble flying ability the relevance of favourable weather conditions for flight is often mentioned (Williams 1961, 1962; Johnson 1969; Pajunen 1970; van Huizen 1979). To test the dependence of flight on weather conditions we carried out some field experiments and analysed flight activity and flight ability in laboratory experiments.

Table VI-3. Flight activity of beetles in field experiments at different rent intensities of radiation from the sky measured in W/cm-^{2} See text for further explanation.
n   = number of experiments within the given radiation range
fl = number of experiments with flight activity
%fl = percentage of experiments with flight activity

RADIATION RANGE	MALES						FEMALES					
	Lowest radiation			Highest radiation			Lowest radiation			Highest radiation		
	n	fl	%fl	n	fl	%fl	n	fl	%fl	n	fl	%fl
0.00-0.09	6	3	50.0	2	0	0.0	8	2	25.0	5	1	20.0
0.10-0.19	19	13	68.4	12	9	75.0	22	17	77.3	13	7	53.8
0.20-0.29	2	2	100.0	5	3	80.0	3	3	100.0	6	4	66.7
0.30-0.39	1	1	100.0	4	3	75.0	1	1	100.0	3	3	100.0
0.40-0.49	6	4	66.7	5	2	40.0	2	1	50.0	6	4	66.7
0.50-0.59	1	1	100.0	3	3	100.0	3	1	33.3	8	4	50.0
0.60-0.69	1	1	100.0	1	1	100.0	1	1	100.0	1	1	100.0
0.70-0.79	2	2	100.0	3	3	100.0	3	3	100.0	2	2	100.0
>0.79	0	-	-	1	1	100.0	0	-	-	2	2	100.0

3.3.2. During a short period in the autumn of 1977 Mrs. A. Kreulen-Jonker was able to perform some field experiments on flight activity in relation to weather (see S 2.3a). Temperature was measured both at the start and at the end of each experiment (duration 5 min) so that the flight activity in each experiment has to be related to both temperature values. Table VI-2 shows that it is more strongly related to the higher temperature value in an experiment than to the lower value. It seems that flight activity does not occur at temperatures lower than 18° C, and that it is most frequent at temperatures higher than 19° C. We have observed both in the field and at the artificial pool that on very warm days (>30° C) the beetles become rather inactive and appear to be looking for shelter from the sun. It seems doubtful that this could be responsible for the low flight activity between 23° C and 25° C. As the number of experiments is small we cannot attach much significance to the reduced flight activity shown

for temperatures between 23° C and 25° C. No differences were found
between the flight activity of males and females (see also Fig I-4,
pag 11).

3.3.3. Relating flight activity in an experiment to radiation from
the sky (Table VI-3), in the same manner as for temperature, we find
increasing flight activity up to a radiation of 0.2-0.3 W/cm^{-2} . At
radiation values higher than 0.5 W/cm^{-2} flight activity occured in
all experiments. The lower flight activity found at radiation values
between 0.3 and 0.5 W/cm^{-2} was observed in the same experiments as
those involving temperatures between 23°C and 25° C. Because tempera-
tures and radiation were measured in the same experiments on the same
few days, and correlate strongly with each other, it is not possible
to ascertain to what extent they are independently responsible for
flight activity.

3.3.4. Wind significantly affects flight activity. For every beetle
that flew away, the flight direction, the wind direction, and the
wind velocity were recorded. As Table VI-4 shows, in general the
beetles did not fly into the wind. Only with low wind velocities were
they able to fly diagonally into the wind (see also Fig I-5, pag 11).

3.3.5. The results mentioned above can be supplemented by some obser-
vations on beetles living in the artificial pool on the shed roof
(see S 2.3.2). Flight attempts were observed on 17 days in 1979 and
1980. On 16 of these days the temperature was more than 19° C at the
boundary of water and air; on one day the temperature was 17° C.

Table VI-4. Flight activity and wind. Wind velocity and flight direc-
             tion of beetles released from a dish (see S 2.3.1). The
             flight directions are described by sectors of 30 of
             deviation from wind direction. The wind velocity in m/sec
             was measured with a rad-anemometer

NUMBER (AND PERCENTAGE) OF BEETLES FLYING IN 6 DIRECTION SECTORS					
Sector	1	2	3	4	5	6
Deviation limits	0-30	30-60	60-90	90-120	120-150	150-180
Wind velocity						
0.0-0.5 m/sec	2 (15.38)	4 (30.77)	3 (23.08)	4 (30.77)	0 (0.00)	0 (0.00)
0.6-1.5	13 (30.86)	7 (16.62)	6 (14.24)	10 (23.74)	3 (7.12)	3 (7.12)
1.6-2.9	19 (41.83)	5 (11.01)	10 (22.02)	5 (11.01)	3 (6.60)	3 (6.60)
3.0-4.0	15 (65.43)	6 (24.54)	1 (4.09)	1 (4.09)	0 (0.00)	0 (0.00)
4.0-4.9	7 (45.92)	3 (19.68)	5 (32.80)	0 (0.00)	0 (0.00)	0 (0.00)
5.0-6.0	1 (100.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
>6.0	12 (100.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
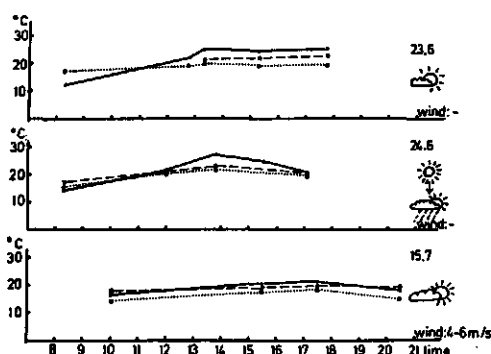
Fig. VI-5. Temperature variation in the course of the day.
Temperature variation during three days at the water surface of the artificial pool (—■——■—), at the surface of a pond of 80 x 200 m (✻--✻), and in the air (··●····●··).

Flight was only observed on sunny days without rainfall and without wind. If beetles were present in the pool flight activity was always observed when the weather conditions became favourable for flight. After some hours all or most of the beetles had left the pool on such days. Probably the conditions in the pool are so unsuitable that as soon as the weather permits, the beetles fly away.

3.3.6. During observations of flight attempts from the pool on the shed importance of wind for take-off became evident. Usually the beetles take off from some object on the surface of the water or climb to the tip of a blade of grass. Sometimes they fly directly from the water surface (cf front cover). Many attempts do not suc- ceed, especially if they occur from a quaking grass blade or a water surface with waves. During a gust of wind attempts are generally not successful, and there are fewer flight attempts during periods of wind.

3.3.7. From the field experiments and from the observations at the artificial pool we may conclude that flight of whirligig beetles occurs if the temperature near the water surface is higher than about 18° C, and if there is sunshine and no wind. Taylor (1963), Heathcote and Cockbean (1966), Johnson (1969), and van Huizen (1979), give similar threshold values for air temperature in relation to flight activity in other insects (wasps, aphids, thrips, locusts, carabid beetles, and others).

3.3.8. A practical question is how frequently the temperature at the water surface in the pools will rise to values above 18° C. Fig VI-5 gives the temperature at the water surface of the artificial pool as well as that for a nearby pond of about 80 x 200 m (a size similar to many ponds in the study area) for 3 days, together with the tempera- ture of the air. On sunny days the surface temperature of the artifi-

cial pool and of the pond rose to higher values than the air tempera-
ture. In the morning the temperature at the surface of the pond was
higher than in the air or at the surface of the artificial pool. On
sunny days with air temperatures above 20° C and with little wind we
always found, without exception, temperatures above 20° C at the
water surface in the study area. Thus, it may be assumed that in the
field water surface temperatures favourable for flight occr at least
as frequently as the corresponding air temperature measured at a
meteorological station 3 km from the study area. In 1976 at least
64 days favourable for flight may have occured, whereas in 1974 there
were no more than 30 such days and in 1977 only 22 days. The number
of days per month favourable for flight from April till October was
on the average in 1974 5.0, in 1976 10.7 and in 1977 only 4.4. The
supposed relationship between the number of days with apparently
favourable weather conditions and the amount of exchange by flight
within the study area is partly supported by the data in Table VI-1.
In 1976 more males were recaptured after flight than in 1974 or in
1977, but we recaptured no more females after flight in 1976 than in
the other years. The field experiments (S 3.3.) indicate that males
and females take off at similar rates, but the experiments were
carried out after the reproduction period. It is possible that flying
females bridge greater distances than males and thus are more likely
to leave the study area. Since the field experiments were carried out
after the reproduction period was finished, another explanation may
be that during reproduction females are less capable of flight and
that most of the favourable days occured during this reproduction
period. In 1974 21 of the 30 days suitable for flight occured during
reproduction, in 1976 56 of the 64, and in 1977 19 of the 22. Hence,
females may have had fewer opportunities than males.

3.4 Flight of males and females in laboratory experiments

3.4.1. In order to compare the flight activity of males and females
we conducted the laboratory experiments described above (see S 2.4).
To measure the possible influence of age on flight we performed these
experiments both with full-grown and with recently hatched beetles.
We did the experiments from May till the end of December and repeated
them in several different years. In order to compare the percentages
of males and of females that flew in the same experiments we use the
natural logarithm ln(V) of the ratio between those percentages, see
Fig VI-6. During the reproduction period (from April until mid-
August) more males than females flew away (ln(V)=0.43±0.47 and after
that period both sexes flew away to nearly the same extent (ln(V)=-
0.01±0.27). During August there is a great variability in ln(V) (area
between the vertical lines in Fig VI-6). The values of ln(V) up to
the end of July are significantly higher than those from September
through December (U-test: Z=4.63, P<0.001, n_1=15, n_2=26), i.e. males
show a greater flight activity than females during reproduction but
not after that period. In the experiments performed after the repro-
duction period significantly more females flew away than during that
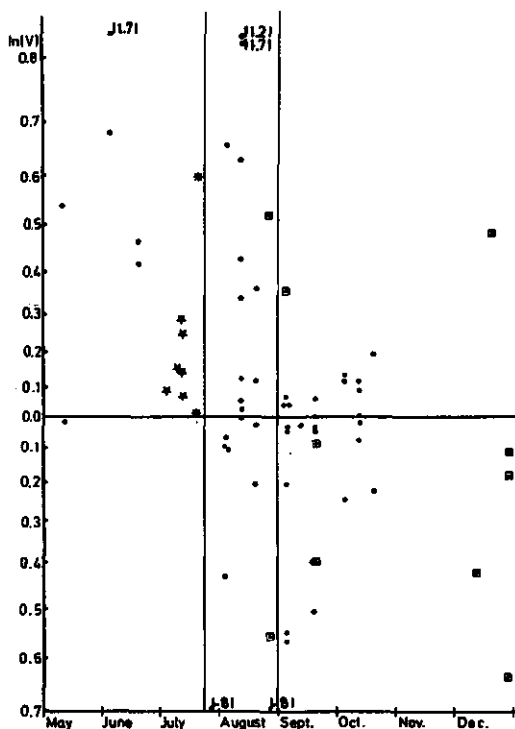
Fig. VI-6. Flight activity of males and females. Natural logarithms of ratios V of the percentages males and females with flight activity in laboratory experiments.

$$ln(V) = ln\left(\frac{\% \text{ males with flight activity}}{\% \text{ females with flight activity}}\right)$$

$\maltese$ = experiments in 1976
$\bullet$ = experiments in 1978
$\ast$ = experiments in 1980
$\boxdot$ = experiments in 1977
$\circ$ = experiments in 1979

Table VI-5. Flight activity and egg production. Average results of 17 experiments on the egg production of females used in flight experiments (standard deviation given in brackets)

	FEMALES SHOWING FLIGHT ACTIVITY	FEMALES NOT SHOWING FLIGHT ACTIVITY
% females reproducing	52.20 (+/-24.51)	65.80 (+/-19.15)
Mean number of eggs per female	12.80 (+/- 8.92)	17.72 (+/- 7.38)
Mean number of eggs per reproducing female	19.70 (+/- 8.90)	23.4 (+/- 5.91)

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period (means: 51.32±28.47% and 71.80±21.32%;   U-test: Z=2.17, P<0.025, n_1=15, n_2=26). There was no significant difference among males (means: 76.24±22.23% and 68.13±26.33%; U-test: Z=0.58, P>0.05, n_1=15, n_2=26).

3.4.2. The most obvous hypothesis to explain the different flight activity of females and males in these two periods is that females fly less during the reproduction period because of the weight and/or volume of the eggs developing in their ovaries. Immediately after an experiment during the period of reproduction was finished, we deter-mined the numbers of eggs in the ovaries of the females by counting the number of eggs laid within 24 hours (cf Chapter IV). The results are shown in Table VI-5. A Wilcoxon test shows significant differen-ces between females that flew and those that did not, both in the percentage of females that thereafter produced eggs (Z= 1.87, p<0.05, n=17), and the mean number of eggs produced by a reproducing female (Z= 1.70, p<0.02, n=17). Females without eggs or with few eggs do not show significantly different flight activity from that of males.

3.4.3. It is likely that the production of eggs hinders females from flying because of the increased body weight and the swollen abdomen filled with eggs. We established the weight of males and of reprodu-cing females in July and of males and of females in September (i.e. after reproduction). Males showed the same average weight in July and September (11.9 mg and 12.3 mg, not significant in t-test: df=83, t=0.14, p>>0.05), but the body weight of females was 2 mg higher in July than in September (mean values 19.8 mg and 17.7 mg, highly significant in t-test: df=111, t=5.24, p<0.001).

3.4.4. In laboratory experiments during reproduction females flew away 10.7 min later than males on the average, but after reproduction the average difference in time for take off was only 2.6 min (not significant: U-test: U=21, p>0.05, n_1=11, n_2=7). It is likely that the production of eggs causes females to need a longer time to take off during the reproduction period than afterwards.

3.5 Flight activity of recently hatched beetles

3.5.1. Whirligig beetles that have just hatched have very soft ely-tra. The process of hardening takes from 10 days to several weeks and seems to depend on the temperature and on food (Nelemans, pers. comm.). As we suppose that their flight muscles cannot operate with a soft, flaccid, cuticula, it seems likely that newly hatched beetles would not be able to fly. The same hypothesis would be suggested by the fact – established for some species of carabid beetles – that the flight muscles are built up during the first period after hatching (Johnson 1969; van Huizen 1979; Nelemans pers. comm.).

3.5.2. We tested the flight abilities of beetles with elytra of
different degrees of hardness. All experiments were done in August
and September, when no differences in flight activity were to be
expected between females and males. The averaged results are shown in
Table VI-6. We found no differences between females an males within
the same class of hardness (sign-test: p>0.10). From Table VI-6 it is
evident that flight ability increases during the first 1-3 weeks
after hatching (Kendall correlation test: n=98, tau=0.44, p<0.001).

Table VI-6. Flight activity and hardening of the elytra. Percentage
            of beetles showing flight activity in laboratory expe-
            riments, in relation to the degree of hardness of the
            elytra. n=number of experiments. Standard deviation given
            in brackets

| HARDNESS | n | % OF INDIVIDUALS SHOWING FLIGHT ACTIVITY | |
		MALES	FEMALES
Hard/r.hard	26	74.13 (+/-18.72)	75.10 (+/-16.53)
Rather soft	18	55.16 (+/-29.17)	61.56 (+/-23.52)
Soft/v.soft	22	16.86 (+/-16.30)	16.61 (+/-19.94)

3.6 Repeated experiments with the same individuals

3.6.1. From the experiments and from our observations at the artifi-
cial pool it appeared that in general not all beetles fly away. There
may be some differences in flight ability between individuals. To
test for this we repeated the flight experiment 1 or 2 days later,
measuring the willingness to fly of the same individuals a second
time (Table VI-7). In five of six trials more beetles from the group
which flew in the first experiment also flew in the second experiment
than from the group that did not fly in the first experiment (Wilcox-
on test: n=12, T=2, p=0.002). (The exceptional sixth trial involved
females and showed no such relationship.) This may mean that in any
given population individuals have differing abilities to leave it by
flight (apart from the effects of reproduction or age). In the labo-
ratory experiments we have observed beetles making many attempts to
fly, but failing to attain stable flight or to surmount the edge of
the dish (1.5 cm high). Differences in flight ability could be caused
by wing or wing muscle polymorphism (Johnson 1969), by morphological
maladjustments, or by other aspects of physical condition of the
individual, but we did not have the opportunity to check these possi-
bilities.

Table VI-7. Flight activity and individual ability. Repeated flight
            tests for the same individuals (see text for further
            explanation)

MALES			NUMBER OF BEETLES IN SECOND TEST		
Date 1st test	Number of beetles		Date 2nd test	without flight	with flight	% with flight
25/5/79	flight	38	27/5/79	3	35	92.1
	no flight	19		6	13	68.4
2/8/79	flight	39	3/8/79	19	20	51.3
	no flight	37		11	16	43.2
7/8/79	flight	18	8/8/79	6	12	66.7
	no flight	25		18	7	28.0
8/8/78	flight	26	9/8/78	1	4	80.0
	no flight	14		14	0	0.0
8/8/78	flight	37	10/8/78	13	24	64.9
	no flight	18		9	9	50.0
5/9/78	flight	129	6/9/78	7	122	94.6
	no flight	76		5	71	93.4

FEMALES			NUMBER OF BEETLES IN SECOND TEST		
Date 1st test	Number of beetles		Date 2nd test	without flight	with flight	% with flight
25/5/79	flight	19	27/5/79	1	16	94.1
	no flight	29		6	22	78.6
26/7/79	flight	13	27/7/79	8	5	38.5
	no flight	82		68	10	12.8
2/8/79	flight	32	3/8/79	8	10	55.6
	no flight	21		17	5	22.7
7/8/79	flight	7	8/8/79	2	4	66.7
	no flight	26		25	1	3.8
8/8/78	flight	35	9/8/78	10	25	71.4
	no flight	8		7	1	12.5
5/9/78	flight	120	6/9/78	11	109	90.8
	no flight	33		1	32	97.0

4 DISCUSSION

4.1. The field data give a picture of flight activity of *Gyrinus marinus* in which the number of beetles that disperse by flight is low, not exceeding a low percentage of the population per year. Although data on recaptures of marked emigrants (Table VI-1) underestimate the extent of exchange within the study area and of the total amount of emigration from a population, experiments with clip-winged beetles and the loss rates found for a number of populations in different years suggest that the loss of individuals as a consequence of emigration by flight is probably so slight that it has no influence on the size of the population as a whole. In the experiments the survival rates or a partially clip-winged population (Fig. 4) vary between 0.43 and 0.67 per month (mean 0.55). At this rate at least 5% of the population would have to emigrate each month before there would be a measurable difference in survival rate (in which case the measured overall survival rate would be 0.467) and emigration would be measurably distinguishable from non-emigration.

4.2. There appears to be some difference in flight activity between females and males. Favourable weather for flight seems to have a different influence on the degree of exchange by flight of females and males between the pools within the area (Table VI-1). From the laboratory experiments it appears that females fly less than males during reproduction. After reproduction the differences disappears. This may mean that females of the new generation, of which most have not reproduced, disperse to a higher degree than their mothers. or to put it differently, that dispersal occurs more by emigration of a new generation of beetles than by distribution of their eggs by reproducing females of the old generation. According to de Jong's (1979) simulations, dispersal of offspring after reproduction would be more favourable in natural sesection than spreading eggs over different sites by dispersal of females during reproduction. In chapter VIII we will examine the effect of the time of dispersal on populations dynamics by means of simulations.

4.3. Little research has been adressed to variability in flight capability or activity of different individuals among insects. On the strength of a review of studies concerning this problem Johnson (1969) supposed that in general young adults have a greater capacity for flight than older ones. Our experiments with recently-hatched beetles give the opposite result, at least during the first few weeks (Table VI-6). Repeated experiments with the same individuals (Table VI-7) indicate that there are full-grown individuals with different flight abilities. These experiments leave open whether the observed differences are due to temporary conditions of individuals, morphological and anatomical qualities, or both. The fact that in the second experiment a large number of beetles which had not flown in the first experiment, did fly (and vice versa), suggests that temporary conditions affecting an individual can be important for flight activity. We concluded above (S 3.4) that the lower dispersal activity of older

females during reproduction compared with the higher dispersal acti-
vity of young females in autumn is probably caused by increased
body weight and swollen ovaries. Since the flight capability of males
seems not to be related to the difference in age in spring and autumn
it is likely that in females the relation with age only reflects the
factor of reproduction, the more so as females with few or no eggs
did not differ from males in flight activity.

4.4. Although the number of our field experiments on the relation
between flight and weather is rather small, when these are taken
together with the observations at the artificial pool we may conclude
that a minimum air temperature of about 18. C is required for flight.
The dependence of flight activity on favourable weather conditions
seems to be the main determining factor in flight activity, at least
given Dutch weather conditions. The occasion for flight may have to
do with factors such as food supply, population size, water pollu-
tion, or drying up of pools, but such factors can apparently only be
effective if the weather permits flight. This is well illustrated by
the experiments in the artificial pool. Although the conditions in
this pool would seem to be continuously unfavourable, the beetles
could leave the pool only when weather conditions favourable for
flight occured. Thus unfavourable habitat conditions can only play a
role in dispersal by flight when they happen to occur in combination
with weather conditions favourable for flight.

4.5. Limited food supply is often considered to be an important
factor in inducing dispersal activity. The diet of whirligig beetles
seems to consist mostly of drowned insects which are abundant along
the shores of pools, where the insects are blown by the wind (Norlin
1964, 1967). The food supply probably is rarely so limited (particu-
larly during good weather) that it will give whirligig beetles occa-
sion to fly away. Overcrowding in the sense of food competition is
unlikely, but it may occur in summer, in the sense that favourable
sites are lacking during daytime for the groups of whirligig beetles.

4.6. Whatever the occasion to fly may be for a whirligig beetle we
must assume that in general emigration and exchange by flight will
occur only to a very small extent. The influence of such marginal
flight activity on population dynamics is not clear. There seems to
be no noticeable effect on the size of the remaining population. It
would seem that the size of the receiving population would also be
very little affected by such a low level of immigration. If so,
beetles which fly away would play a role in population dynamics
primarily by founding new populations.

4.7. Discussions of dispersal activity generally attribute it to some
adverse condition, because it is supposed that in general a disper-
sing individual is in a disadvantageous position compared with the
remaining individuals. Therefore only an individual which is unable
to continue in his habitat will tend to leave it. Too little atten-
tion has been paid to the suggestion of den Boer (1970, 1977, 1981,

1985) that dispersal can have advantages for the dispersing as well
as for the remaining individuals in accordance with the principle of
spreading of risk. In any event, the capture-recapture data in this
study give no support to the idea that only adverse conditions occa-
sion flight activity. The hypothesis that beetles fly just because
the conditions for flight are favourable cannot be rejected. The
significance of dispersal for the founding of new populations is
self-evident. Further discussion of this question must await an
analysis of the significance of dispersal for a population, in which
the costs of dispersal as well as its advantages are considered. The
consequences of different distributions of emigration activity over
populations, over individuals, or over time must be analysed. Kuno
(1981) devotes attention to the mathematical consequences exchange of
individuals between habitats will have on the course of the popula-
tion sizes in those habitats. A thorough analysis of the significance
of the described flight activity of whirligig beetles for population
dynamics will be undertaken in chapter VIII.

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CHAPTER VII. DISPERSAL BY SWIMMING

SUMMARY

The amount of exchange by swimming between local populations of the water beetle *Gyrinus marinus Gyll.* is estimated by capture-recapture methods. The mean emigration chance per week decreases not signifi-cantly from about 0.36 in spring to 0.20 in late summer and autumn. Males emigrate more frequently than females.   The emigration from pools with several passages to other pools is greater than that from pools with a single outlet. The pools in the centre of the study area therefore show a greater exchange with other ones than the border pools.   The exchange between two pools also depends on the number of pools between and on the number of possible routes. Large populations have lower emigration rates and receive a greater proportion of the immigrants than small populations, i.e. there is a tendency to stay and to go to places with relatively high numbers of beetles.

Exchange by swimming occurs at night and is more intensive at nights with high temperatures, and possibly during rain.
A mean survival chance during exchange of 0.70 is estimated (chance to immigrate elsewhere).
During the year and between populations both emigration and immigra-tion vary considerably.   In general the number of beetles emigrating from a population is higher than the number of beetles that immi-grate. However, in eight out of 24 cases immigration was greater than emigration. On the average, three weeks after release of marked beetles 50 per cent of a local population appears to consist of immigrants.

1. INTRODUCTION

1.1. Whirligig beetles (*Gyrinus marinus Gyll.*) can disperse by flight and by swimming. Flight activity only occurs during special weather conditions, and is shown by only a small proportion of the beetles (Chapter VI). Flight seems seems to be a reaction to conditions favourable to flying. Swimming, on the contrary, is the normal way of moving, to find food, shelter, or other whirligig beetles. During the daytime, movement is generally limited to an area of a few meters around groups of beetles along the bank, but at sunset the beetles become very active, swarming around for at least several hours. At sunrise the beetles are found again within groups or they have shel-tered in the bank vegetation or under water. Apart from the possible functions of swarming (Heinrich and Vogt 1980), a number of the swarming beetles may leave the pool (by accident ?) and keep swimming until they meet another group of whirligig beetles. The company of other whirligig beetles is probably an important stimulus for an individual to stay at a given place (Grooters and Groothuis 1979b,
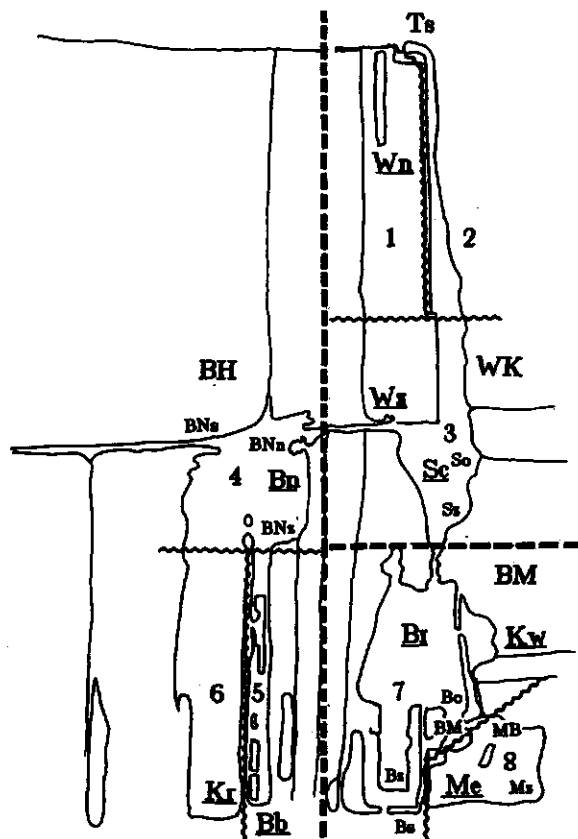
Fig. VII-1.
Division of the Br-complex into
populations, pools, sectors and
pool-groups.
Wn,...,Bb   : pool or population
Wn,..,Bb   : (sub)population
1-8   : sector   (~~~~)
BH, WK, BM : pool-group (═ ═)

Zijlstra 1979). It can thus be expected that a beetle that has swum
away from its pool will be found in a group in another pool, unless
it has died. It also implies that the time between leaving one pool
and immigrating into another will probably be short, i.e. less than
24 hours.

1.2. During daytime whirligig beetles are concentrated for the grea-
ter part in groups along the banks of pools. We have never observed a
group of beetles more than two meters from the bank. Fig III-3 (pag
36) shows that certain parts of the banks were always occupied in the
course of several years, whereas other places were occupied for res-
tricted periods only; along considerable parts of the banks groups of
beetles were never observed. Apparently, certain areas along the
banks are not attractive for the beetles and can be considered a kind
of "desserts" that they have to cross to reach another inhabitable
place.

2. METHODS

2.1. The study area is situated in the northern part of the Nether-
lands, near Groningen. It is an area of pools and ditches. The pools
of the Br-complex (Fig III-3) are connected by water, the others are
not.

2.2. Exchange between different pools can be traced by releasing and
recapturing marked beetles. The beetles are marked by means of pin
pricks (individual marks) and by paint dots (group marks). The indi-
vidual-mark method gives information about displacements of indivi-
duals and about the composition of local populations of both autoch-
tonous beetles and of immigrated ones from different sources. How-
ever, information about the daily dispersal activities is lost,
because in most cases beetles can not be sampled more frequently than
once every 10 days. Moreover, the capturing and releasing of beetles
will disturb the normal dispersal behaviour. A detailed description
of the marking technique is given in Chapter VI.·

2.3. The method of marking with paint spots enables a daily recording
of the distribution of the differently coloured beetles throughout
the study area. The beetles do not have to be disturbed: they can be
observed and counted with the help of binoculars while swimming
around or in groups. Painting was applied in 1978 only, after some
years of experimenting to develop a safe, harmless technique. We used
non-toxic paint, and before application the central surface of the
elytra was sanded gently with fine waterproof sandpaper in order to
remove the wax-layer and to make a rough surface. After some expe-
rience we were able to mark the beetles without harming them. The
marks kept well for a long time (we even recaptured some marked
beetles the next spring). Before release, the painted beetles were
kept in an isolated ditch for 24 hours, to be sure that only vital
individuals were released.
Flight activity is made practically impossible by the painting,
because in most beetles the elytra are fixed by the paint dots.

2.4. After the beetles were released, the numbers of each color and
that of unmarked beetles were recorded daily at every suitable place
in the entire area. After about six weeks the variously coloured
beetles were too dispersed over the whole area to permit further
registration of displacements. Moreover, their numbers had decreased
to such a low level by mortality as well as by some loss of marks,
that a new series of paint-marked beetles had to be released. Before
a new series of marked beetles was released as many beetles as possi-
ble were captured and checked to avoid confusion with beetles of a
previous series, as well as to look for beetles with remains of lost
paint-marks. It was possible to release such series in four periods:
period I (spring): 29.4 - 6.6 (week 18 -23), period II (summer): 19.6
- 27.7 (week 25 - 30), period III (late summer): 1.8 - 15.9 (week 31
- 37), period IV (autumn): 15.9 - 30.10 (week 37 - 44).

2.5. The paint-marked beetles were released in the northern part of the study area, the "Br-complex" (cf Fig. III-3, pag 36), where the pools are connected by brooks or other passages. The greatest distance between two pools is about 1.5 km. Since only the colours red, blue, green, yellow, orange and white give marks distinguishable from a distance, marked beetles were released at only part of the pools. In period III the colour combinations yellow-blue and orange-red were added.

2.6. Because some places where beetles congregate were situated close to each other at both sides of a passage between two pools (for example at Wz and Sc, cf Fig VIII-1), the exchange between such groups can hardly be considered exchange between different local populations. We therefore divided the Br-complex into eight sectors (Fig VIII-1). Only exchange between different sectors is regarded as exchange between local populations. The pools can also be classified in groups, the BH-group (Kr, Bb, Bn), the WK-group (Wn, Wz, Sc,Ts) and the BM-group (Br, Bs, Me, Kw, see Fig. VIII-1).

A local population will be defined as a cluster of groups of individuals (sometimes only a single one) that is clearly separated from other such clusters.

2.7. Within the Br-complex there are pools with only one passage to other pools (Kr, Bb, Me, Wn, cf Fig. VIII-1), and others with two or more passages (Bn, Wz, Sc, Br, Kw). Because the pools with a single outlet are mostly situated at the outer edges of the complex these pools will be indicated throughout this article as "border" pools, as opposed to the "centre" pools.

2.8. The period that beetles are present at a site is determined by the balance between emigration (+ mortality) and immigration (+ natality). But dispersal activities may be influenced by local conditions, so that certain sites are more attractive than others (Grooters and Groothuis 1979b). To compare the emigration and immigration at places with different degrees of "occupation" (attractiveness) marked beetles were released at places where beetles were generally found as well as at places where they have been observed only during relatively short periods.

2.9 In the following the survival chance Q refers to the proportion of the population still present after some period, whereas the decrease rate (DR) is the proportion lost from a population or site by death or by emigration, i.e. $Q = 1 - DR$.
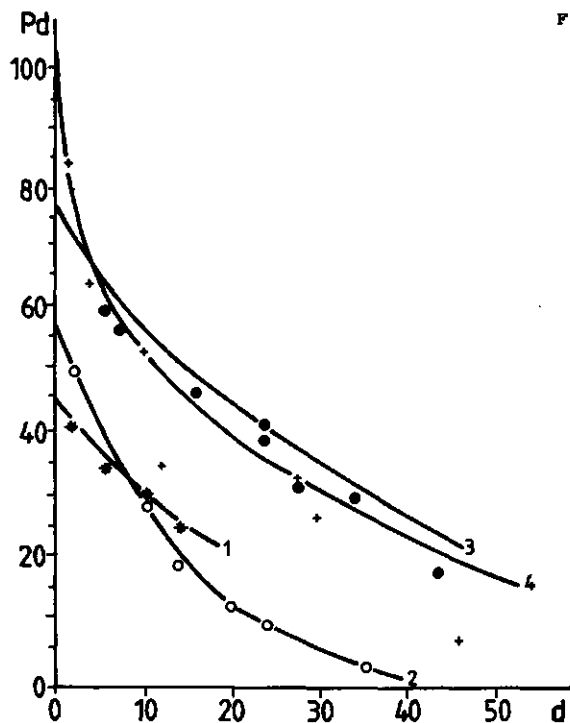
Fig. VII-2. Example of the estimation of the decrease rate of the number of autochtonous, marked beetles in a pool (Wn).
d = number of days after release
P_d = minimum number of beetles present d days after release, according to the curve number of marked beetles at least present:

⊕ = in period 1
○ = in period 2
● = in period 3
+ = in period 4

3. RESULTS

3.1. Emigration rates of prick-marked males and females in 1974-'77

3.1.1. The capture-recapture data concerning the prick-marked beetles do not allow a detailed analysis of swimming, but when the numbers of females and males released in 1974 - 1977 in the different pools of the Br-complex are compared with the numbers of females and males recaptured as immigrants elsewhere in the complex, males were more frequently recaptured as immigrants than females (Table VII-1, Wilcoxon test: n=18, R=25.5, P<0.02). Males apparently show a higher swim-dispersal activity than females, as was also found for flight-dispersal activity (Chapter VI).

Table VII-1. Number of marked beetles released per pool in the Br-
complex during 1974 - 1977 and the number recaptured as
immigrants elsewhere.
N = number of marked beetles released up to August 30th
R = number of beetles recaptured as immigrant
%R = the proportion (R/N)*100

POOL	MALES			FEMALES		
	N	R	%R	N	R	%R
Wn-74	1710	16	0.94	1366	6	0.44
Kr-74	1205	16	1.33	1085	11	1.01
Br-76	1090	51	4.68	643	11	1.71
Wn-76	235	62	26.38	107	22	20.56
Wz-76	384	94	24.48	240	35	14.58
Bn-76	460	164	35.65	377	80	21.22
Bb-76	640	82	12.81	528	68	12.88
Kr-76	976	156	15.98	683	75	10.98
Wn-77	126	66	52.38	127	47	37.01
Wz-77	230	25	10.87	145	19	13.10
Sc-77	136	56	41.18	86	28	32.56
Bn-77	290	64	22.07	250	55	22.00
Kr-77	481	64	13.31	200	79	39.50
Bb-77	252	47	18.65	300	37	12.33
Br-77	398	105	26.38	611	85	13.91
Me-77	160	34	21.25	148	26	17.57
Sl-77	101	22	21.78	72	11	15.28
TOTAL 74	2915	32	1.10	2451	17	0.69
TOTAL 76	3785	609	16.09	1935	280	14.47
TOTAL 77	2174	483	22.22	1939	387	19.96
TOT 76/77	5959	1092	18.33	3874	667	17.22

3.2. Emigration rates of paint-marked beetles in 1978

3.2.1. After beetles were released in a given pool only some of them
could be recorded during the next few days in that pool or elsewhere
in the Br-complex. Some may have been overlooked, but a number of the
missing beetles presumably died soon after release and should thus be
considered as not released. The number of marked beetles effectively
released in a pool can be estimated by extrapolating back to day 0
from the decreasing course of the number of beetles of the concerned
colour released in that pool, cf Fig VII-2. The points in the figure
give the minimum numbers of beetles still present, i.e. the actual
regression curve has to run through or above these points. The de-

crease rate (DR) determined by survival chance and rate of emigration from the pools concerned can be estimated as

$$DR = \frac{\sum_{d=1}^{n} Q_d}{n},$$

if $Q_d = (P_d/P_o)^{265/d \cdot 52}$, P_o=number of beetles effectively released, P_d = number of beetles present d days after release, according to the regression curve (cf. Fig VII-2) and n = the number of days on which an reliable estimate of the number of beetles is made; e.g. for pool Wn the points in Fig VII-2 (see Table VII-2). Since an only very small variation in survival chance was found between different iso-

Table VII-2. Decrease rates of marked beetles per week in four periods in 1978.
$Q = 1 - DR$ (DR = decrease rate (cf Fig 3) in interconnected pools)
r = rank number
Q_m, Q_f = mean survival chance of males or females in isolated populations in 1974 - 1977
i.p. = isolated pools.
$Q_m - Q$, $Q_f - Q$ = mean emigration rates estimated in Table VII-3.
See text for further explanation.

| NR PERIOD | I | | II | | III | | IV | | MEAN | |
| PERIOD | 29.4 - 6.6 | | 19.6 - 27.7 | | 1.8 - 15.9 | | 15.9 - 30.10 | | | |
Pool	Q	r	Q	r	Q	r	Q	r	Q	r
Wn	0.7687	18	0.5894	8	0.8340	22	0.7164	13	0.7271	15.25
Wz	0.7024	12	0.4995	5	0.7308	16	0.5874	7	0.6300	10.00
Br	0.4865	4	0.6334	10	0.7998	21	0.5402	6	0.6150	10.25
Me	0.3164	1	0.6914	11	0.8414	23	0.7891	20	0.6595	13.75
Bb	0.7257	15	0.8804	24	0.7883	19	-	-	0.7981	19.33
Sc	0.4830	3	0.6242	9	-	-	-	-	0.5536	6.00
Kw	0.4747	2	-	-	-	-	-	-	0.4747	2.00
Kr	-	-	-	-	0.7535	17	-	-	0.7535	17.00
Bn	-	-	-	-	0.7219	14	-	-	0.7219	14.00
MEAN Q	0.5653	7.86	0.6531	11.17	0.7814	18.86	0.6583	11.50	0.6658	12.50
Q_m (i.p.)	0.9056		0.8872		0.8687		0.7836			
Q_f (i.p.)	0.8912		0.8763		0.8613		0.7701			
$Q_m - Q$	0.3403		0.2341		0.0966		0.1253			
$Q_f - Q$	0.3259		0.2232		0.0799		0.1118			

lated pools (Chapter V) the differences between the rates of decrease
in inter-connected pools can be regarded as a relative measure for
the differences in emigration rate from these pools.
The emigration rates can be estimated roughly for males as $E_m = Q_m$ -
Q, and for females as $E_r = Q_r - Q$, when Q is the survival chance in
interconnected pools (Q = 1- DR), and Q_m and Q_r are the mean survival
chances of males and females in isolated pools in 1974 - 1977 (Table
VII-2, VII-3).

Table VII-3. Emigration rates estimated as $E = Q_m - Q$ (males) and as
             $E = Q_f - Q$ (females), see table VII-2; v.c. = variation
             coefficient.

PERIOD MALES	I	II	III	IV	MEAN	v.c.
Wn	0.1369	0.2978	0.0347	0.0672	0.1342	0.87
Wz	0.2032	0.3877	0.1379	0.1962	0.2313	0.44
Br	0.4191	0.2538	0.0689	0.2434	0.2463	0.58
Me	0.5892	0.1958	0.0273	0.0000	0.2031	1.34
Bb	0.1799	0.0069	0.0804	-	0.0890	0.98
Sc	0.4226	0.2630	-	-	0.3428	0.33
Kw	0.4309	-	-	-	0.4309	-
Kr	-	-	0.1152	-	0.1152	-
Bn	-	-	0.1468	-	0.1468	-
MEAN	0.3403	0.2342	0.0873	0.1267		
v.c.	0.49	0.55	0.55	0.89		
FEMALES						
Wn	0.1225	0.2869	0.0273	0.0537	0.1226	0.95
Wz	0.1888	0.3768	0.1305	0.1827	0.2197	0.49
Br	0.4047	0.2429	0.0615	0.2299	0.2348	0.60
Me	0.5748	0.1849	0.0199	0.0000	0.1949	1.37
Bb	0.1655	0.0000	0.0073	-	0.0795	1.04
Sc	0.4082	0.2521	-	-	0.3302	0.33
Kw	0.4165	-	-	-	0.4165	-
Kr	-	-	0.1078	-	0.1078	-
Bn	-	-	0.1394	-	0.1394	-
MEAN	0.3259	0.2239	0.0705	0.1166		
v.c.	0.52	0.57	0.78	0.92		

3.2.2. Starting from these rough estimates of emigration rates and from the survival chances as derived in Chapter V more accurate esti- mates of emigration rates can be made with the help of an iterative computer-model. Introducing a given survival chance (Q) and emigra- tion rate (E) and a given survival chance during dispersal ($Q_e = I/E$), the model calculates the number of beetles expected to be still present in the population (P_e), the number of beetles that have died (V), the number of beetles that have emigrated (E_e), and the number of the (E_e)-beetles that have immigrated elsewhere (I_e). By comparing the expected numbers with those actually observed the estimates can be corrected such that the best fit all field data. The method is explained in detail in Appendix C. The dispersal-ratio, which is the ratio between the number of immigrated beetles in a population and the number of emigrants from the same population can also be esti- mated. The results are given in Table VII-4.

3.2.3. In most cases, especially in periods III and IV, the values of the emigration rate in Table VII-4 are somewhat higher than those estimated in Table VII-3. Emigration rates decrease from the first (mean $E = 0.36$) to the fourth (mean $E = 0.20$) period, but not signi- ficantly (Kruskall-Wallis H-test: $z=0.615$, $P>0.20$), also not when the pools are divided in border pools and centre pools.
The border pools show lower emigration rates than the centre pools, i.e. the emigration from a pool is higher when the possibilities to leave the pool are greater (Mann-Whitney U-test: $z=2.14$, $P<0.05$).
Some sites (Sc, Kr, Kw and Bn) were in 1978 only temporarily occupied by groups of beetles. The emigration rate from these sites seems to be greater than from places occupied more permanently, but this difference is not significant (U-test: $n_1 = 5$, $n_2 = 19$, $U = 24.5$, $P>0.10$).

3.2.4. The variation in emigration rates can be considered both per population between periods (variation-in-time) and per period between populations (variation-in-place). The variation coefficient of the emigration rates of populations with marked beetles released in all four periods varies between 0.49 and 1.00 (mean v.c: 0.64), but part of this variation in time is due to the decrease in emigration rates from period I to IV. When the values of the emigration rates in period t are corrected for this decreasing trend by $E_t = E_t \times (\text{mean } E_1)/(\text{mean } E_t)$ the mean variation-in-time coefficient becomes 0.50.
Between populations in the same period variation-in-place coeffi- cients are found between 0.47 in the first period to 0.85 in the third period. Mean variation-in-place for all periods = 0.59; i.e. no important differences occur between the variation in time and in place.

Table VII-4. Estimates of the emigration rate, survival during dispersal and the dispersal-ratio as derived by an iterative method best fitting the field data.
R = number of beetles released; Em = number of beetles emigrated; Ie = number of emigrants found as immigrant elsewhere; I = number of immigrants from elsewhere; E = emigration rate/week; Q_ϕ = survival chance during dispersal; Db = dispersal-ratio; v.c. = variation coefficient (standard deviation/mean)

POPULATION		Wn	Bb	Me	Kr	MEAN	v.c.	Br	Wz	Sc	Kv	Bn	MEAN	v.c.	MEAN	v.c.
	period															
R	I	46	70	68	-			49	84	41	68	-				
R	II	70	58	60	-			25	70	70	-	-				
R	III	90	40	100	85			85	75	-	-	87				
R	IV	100	-	80	-			90	120	-	-	-				
Em	I	14	39	45	-			37	57	31	54	-				
Em	II	49	14	33	-			15	52	46	-	-				
Em	III	45	15	28	43			19	58	-	-	66				
Em	IV	32	-	21	-			44	42	-	-	-				
I_e	I	12	23	26	-			33	40	16	41	-				
I_e	II	38	5	7	-			10	45	37	-	-				
I_e	III	42	13	28	29			10	56	-	-	62				
I_e	IV	30	-	19	-			29	16	-	-	-				
I	I	30	2	40	3			43	17	38	6	12				
I	II	14	0	7	2			26	49	26	2	16				
I	III	45	20	16	49			77	9	0	0	17				
I	IV	6	1	16	2			11	31	24	0	3				
E	I	0.13	0.18	0.58	-	0.30	0.83	0.50	0.27	0.42	0.45	-	0.41	0.24	0.36	0.47
E	II	0.32	0.07	0.19	-	0.19	0.65	0.30	0.38	0.35	-	-	0.34	0.12	0.27	0.44
E	III	0.18	0.17	0.07	0.18	0.15	0.36	0.08	0.65	-	-	0.50	0.41	0.72	0.26	0.85
E	IV	0.12	-	0.10	-	0.11	0.13	0.36	0.23	-	-	-	0.30	0.31	0.20	0.59
Q_e	I	0.86	0.58	0.58	-	0.67	0.24	0.89	0.70	0.52	0.77	-	0.72	0.21	0.70	0.21
Q_e	II	0.78	0.35	0.21	-	0.45	0.67	0.68	0.86	0.81	-	-	0.78	0.12	0.62	0.44
Q_e	III	0.93	0.89	1.00	0.67	0.87	0.16	0 52	0.97	-	-	0.93	0.81	0.31	0.84	0.21
Q_e	IV	0.95	-	0.89	-	0.92	0.05	0.65	0.38	-	-	-	0.52	0.37	0.72	0.36
Db	I	2.16	0.05	0.89	-	1.03	1.03	1.15	0.30	1.23	0.11	-	0.70	0.82	0.97	0.76
Db	II	0.29	0.00	0.21	-	0.17	0.90	1.76	0.94	0.57	-	-	1.09	1.09	0.63	1.02
Db	III	1.00	1.37	0.58	1.14	1.02	0.32	4.02	0.16	-	-	0.26	1.48	1.49	1.22	1.08
Db	IV	0.19	-	0.75	-	0.47	0.84	0.25	0.73	-	-	-	0.49	0.69	0.48	0.63

(BORDER POOLS: Wn, Bb, Me, Kr; CENTRE POOLS: Br, Wz, Sc, Kv, Bn; ALL POOLS)

3.2.5. As could be expected, not every emigrant arrived in another population; some were lost on the way, because they die from predation or some other cause. On the average the chance Q_d to survive during swim-dispersal (i.e. the chance that an emigrated individual will arrive in another population in the area) is found to be 0.72 (st.dev. = 0.21, v.c. = 0.30): that is, about a quarter of the emigrants is lost. The Q_d-values of border pools and of centre pools

are not significantly different (U-test: z=0.347, P>0.20), nor are those of permanently occupied pools and of pools that were occupied temporarily (Table VII-4, U-test: n_1=5, n_2=19, U=45, P>0.20). The survival chance during dispersal in the third period appear to be higher than in the other periods (Table VII-4), even if we assume that the values in the third period are somewhat overestimated (U-test: n_1=7, n_2=17, U=27.5, P<=0.05).

3.2.6. The emigrants from each population can be arranged according to the distance at which they were reobserved. From these data the mean survival chance per 100 m. can be estimated. Starting from the actual distribution of the emigrated beetles according to distance, the expected distribution is estimated for an introduced survival chance per 100 m. The total number of thus estimated immigrants elsewhere is compared with the number of emigrants as found in Table VII-4. By iteration several survival chances per 100 m are tried out until the thus estimated total number of redistributed beetles equals the number of emigrated beetles from Table VII-4.
A mean survival chance of 0.92 per 100 m is thus estimated (st. dev. = 0.07, v.c. = 0.07). Since different survival values per 100 m for emigrants from different populations were found (cf Table VII-5) the survival chance per unit of distance seems not to be constant. The survival chances of emigrants from population Wn (mainly immigrating into Wz) and from Br (mainly immigrating into Me) are rather stable (v.c. = 0.03 and 0.02 respectively), but those of emigrants from populations Wz and Me that immigrated into a number of other populations varied much more (v.c. = 0.10 and 0.12 respectively). Apparently, the risks at the routes between different populations differ, and also change between periods.

Table VII-5. Survival chance per 100 m. during swim-dispersal. Explanation in text.

PERIOD	BORDER POOLS				CENTRE POOLS					MEAN	v.c.
	Wn	Bb	Me	Kr	Br	Wz	Sc	Kv	Bn		
I	0.980	0.952	0.917	-	0.970	0.927	0.890	0.945	-	0.940	0.030
II	0.963	0.895	0.835	-	0.945	0.967	0.950	-	-	0.626	0.060
III	0.992	0.995	0.999	0.970	0.935	0.993	-	-	0.992	0.980	0.025
IV	0.993	-	0.990	-	0.943	0.860	-	-	-	0.950	0.066

3.2.7. Generally, in theoretical analyses of the dispersal phenomenon the dispersal-ratio (Db) plays - sometimes implicitly - an important role. In most theories it is assumed that a population will lose more individuals by emigration than it wins by immigration. In our experiments on the average a population indeed lost more beetles by emigration than it received as immigrants (mean Db = 0.84, st.dev. = 0.88, v.c = 1.05), but we also found that in eight out of 24 cases a population got more immigrants than it lost emigrants (cf Db>1, Table VII-4). No significant differences were found between different kinds of pools, nor between different periods (U-tests and H-tests P>0.20). Different patterns were, however, found between certain pools.

3.2.8. Whether exchange between pools is substantial in relation to the survival chances in the populations (Chapter V) can be examined by comparing the exchange-rates of the populations with the survival chances. The exchange-rate is the net emigration or immigration rate, estimated as E_x = E.(1-Db). The same conclusions can be drawn here as in regard to the Db-values. Between different pools and between different periods at the same pool considerable differences in the flow of beetles occur, e.g. Wn in periods 1 and 2, or Br in periods 3 and 4 (Table VII-6). The differences between the border pools and the centre-pools are more evident here than they were in Table VII-5 with respect to the Db-values, but far from significantly different (U-test: z=0.75, P>0.20). On the average 3 per cent each week is lost from border-pools (v.c. = 2.10), and 11 per cent from centre-pools. By way of comparison, the estimates of the survival chances in isolated populations (Chapter V) give a mean loss by mortality increasing during period I to IV from 11 to 24 per cent per week (Table VII-6). On the average the losses by dispersal activity and by mortality do not differ significantly, although in cases that E_x<0 dispersal gave a net gain of individuals (Wilcoxon pair test: E_x-values

Table VII-6. The net exchange rate per week.
E_x = E.(1-Db); E_x<0 = net immigration rate, E_x>0 = net emigration rate. The mean values of E_x are calculated from the mean values of e and Db per category of pool MORT.RATE = mean mortality rate per week.

PERIOD	BORDER POOLS					CENTRE POOLS						MEAN ALL POOLS	MORT.RATE
	Wn	Bb	He	Kr	MEAN	Br	Wz	Sc	Kv	Bn	MEAN		
1	-0.15	0.17	0.06	-	0.03	-0.08	0.19	-0.10	0.40	-	-0.12	0.01	0.11
2	0.23	0.07	0.15	-	0.16	-0.23	0.02	0.15	-	-	0.16	-0.03	0.13
3	0.00	-0.06	0.03	-0.03	-0.003	-0.24	0.55	-	-	0.37	-0.20	-0.06	0.15
4	0.10	-	0.03	-	0.06	0.27	0.06	-	-		0.06	0.15	0.24
MEAN	0.02		0.09		0.03	-0.25	0.18				0.11	0.07	0.16

Table VII-7. The proportional contribution of the emigrants per pool to the total number of beetles dispersing per period.
N = number of beetles released
Em = number of beetles emigrated
E_{ex} = expected proportional distribution of the total number of emigrants per period over pools according to the ratio of N to total N per period
E_{fn} = proportional distribution of emigrants over pools as observed per period in relation to the total number of dispersing beetles per period; $D = \ln(E_{fn}/E_{ex})$
$D>0$ / $D<0$ = more / less emigration than expected

PERIOD		BORDER POOLS				CENTRE POOLS					TOTALS
		Wn	Bb	Me	Kr	Br	Wz	Sc	Kw	Bn	
I	N	46	70	55	-	49	81	41	68	-	410
	Em	14	39	45	-	37	57	31	54	-	277
	E_{ex}	11.2	17.1	13.4	-	12.0	19.8	10.0	16.6	-	100%
	E_{fn}	5.1	14.1	16.3	-	13.4	20.6	11.2	19.5	-	100%
	D	-0.80	-0.19	0.19	-	0.11	0.04	0.11	0.16	-	
II	N	70	58	60	-	25	70	70	-	-	353
	Em	49	14	33	-	15	52	46	-	-	209
	E_{ex}	19.8	16.4	17.0	-	7.1	19.8	19.8	-	-	100%
	E_{fn}	23.4	6.7	15.8	-	7.2	24.9	22.0	-	-	100%
	D	0.17	-0.90	-0.07	-	0.01	0.23	0.10	-	-	
III	N	90	40	100	85	85	75	-	-	87	562
	Em	45	15	28	43	19	58	-	-	66	274
	E_{ex}	16.0	7.1	17.8	15.1	15.1	13.4	-	-	15.5	100%
	E_{fn}	16.4	5.5	10.2	15.7	6.9	21.2	-	-	24.1	100%
	D	0.03	-0.26	-0.55	0.04	-0.78	0.45	-	-	0.44	
IV	N	100	-	80	-	90	120	-	-	-	391
	Em	32	-	21	-	44	42	-	-	-	139
	E_{ex}	25.6	-	20.5	-	23.1	30.	-	-	-	100%
	E_{fn}	23.0	-	15.1	-	31.7	30.2	-	-	-	100%
	D	-0.11	-	-0.31	-	0.32	-0.02	-	-	-	
	mean D	-0.18	-0.45	-0.19	0.04	-0.09	0.18	0.11	0.16	0.44	
I-IV	$\sum$N	306	168	295	85	249	346	111	68	87	1715
	Em	140	68	127	43	115	209	77	54	66	899
	E_{ex}	17.8	9.8	17.2	5.0	14.5	20.2	6.5	4.0	5.1	100%
	E_{fn}	15.6	7.6	14.1	4.8	12.8	23.3	8.6	6.0	7.3	100%
	D	-0.14	-0.26	-0.20	-0.03	-0.13	0.14	0.28	0.41	0.37	

against the mortality rates as expected values: n=17, T=75, P>0.20).
In chapter VIII, dealing with simulation of the field data, it will
appear that there is an important relation between dispersal activi-
ty, survival from dispersal and survival in the population.

3.3. Exchange between pools of the Br-complex

3.3.1. The distribution of the emigrants from a certain site over the
other sites will now be considered, together with the distribution of
the origins of the immigrants at a certain site.

3.3.2. If the emigration rate were determined by random processes,
each pool (subpopulation) should proportionally contribute to the
number of marked beetles released to the total number of dispersing
beetles in the complex. In Table VII-7 the expected random distribu-
tion is compared with the observed distributions of paint-marked emi-
grants. The contribution of emigrants from each population to the
total number of dispersing beetles indeed shows some relationship to
the number of beetles released per population (corr.test: n=24,
r=0.51, z=2.59, P<0.01). On the average fewer emigrants depart from
the border pools (Wn - Kr) than expected (D<0), whereas from the
centre pools (Br - Bn) usually more emigrants depart than expected
(U-test on E_{fm} -values, $n_1 = n_2 = 12$, U=38.5, P<=0.05). Temporarily
occupied pools (Kw, Sc, Bn) did not give significantly more emigrants
than the permanently occupied ones (U-test on E_{fm} -value: $n_1 = 5$, $n_2 =
19$, U=24, P>0.05), but there is a weak tendency in that direction. We
would have expected that if the temporarily occupied sites were less
favourable, emigration would be higher there than from permanently
occupied sites. The flow of emigrants is not very consistent per
population (cf D-values of pools with series in three or four pe-
riods, Table VII-7). For the relationship between emigration and
population size see 3.4.3.

3.3.3. The expected distribution of immigrants over the pools would
only be random if it is assumed that there is no relation with the
relative position of the pools in the complex (accessibility, distan-
ce to other pools). In Table VII-8 the observed distribution of
immigrants is compared with such an expected one. In the pools of the
BH-group (cf Fig VII-1) fewer immigrants are found than in the other
pools. The Bn pool is only temporarily occupied by beetles, and it
may be less attractive for passing beetles to stay there when no
other beetles are available. The Bb and the Kr pools are probably
less accessible than the others: the opening to Bb is in summer
filled with water-lilies and the route to Kr is relatively long,
irregular and with a number of alternative routes. As could be
expected, fewer immigrants arrived in in the border pools than in the
centre pools (U-test on I_{fm} -values: $n_1=8$, $n_2=12$, U=20, z=2.162, P <
0.05); this is also the case for temporarily and permanently occupied
pools respectively (U-test: $n_1=16$, $n_2=20$, U=103, P<=0.05).

Table VII-8. The proportional distribution of immigrants per pool
from the total number of dispersing beetles per series.
I = number of beetles immigrated
I_{ex} = expected proportional distribution of the total
number of dispersing beetles according to a random dis-
tribution
I_{fn} = proportional distribution of the total number of
dispersing beetles per population as observed
D = $\ln(I_{fn}/I_{ex})$, D>0 / D<0 = more / less immigration
than expected

PERIOD	BO R D E R	P O O L S			C E N T R E	P O O L S				ALL
	Wn	Bb	Me	Kr	Br	Wz	Sc	Kw	Bn	POOLS
I										
I	30	2	40	3	43	17	38	6	12	191
I_{ex}	11.1	11.1	11.1	11.1	11.1	11.1	11.1	11.1	11.1	100%
I_{fn}	15.7	1.1	20.9	1.6	22.5	8.9	19.9	3.1	6.3	100%
D	0.4	-2.4	0.6	-2.0	0.7	-0.2	0.6	-1.3	-0.6	
II										
I	14	0	7	2	26	49	26	2	16	142
I_{ex}	11.1	11.1	11.1	11.1	11.1	11.1	11.1	11.1	11.1	100%
I_{fn}	9.9	0.0	4.9	1.4	18.3	34.5	18.3	1.4	11.3	100%
D	-0.1	-	-0.8	-2.1	0.5	1.1	0.5	-2.1	0.0	
III										
I	45	20	16	49	77	9	-	-	17	233
I_{ex}	14.3	14.3	14.3	14.3	14.3	14.3	-	-	14.3	100%
I_{fn}	19.3	8.6	6.9	21.0	3.9	3.9	-	-	7.3	100%
D	0.3	-0.5	-0.7	0.4	-1.3	-1.3	-	-	-0.7	
IV										
I	6	1	16	2	31	31	24	-	3	94
I_{ex}	12.5	12.5	12.5	12.5	12.5	12.5	12.5	-	12.5	100%
I_{fn}	6.4	1.1	17.0	2.1	33.0	33.0	25.5	-	3.2	100%
D	-0.7	-2.5	0.3	-1.8	1.0	1.0	0.7	-	-1.4	
I-IV										
> I	95	23	79	56	157	106	-	-	48	564
I_{ex}	14.3	14.3	14.3	14.3	14.3	14.3	-	-	14.3	100%
I_{fn}	16.8	4.1	14.0	9.9	27.8	18.8	-	-	8.5	100%
D	0.2	-1.3	-0.0	-0.4	0.7	0.3	-	-	-0.5	

Table VII-9. The exchange between sectors in 1978 in relation to distance, expressed as the proportional distribution of the beetles, emigrated from one sector (X), over the other sectors of the Br-complex. Rank: The sectors are ranked 1 - 8. Starting from sector X, with rank 0, the other sectors are ranked anew according to their spatial positions to X:can be reached directly, or can only be reached via one other sector, two other sectors, etc.

Pool-group			BH			WK		BM	
	Sector		Kr	Bb	Bn	Sc/Wz	Wn	Br	Me
Sector	Period								
		Rank	0	1.5	1.5	3	4.5	4.5	6
Kr	III		X	29.1	16.7	2.0	16.7	29.1	6.3
		Rank	1.5	0	1.5	3	4.5	4.5	6
Bb	I		13.6	X	27.3	18.2	22.7	9.1	9.1
	II		16.7	X	33.3	33.3	16.7	0.0	0.0
	III		30.8	X	11.5	3.8	19.2	30.8	3.8
		Rank	2	2	0	2	4.5	4.5	6
Bn	III		49.5	13.0	X	5.1	6.5	22.1	3.9
		Rank	5	5	2	0	2	2	5
Sc/Wz	I		0.0	5.0	8.0	X	31.0	36.6	19.4
	II		2.4	0.0	18.2	X	17.6	57.8	4.0
	III		18.6	4.9	7.4	X	32.4	30.8	5.8
	IV		7.3	0.0	0.0	X	35.5	35.5	21.7
		Rank	5	5	2.5	1	0	2.5	5
Wn	I		0.0	0.0	6.5	86.5	X	7.0	0.0
	II		2.4	0.0	9.1	65.0	X	18.7	4.8
	III		12.8	0.0	9.2	12.3	X	39.6	26.1
	IV		5.2	0.0	0.0	65.1	X	22.1	7.6
		Rank	5.5	5.5	3.5	1.5	3.5	0	1.5
Br	I		0.0	0.0	1.4	28.6	16.0	X	54.0
	II		0.0	0.0	13.9	46.3	6.6	X	33.2
	III		15.8	0.0	5.3	20.0	18.7	X	40.2
	IV		0.0	0.0	0.0	61.8	0.0	X	38.2
		Rank	5.5	5.5	3.5	2	3.5	1	0
Me	I		0.0	0.0	0.0	23.9	6.2	69.9	X
	II		0.0	0.0	0.0	10.1	10.2	79.7	X
	III		11.6	0.0	4.8	2.5	8.9	72.2	X
	IV		0.0	0.0	0.0	76.5	10.7	10.8	X

3.3.4 Obviously the exchange between two pools depends on the distances between them. The proportional distribution of the emigrants from one sector over the other sectors in 1978 is shown in Table VII-9. The distances from one sector, from which the beetles emigrated, to the other sectors are expressed as rank numbers that are related to the numbers of pools between. There is an overall inverse relationship between distance and amount of exchange between two sectors (Spearman-test: R_s = -0.777, df = 8, P < 0.001). But there are also exceptions, e.g. in period III the flow of individuals from Bb to Br and that from Br and Me to Kr (see Table VII-9); obviously other aspects than distance are important too.

3.3.5. On the average there is a relatively high influx of immigrants into pool Br and a relatively small one into the pools Kr, Bb and Bn (Table VII-9). Remarkable is that most emigrants from Wn stay behind in Wz/Sc, whereas beetles from other pools that arrive in Wz/Sc usually continue dispersal activities.
The distribution of emigrants from one sector can be different in different periods. One cause of this may be the growth of water-plants, such as water-lilies, so that local situations may change such that the routes and choices of direction of the beetles will be affected.

3.3.6. At places where beetles have to choose between two or three possible routes, the choice seems to be influenced by the direction in which they were already moving. Proportionally beetles from pool Bb swim less to Kr than beetles from Kr go to Bb, whereas beetles from Bn mainly move to Kr. In Table VII-10 the choice of direction of beetles passing through Wz/Sc is compared with that of the beetles released in Wz/Sc. In 6 of the 12 comparisons the choices of the passing beetles do not differ distinctly from those of Wz/Sc; in one case the passing beetles on the average went in the opposite direction; and in the other five cases their movements were intermediate between those of the Wz/Sc-beetles and the opposite direction. These differences are significant according to the Fisher-test (n=24, A=12, B=0, C=6, P=0.05)

3.4. The relationship between exchange between subpopulations and population size and composition

3.4.1. The composition and size of the population at each pool will change as a result of exchange. Table VII-11 shows for each subpopulation in which paint-marked beetles were released, the proportion of immigrants after about three weeks of dispersal activities (after correction for the number of marked beetles released). From the table it appears that after some weeks immigrants are a substantial part of most subpopulations. In centre-pools immigrants dominate more than in the border pools (U-test: n_1 =9, n_2 =12, U=20.5, P<0.025). Sometimes the high proportion of immigrants will only be due to the small size of the subpopulation concerned (e.g. Wz/Sc and Bn in period III), but

in general no relationship was found between population size and the proportion of immigrants in the subpopulation (cf Table VII-12). See also 3.4.3.

Table VII-10. Comparison of the choice of direction of beetles re-
leased at pool Wz/S and of beetles that arrive at Wz/S.
= : choices in both groups of beetles similar
x : intermediate choices of both groups
xx : choices in both groups opposite to each other.

EMIGRANTS FROM	PERIOD	MAIN DIRECTION OF Wz/S-BEETLES	ACCORDING TO OTHER BEETLES	COMPARISON
Bh (=Bb,Kr,Bn)	I	Br > Wn	Br = Wn	x
	II	Br > Wn	Br < Wn	xx
	III	Br = Wn	Br > Wn	x
	IV	Br > Wn	Br > Wn	=
Wn	I	Br > Bh	Br = Bh	x
	II	Br > Bh	Br > Bh	=
	III	Br = Bh	Br > Bh	x
	IV	Br > Bh	Br > Bh	=
BM (=Br,Me)	I	Wn > Bh	Wn > Bh	=
	II	Wn = Bh	Wn = Bh	=
	III	Wn = Bh	Wn > Bh	x
	IV	Wn > Bh	Wn > Bh	=

Table VII-11. The proportion of immigrants in the paint-marked sub-
populations of each pool as a result of exchange over 3
to 4 weeks.

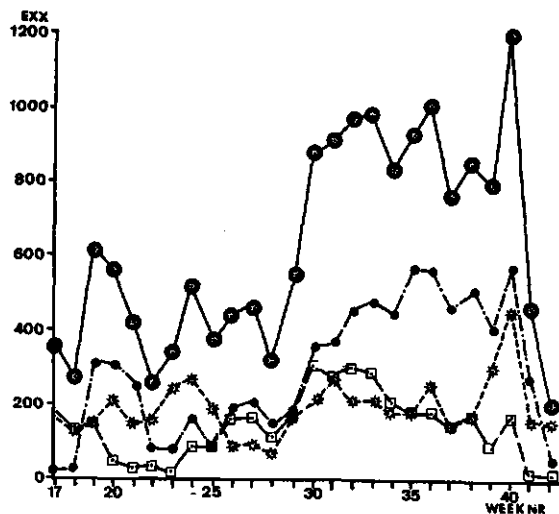|	BORDER POOLS						CENTRE POOLS					MEAN	v.c.
Pool	Wn	Bb	Me	Kr	MEAN	v.c.	Br	Wz/Sc	Bn	MEAN	v.c.		
Period													
I	32	14	73	-	39	0.76	75	53	-	64	0.24	49.4	0.53
II	30	0	41	-	24	0.90	30	66	-	48	0.53	33.4	0.71
III	47	26	42	74	47	0.42	56	100	58	71	0.35	57.6	0.41
IV	36	-	38	-	37	0.04	61	55	-	58	0.07	47.5	0.26
MEAN	36.3	13.3	48.5		38	0.56	55.5	68.5	-	62	0.31	48.0	0.48

Fig. VII-3.

Number of individuals (marked + unmarked) counted per pool-group and in the whole Br-complex.

☼   = pool-group WK
▣   = pool-group BH
●   = pool-group BM
◉   = whole Br-complex

3.4.2. In Fig VII-3 the number of beetles observed per week in each pool-group and in the whole Br-complex is given (unmarked and marked together). The total numbers decrease in spring and increase in summer and autumn. But the course in numbers is not similar in the three pool-groups. In BM the numbers follow those of the total com- plex, but in the WK and BH the numbers decrease after week 31 (period III) in contrast with the increasing numbers in pool-group BM. These differences between pool-group BM and the others may be explained by a) a possibly higher number of emerged tenerals (as a consequence of the higher number of adults during egg production in spring en sum- mer) anb by b) an exchange between the pool-groups favouring BM. The Db-values per pool-group can be calculated from the I- and E-values in Table VII-4, see Table VII-12. In all four periods Db-values for all pool-groups are below 1 (emigration)immigration), except for BM in the third period with DB=1.98, i.e. in that period BM got twice as much immigrants than it lost beetles by emigration. In accordance with this we can derive from Table VII-7 and VII-8 that in the third period BM lost less emigrants than expected and got more immigrants than expected (Table VII-12). WK got also proportionally more immi- grants in the last period, which may explain its strong increase in numbers in week 40 and 41.

3.4.3. As an example of how changes in the distribution occur on a more detailed scale Fig VII-4 shows the course in numbers at five sites in the BM-pool-group. In spring the beetles are concentrated at the east side of the pool-group (Kw, Mz and B/M). Rather quickly all
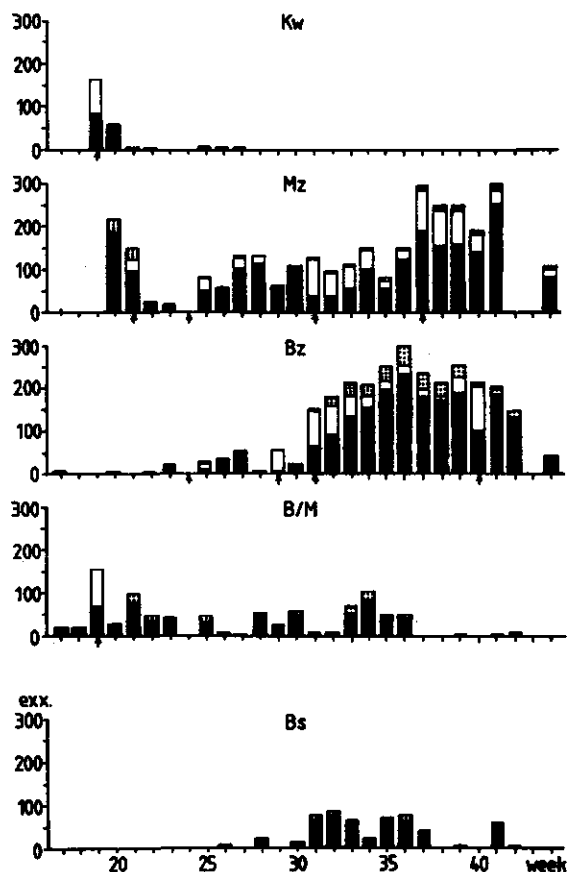
- 111 -

Fig. VII-4.

Number of beetles counted at locations in the BM-pool-group.

■ = number of unmarked beetles

□ = number of autochtonous marked beetles

⊞ = number of immigrated marked beetles;

↑ = date of release.

beetles disappear at Kw, and Mz and Bz become the more important sites with groups of beetles. During summer also a concentration of beetles is observed in the blind ditch Bs.

3.4.4. If we consider the total number of beetles observed per subpopulation as a measure for the population size, and compare that number per period with the emigration rate estimated in Table VII-4, then it appears that emigration from large subpopulations is less than from small ones, whereas the former got relatively more immigrants than the smaller subpopulations (Table VII-12: E_m increases from left to right, whereas I_m decreases).

Table VII-12. Comparison of population size with some dispersal para-
meters. The subpopulations are classified per period
according to their size (cf. Fig VII-3).
class 1 > 129 beetles observed; class 2 = 75 - 129
beetles observed; class 3 = 36 - 74 beetles observed;
class 4 = 5 - 35 beetles observed; class 5 < 4 indivi-
duals observed.
E = emigration rate (cf. Table VII-4)
E_x = net exchange rate (Table VII-6)
Db = dispersal ratio (Table VII-4)
E_{fn} = proportional contribution of emigrants to the
total number of emigrants
I_{fn} = proportional distribution of immigrants
I% = % immigrants per subpopulation after about 3
weeks (Table VII-11). Given are the mean values and
between brackets the variation coefficients.

SIZE CLASS	1		2		3		4		5		KRUSKALL-WALLIS TEST		
POPULATION	Me-1 Br-3 Me-4		Wn-1 Bb-1 Wz-1		Br-1 Sc-1 Kw-1		Kr-1 Wn-2 Br-2		Kr-2 Kw-2 Kw-3		H	z	P
	Br-4 Wz-4		Bb-2 Me-2 Wn-3		Bn-1 Wz-2 Bn-2		Sc-2 Wz-3 Sc-3		Kw-4				
			Bb-3 Me-3 Kr-3		Bn-3 Wn-4 Bb-4		Bn-4						
			Sc-3		Kr-4								
E	0.27	(0.77)	0.16	(0.39)	0.40	(0.36)	0.40	(0.41)	-		9.46	2.11	<0.05
E_x	0.04	(5.05)	0.04	(2.79)	0.12	(1.85)	0.23	(1.83)	-		1.16	0.72	>0.40
Db	1.33	(1.15)	0.76	(0.95)	0.65	(0.80)	0.70	(1.05)	-		0.59	1.15	>0.20
E_{fn}	3.81	(0.38)	3.56	(0.48)	5.04	(0.31)	4.67	(0.45)	-		3.52	0.42	>0.60
I_{fn}	23.14	(0.41)	11.19	(0.78)	11.45	(0.95)	7.87	(0.99)	0.71	(1.15)	12.54	2.36	<0.02 [1])
I%	56.60	(0.22)	36.56	(0.60)	58.75	(0.28)	53.55	(0.76)	-		4.51	0.77	>0.40

1) without class 5: H = 8.08, z = 1.28, P>0.05

3.5. Dispersal activities and weather

3.5.1. Since the paint-marked beetles were recorded daily we can
examine whether there are particular days with more or with less
dispersal activity. A Kolmogorov-Smirnov test and a chi^2 goodness-of-
fit test show that the numbers of beetles daily exchanged (X in
Table VII-13) deviate significantly from the expectations according
to a normal distribution of exchange-events (K-S test: n = 32, D =
0.340, P < 0.001; chi²-test: df = 1, X^2= 12.56, P < 0.001). High or
low dispersal activities may be connected with particular weather
conditions. In Table VII-13 some data concerning weather are added,
and the numbers of beetles exchanged under different weather condi-
tions are compared with the U-test. We only found a significant
relation between exchange and minimum temperature. As exchange by
swimming occurs mainly at night the lack of a correlation with maxi-
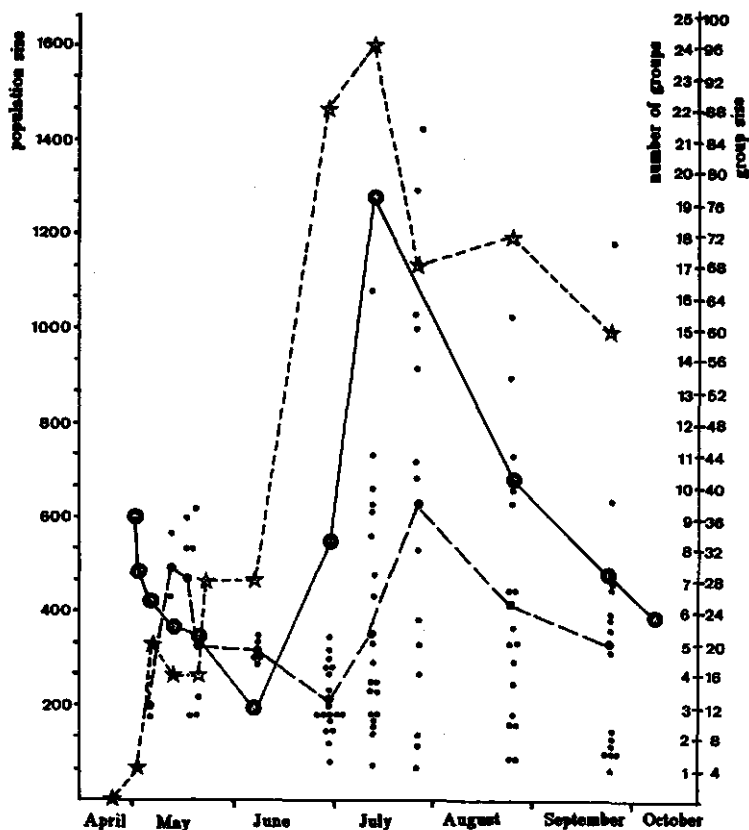
Fig. VII-5. Population size, number of groups, group size and
       percentage of individuals outside the groups during
       the year in pool SpG in 1969.

       ☆ = number of groups

       ● = mean group size (• = size of individual groups)

       ◉ = population size

U-test: X-values during some weather condition (Table VII-13)

		n_1	n_2	mean$_1$	mean$_2$	U	z	P
Tmax	: >21°C - <17°C	7	8	7.57	4.75	14	-	>0.20
Tmin	: >10°C - <8°C	11	7	7.45	3.14	13	-	<0.05
rain mm	: >1.3 mm - dry	10	12	8.70	5.08	33.5	1.76	>0.05
rain time	: >4 hours - dry	14	12	7.43	5.08	62	1.14	>0.20
wind	: >8 m/s - <6 m/s	8	8	6.75	5.25	21.5	-	>0.20
radiation	: <1500 - >2000 J/cm²	11	13	6.91	5.69	60.5	0.64	>0.20
weather I	: Tmin + rain (mm)	8	8	7.13	3.63	24.5	-	>0.20
weather II:	rain (mm) + (time)	8	12	8.50	4.25	33.5	-	>0.20

Table VII-13. The number of beetles exchanged per day between popula-
tions in the Br-complex and some weather data per day
in the first two weeks of periods I - III. X = number
of exchanged beetles; T_{max}, T_{min} = maximum, minimum
temperature per day; RAIN time = number of hours with
rain; WIND = mean wind velocity per day; RADIATION =
global radiation of the sky

PERIOD	DATE		EXCHANGE X	Tmax °C	Tmin °C	RAIN mm	WIND time	m/s	RADIATION J/cm²
I	May	24		13	10	0.1		12	498
		25	4	12	10	0.8	11	8	525
		26	10	17	8	0	3	6	2118
		27	3	21	6	0	0	5	2151
		28	1	21	6	0	0	6	2897
		29	4	22	8	0	0	6	2297
		30	4	27	9	0	0	7	2385
		31	3	29	12	0	0	6	2646
	June	1		32	14	0	0	4	2400
		2	4	27	12	1.1	2	5	2300
		3		26	10	0	0	6	2587
		4	13	27	12	0	0	5	2193
		5	11	25	13	0	0	6	1883
II	June	27		13	8	3.6	?	10	861
		28	0	16	9	1.0	8	8	1096
		29	1	18	12	2.5	14	8	675
		30	8	17	10	3.1	17	9	1263
	July	3		16	9	5.7	?	10	1205
		4	13	16	9	2.9	13	9	1521
		5	2	16	8	3.7	9	5	1487
		6	1	16	10	4.3	18	12	1603
		9		15	9	1.7	?	9	1202
		10	4	19	7	0	3	4	2345
		11	2	20	6	0.1	1	4	2756
		12	1	18	6	0	0	4	2869
		13	1	18	6	0	0	6	1654
		14	0	14	11	0	15	9	721
III	Aug.	6		19	11	0.9	?	6	1112
		7	8	18	8	1.0	8	7	1001
		8	9	19	9	1.4	5	8	1439
		9	4	19	8	0	0	6	1519
		10	1	20	11	0	0	7	1920
		11	10	16	12	0.5	9	8	820
		13		24	10	0	0	3	1490
		14	12	18	11	2.2	6	7	558
		15	7	26	12	0	1	10	2079
		16	9	20	11	2.1	2	9	1335
		17	22	19	8	5.5	9	10	1603
		18	5	20	6	0	0	4	2475

mum temperature or radiation (i.e. sunshine) is understandable. More exchange at higher minimum temperatures could be expected. On the one hand more exchange can also be expected during rain and wind, because the beetles may be disturbed by rain and waves, and the chance that they lose their way may increase. On the other hand, swim activity might be diminished during rain and wind, so that fewer beetles will run the risk of disappearing from a subpopulation. Possibly, both phenomena occur, because no significantly different exchange was found between dry days and days with rain.

4. DISCUSSION

4.1. Comparison of flight and swim activity

4.1.1. Exchange between populations by swimming can be interpreted as a result of random dispersal of individuals during activities such as looking for food. However, in the case of *Gyrinus marinus* flight may be real dispersal behaviour. It is likely that the beetles do not leave the population by flight accidentally, but because they are motivated in some way to fly. Flight is highly determined by good weather conditions.
For exchange between pools by swimming no such strong dependence on weather was found, although there is some relation with temperature.

4.1.2. Flight activity is observed in only a small part of the beetles (< 5 %) and obviously population sizes will not be changed substantially by the number of beetles emigrating or immigrating by flight. However, exchange by swimming may change populations substantially. In general this exchange will occur between populations relatively close to each other. Flight occurs over a large area but with low frequency, probably with high risks, and is possibly especially important for the (re)founding of populations, whereas swimming occurs on a smaller scale with high frequency, probably with lower risks and with direct effects on the distribution of the beetles over the habitats in the area.
See also below (4.4.)

4.2. Exchange between pools

4.2.1. The emigration from and the immigration into a pool occur not randomly, but also depend on local circumstances. Such as the layout of the habitat: the position of the openings to other pools, the number of alternative routesway, distances between populations, etc. Since we rarely found beetles along marshy or bare banks we may assume that local qualities are also important. From experiments we know that a group of beetles is attractive to a swimming beetle and may cause a beetle to stay in that group (Grooters and Groothuis 1979a/b, Zijlstra 1979). The groups change in size and location. This

may account for the variation in exchange rate between one pool and the rest of the pools. For example, the exchange between the pools Bb and Kr and the rest of the complex is more intensive in the third period, when several groups are present in Bn, than in the previous periods when no groups were present in Bn. That beetles emigrate less from and immigrate more to subpopulations of large size than from or into populations of small sizes may also be due to the attraction of groups. In a preceding study it was found that with increasing population size not so much the size of the groups, but the number of groups increased (Fig VII-6). We may assume that with more groups per pool the chance will increase that a beetle will have found a group before leaving the pool; the same holds for an immigrating beetle.

4.3.2. The effects of dispersal activities upon the composition and size of the subpopulation will be different for each pool, and also the influence of the course of events in one pool upon the dynamics in other pools will be different from pool to pool. Although we know some of the factors that play a part, the total process of exchange as a whole is highly stochastic, i.e. many factors are unknown and variable in time and/or place in an unpredictable way.

4.4. The effects of exchange between pools upon population size

4.4.1. Exchange by swimming between pools can be considerable, a subpopulation can consist for an important part of immigrants (cf pool Br), and population size can thus be changed substantially by emigration and immigration. We found that in most cases the loss of individuals from a population by emigration is greater than the gain by immigration. In some populations sizes are decreased substantially by emigration. To this extent exchange by swimming seems to be unfavourable for the maintenance of a population. On the other hand, in one-third of the cases, not restricted to some subpopulation or period, a dispersal-ratio greater than 1 was found, i.e. more beetles were immigrating than were emigrated. Six of the nine populations studied gave at least once a Db>1, and Db-values greater than 1 occured in periods I to III. This variation in displacement of beetles in time and in space will decrease the chance of local extinction and will cause some sites to be re-occupied by a new local subpopulation. In this way the risk of unfavourable changes in the overall dynamics are spread over a variable number of places, which also change in position, so that the chance of extinction of the population as a whole in the complex may decrease ('spreading of risk', e.g. den Boer 1968, 1981)

4.4.2. Theoretically the exchange between subpopulations may result in a greater stability of population numbers (e.g. den Boer 1981). This is also confirmed by simulations (e.g. Reddingius and den Boer 1970). Furthermore Kuno (1981) added a special effect of exchange between subpopulations that fluctuate asynchronously. In such case

mean population size even increases due to exchange of individuals followed by reproduction (see also Metz et al 1983).
Obviously the risks of dispersal are crucial to population dynamics and may generate alternative hypotheses to understand dispersal activities: Why should an individual leave its population when the risk of death during dispersal is high? Why should emigration occur if the loss by emigration is greater than the gain by immigration?

4.4.3. To judge the significance of exchange between populations the negative effects (losses by death, disappearance from the complex of subpopulations) have to be weighed against the positive effects (spreading of risk, the 'Kuno'effect, (re)founding of subpopulations). Theoretically, variation in the numerical processes within and between populations are determining the power of the positive effects of dispersal activities (Southwood 1962, den Boer 1981, Kuno 1981). Therefore, such a weighing of negative and positive effects of dispersal activities can hardly occur without simulation experiments. Such experiments will be discussed in Chapter VIII. At the moment we can only report empirical findings that (1) there is a considerable emigration by swimming, (2) swim-activities are probably necessary for daily life, (3) exchange between pools possibly occurs by accident, (4) exchange between subpopulations depends on the distance between them, the structure of the route and the number of alternatives, (5) emigration can lead to extinction of local subpopulations as well as to founding of new ones, (6) the dispersal ratio can be greater than 1, and (7) the composition and size of subpopulations can change considerably because of exchange by swimming.

4.4.4. The irregular exchange rates between different subpopulations and sites within the whole population in the BR-complex leads to confusion in regard to defining of subpopulation and interaction group (e.g. den Boer 1977, pag 23) and to complications in using mark-recapture methods for estimating population numbers (e.g. methods of Jolly (1965) and Fisher and Ford (1947). The boundaries of an interaction group become variable by the changing movements of the individual beetles and changes in the distribution in a pool. When not all samples concern the whole area of such a population the assumption of equal chances for each individual to be caught can not be fulfilled. In such situations samples that are taken from a part of a habitat may also be inaccurate in estimating the quantitative presence of some species.

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FIRST PERIOD (SPRING - 11 weeks)

NUMBER OF FEMALES | NUMBER OF MALES

max. natality

$k_{5,6}$ mortality in the population

MAX. EGG PRODUCTION

k_1 reduction of max. egg production

$k_{7,8}$ mortality during flight

EGG PRODUCTION

k_2 egg mortality

$k_{9,10}$ mortality during swimming

FIRST LARVAL INSTAR

k_3 larval and pupal mortality

TENERALS | SURVIVING FEMALES | SURVIVING MALES

k_4 mortality during hardening

NEW FEMALES | NEW MALES | added to next generation in succeding weeks

SECOND PERIOD (SUMMER - 7 weeks)

NUMBER OF FEMALES | NUMBER OF MALES

same processes of reproduction and adult survival as in first period, but with other values (k_{11} - k_{20})

THIRD PERIOD (AUTUMN - 6 weeks)

NUMBER OF FEMALES | NUMBER OF MALES

no reproduction

processes of adult survival as in first period (k_{21} - k_{26})

FOURTH PERIOD (WINTER)

NUMBER OF FEMALES | NUMBER OF MALES

no reproduction

$k_{27,28}$ mortality during hibernation
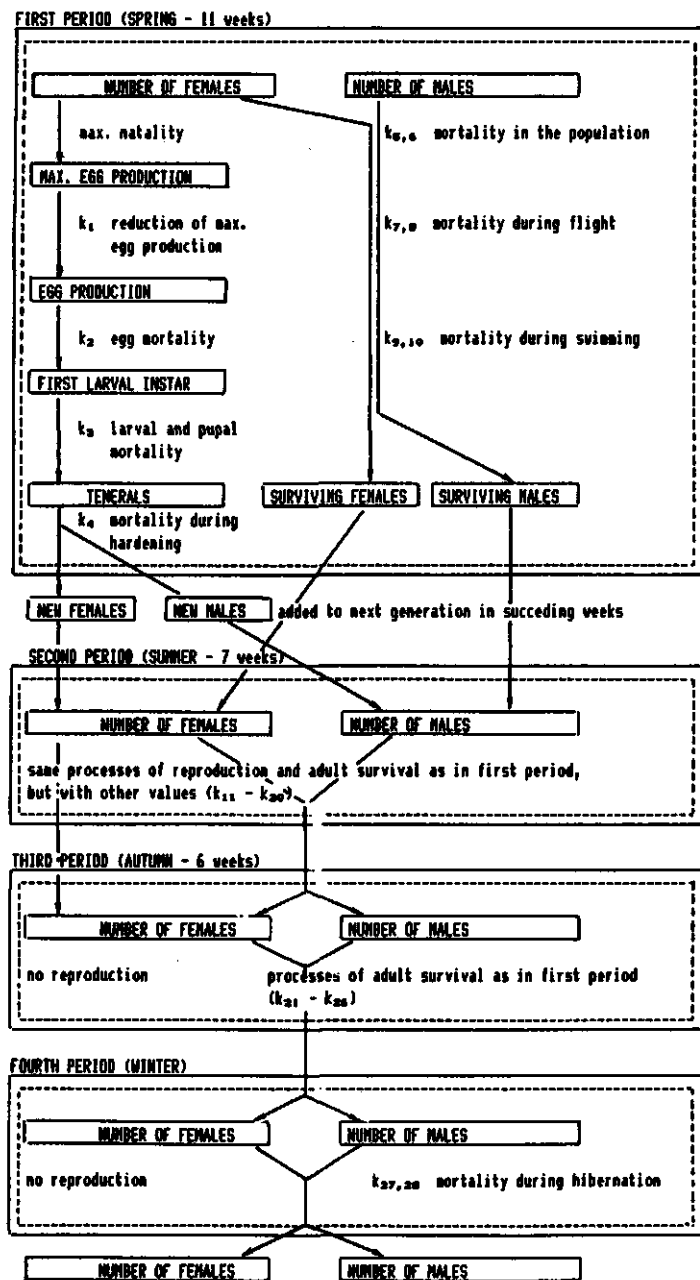
NUMBER OF FEMALES | NUMBER OF MALES

Fig. VIII-1. Diagram of the simulation model as source for the key-factor analysis.

CHAPTER VIII.   DISCUSSION AND SIMULATIONS

This chapter will also be published with minor changes in text in Oecologia (in press)

SUMMARY
The results of a field study of the population dynamics of the water
beetle *Gyrinus marinus Gyll.* with the aim of tracing the effects   of
dispersal activities are checked and assessed by k-factor analysis as
well as by stochastic simulation modelling.
The key-factor analysis establishes that survival of adult beetles
from hibernation is the key-factor and highly determines population
size after hibernation. Survival during larval and pupal development
in spring is less, but still significantly determining the size   of
population fluctuations. According to the key-factor analysis survi-
val   at   all other developmental and adult stages are immaterial   for
the fluctuations in population size.
Computer simulations show that even a small dispersal activity (three
per cent of the individuals) with immigration into other populations
significantly restricts the fluctuations in population size,   both
decreasing the chance of extinction of the population and the range
of population sizes, in spite of the extra losses during dispersal
activities. These effects of dispersal are most decisive when survi-
val chances in the populations are low and when dispersal occurs   at
least also out of the period of reproduction.   There is a rather
complicated relationship between the survival chances during and out
of the reproduction season, the success of reproduction, the survival
from dispersal and the optimal level of dispersal activities.   When
the number of suitable habitats is low or when the exchange between
habitats highly depends on the distances between habitats,   the ef-
fects of dispersal are less than with a high number of habitats   or
when exchange is less distance-dependent. Dispersal as a result   of
high population densities restricts fluctuations in population size
to a similar extent as randomly occuring dispersal, but though it
longer keeps populations at higher densities as soon as the popula-
tion density has become low the chance of extinction will be high.
Dispersal as a direct result of adverse conditions only restricts
fluctuations if dispersal occurs in most of the habitats. This situa-
tion is probably less predictable than when dispersal is due   to
density-dependent or random processes. A decrease of the variation in
space (more synchronisation between habitats) increases the chance of
extinction, whereas a decrease of the variation in time decreases it.
Simulations that imitate the field situation as closely as possible
show that even the very limited flight activity of *Gyrinus marinus*
may highly decrease the chance of extinction. In simulation experi-
ments with natural selection between Mendelian genotypes with reces-
sive dispersal ability (M) on the one hand and without dispersal
ability (B) at the other, the relative frequency of the M-genotype
decreases with increasing population sizes, and increases with de-
creasing sizes. The M-genotype tends to low frequencies, as is known
from some carabid beetles species with macropterous and brachypterous

genotypes. The fluctuation in numbers of the M-genotype is relatively restricted, as compared with that of the B-genotype. The heterozygote functions as a buffer, lowering the chance of disappearance of one of the homozygote genotypes.

1. INTRODUCTION

1.1. In the previous chapters IV - VII reproduction and recruitment, as well as survival and dispersal both by flight and by swimming were analysed in the context of a comprehensive study of the population dynamics of the waterbeetle *Gyrinus marinus Gyll.*
In this chapter the estimates from the field study are brought to-gether into simulation models to assess the significance of the dispersal activities found for population dynamics in general, and for *Gyrinus marinus* in particular. But first, using key-factor analysis, we will establish the relative importance of the consecutive stages during the development from egg to adult beetle for the changes in population size.

1.2. In Table VIII-1 the mean values and variation coefficients for reproduction, survival and dispersal from our field study are recapi-tulated. A substantial variation was found in the viability of eggs, the number of tenerals per oviposition, the survival of tenerals, the succes of hibernation, and the degree of dispersal both by flight and by swimming.   The survival chance per week as well as egg production showed a low variation coefficient.   The variation of survival during exchange by flight cannot be important, because it concerns only a small fraction of the beetles. The mortality during the different stages of development from egg until reproducing beetle can be mu-tually compared by k-factor analysis (Morris 1963, Varley and Grad-well 1960). The situation is complicated however, when an entire year is considered, since we have to deal then with two succeeding repro-duction seasons, followed by a non-reproductive period in autumn and by hibernation.

2. KEY-FACTOR ANALYSIS

2.1. Introduction and methods
2.2.1. Key-factor analysis is a method to establish which stages during the development from adult to the next adult generation govern changes in population size (Varley and Gradwell 1960, Morris 1963, Podoler and Rogers 1975, Southwood 1978). Demographic processes among adults, such as mortality and dispersal are also considered stages in this model. The survival in each stage is defined by the chance of the individuals to reach the next one. The method requires the avai-lability of data for a sequence of generations. For each generation the number of individuals (P_t) that is alive at the beginning of each stage (t) is calculated. The variables S_t, defined as $\log(P_t)$, and

Table VIII-1. A review of mean values and variation coefficients per week for reproduction, recruitment, survival and dispersal. Survival in larval and pupal stages was not estimated in the field.

PROCESS/STAGE	MEAN VALUE (+ VARIATION COEFFICIENT)		
	FEMALES	MALES	ALL INDIVIDUALS
REPRODUCTION			
spring generation			
max egg prod. per oviposition	38		
mean eggs laid per oviposition	32 (0.31)		
viability of eggs			0.60 (0.60)
survival larval and pupal stage			0.09 (-)
tenerals per oviposition			1.80 (0.54)
summer generation			
max egg prod. per oviposition	32		
mean eggs laid per oviposition	25 (0.42)		
viability of eggs			0.60 (0.60)
survival larval and pupal stage			0.10 (-)
tenerals per oviposition			1.50 (0.32)
SURVIVAL CHANCE OF ADULTS			
restricted survival of tenerals[1]	0.89 (0.36)	0.96 (0.26)	
survival in spring	0.89 (0.05)	0.91 (0.04)	
survival in summer	0.86 (0.06)	0.88 (0.05)	
survival in autumn	0.77 (0.07)	0.78 (0.09)	
survival in winter	0.35 (0.82)	0.32 (0.73)	
DISPERSAL ACTIVITIES			
emigration by flight [2]	0.025 (1.44)	0.050 (0.70)	
survival during flight	≤ 0.40	≤ 0.40	
emigration by swimming			
in spring	0.33 (0.52)	0.36 (0.47)	
in June/July	0.24 (0.57)	0.27 (0.44)	
in August/September	0.23 (0.60)	0.26 (0.55)	
in September/October	0.18 (0.60)	0.20 (0.59)	
survival during swimming			
in spring			0.70 (0.21)
in June/July			0.62 (0.44)
in August/September			0.84 (0.21)
in September/October			0.72 (0.36)

[1] The survival chance of tenerals is found by multiplication this reduction factor with the survival chance per season mentioned below.

[2] Flight depends on weather, and, for females, reproductive activity (less flight activity during reproduction)
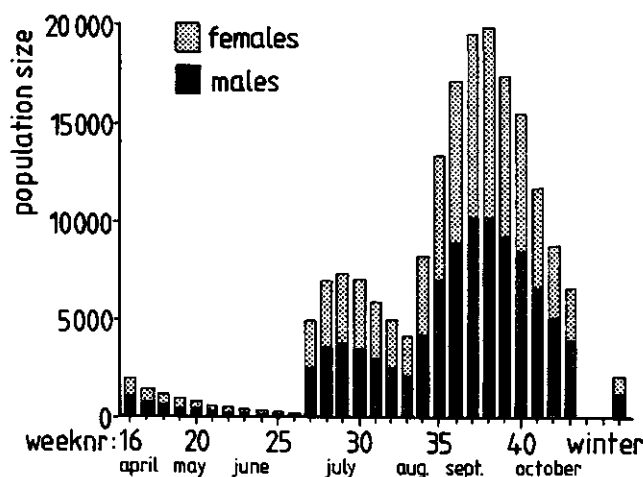
Fig. VIII-2.

Fluctuation in population size during a single year due to reproduction and survival, as an average of 100 stochastic simulations (see text).

k_t, defined as $S_{t-1} - S_t$, are calculated for each stage in each generation. The sum of the k_t-values gives the value of K (generation mortality). The mean k_t-value per stage indicates the average decrease in numbers from the beginning to the end of that stage, so that a higher mean k_t-value indicates that greater losses during that stage and thus a higher mortality is expected. As k-values are differences between two logarithms at base 10, k=0.05 corresponds with a mortality of 0.11, K=0.3 with one of 0.5 and k=1.0 with a mortality of about 0.9.

2.2.2 In our case only a small number of generations was studied, and for most generations only part of the required data could be directly estimated. Nevertheless, for most stages we could reasonably estimate a mean survival chance and a variation coefficient. These two parameters per stage suffice to simulate a number of generations, which can then be subjected to a key-factor analysis.

2.2.3. In the model the year is divided into four seasons: two reproductive seasons (spring and summer) each with a separate generation, a post-reproductive season (autumn) with the third generation which has to survive the fourth season (winter), cf. Fig VIII-1, VIII-2. For each season the K_s-value is the sum of the relevant k_t-values ($\sum k_t$), i.e. season-mortality. K_y is the grand sum of all k_t-values $\sum\sum k_t$).
In the first two seasons two processes occur at the same time: (1) reproduction, with stages from egg production to the hardening of tenerals and (2) mortality of adult beetles, which can be divided

into mortality in the population and mortality during dispersal by flight and by swimming. Only dispersal losses can be taken into account in a key-factor analysis, not dispersal itself or the resulting exchange between populations.

2.2.4. The survival per stage is simulated for each year and for each generation by drawing random values from the frequency distribution fitted to the suvival values from the field. The simulation is repeated 100 times, starting each year with 1000 females and 1000 males emerging from hibernation. The average course of numbers during the year according to this simulation is shown in Fig VIII-2. The listing of the simulation-program is available on request.

Table VIII-2. The 10 stages between egg and adult with the greatest losses according to a key-factor analysis on simulated field values (see text). Ranked from high to low.

stage	rank	k
mortality of males during hibernation	1	1.307
mortality of females during hibernation	2	1.246
mortality during larval and pupal development in spring	3	0.793
mortality during larval and pupal development in summer	4	0.787
mortality of females in autumn	5	0.382
mortality of female tenerals in summer	6	0.369
mortality of females in summer	7	0.368
mortality of males in autumn	8	0.362
mortality of female tenerals in spring	9	0.351
mortality of males during dispersal by swimming in spring	10	0.328

2.3. Results of key-factor analysis

2.3.1. The 10 stages with the greatest losses are shown in Table VIII-2. On the average 43.0 per cent of the losses occur during hibernation and 26.6 per cent during larval and pupal development. The losses from dispersal by swimming or by flight are negligible except for swimming activities in spring. Note that five of the stages concern mortality in females, and only three stages concern male mortality. Neither reduction of maximal egg production (k_1) nor egg mortality (k_2) result in great losses.

2.3.2. Besides the magnitude of the mean k-value, the variation around the mean is significant because it determines the fluctuations of population size. It is clear that a high k-value with a small variation makes only a small contribution to the variation in popula-

tion size. The same applies to small k-values, irrespective their
variances. Therefore, the product of the mean k_i-value and its
standard deviation (sd) will give a good indication of the relative
contribution that each stage may give to the variation of population
size. Ranking the stages again, the order is not changed in compa-
rison to Table VIII-2 for the first five stages, see Table VIII-3.
Mortality during hibernation and, to a much smaller degree during
larval and pupal development apparently govern the fluctuations in
population size of adult beetles. It is important to note that the
activities of adult beetles may have no influence on such losses, see
below. Mortality of adults during the active seasons, and egg losses
seem to be of only minor importance.

2.3.3. The contribution of the mortality in each stage to the varia-
tion in population size at the end of each season, and to that after
hibernation at the end of one year-cycle is indicated by the product-
moment correlation coefficients between the k-values concerned and
(1) the K-factors of each period (K_p) and (2) the K-factors of the
total year (K_y).

Table VIII-3. The age-stages ranked according to k×sd-values as found
with a key-factor analysis of the data from a simula-
tion of the field data (see text).

stage	rank	k×sd	r_p	r_y
mortality of males from hibernation	1	0.459	0.706	0.582
mortality of females from hibernation	2	0.438	0.732	0.677
mortality from development[1] in spring	3	0.091	0.622	0.226
mortality from development in summer	4	0.076	0.167	0.130
mortality of females in autumn	5	0.035	0.194	-0.036
mortality of males from swimming[2] in spring	6	0.025	-0.338	-0.049
mortality of eggs in summer	7	0.024	-0.086	0.002
mortality of males in summer	8	0.024	-0.321	-0.135
mortality of eggs in spring	9	0.022	0.084	0.066
mortality of females in autumn	10	0.021	0.034	0.192
mortality of males in autumn	11	0.021	-0.029	0.132
mortality of females from swimming in spring	12	0.019	0.122	0.150
mortality of females in spring	13	0.015	-0.072	-0.143
mortality of males from swimming in summer	14	0.013	-0.118	-0.017
mortality of females from swimming in summer	15	0.012	-0.210	0.131

[1] development = larval + pupal development
[2] swimming = dispersal by swimming

2.3.4. In our case a product-moment correlation is significant for r
> 0.20 (df=98, P<0.05, Sachs 1984). The k-values of most stages are
not correlated with K_P or K_y, see Table VIII-3. Stages important to
the fluctuations in population size must have a substantial Kxsd-
value and also have significant r-values with K_P- or K_y-values. It
appears that fluctuations in the yearly population size are highly
determined by hibernation and to a lesser degree by the developmental
stages from egg until teneral in spring. The influence of the other
stages upon the fluctuations of yearly population size is of seconda-
ry importance only.

3. EXCHANGE BETWEEN POPULATIONS

3.1. Introduction

3.1.1. Besides hibernation and development in spring, the other
stages in the key-factor analysis above, including dispersal acti-
vities of adults, have only low values for $k_1$xsd and/or for r. There-
fore, it seems immaterial for the fluctuations of population size
what happens to the adults during the seasons in which they are
active.
But a key-factor analysis deals only with a single population unit,
whereas the significance of dispersal may be the exchange between
different population units. Moreover, the key-factor analysis only
deals with the variation in the costs of dispersal, not with its
possible advantages: the analysis can only consider changes in num-
bers of individuals, not changes in the distribution of numbers of
individuals over the population area.

3.1.2. The field data show a considerable variation in survival
during hibernation (Table VIII-1). Thus, the future of a population
unit is rather uncertain, and therefore the units can be considered
unstable. Two processes may decrease the variation in population size
caused by mortality during hibernation: (1) density-dependent proces-
ses and (2) exchange between (sub)populations.
According to our key-factor analysis density-dependent processes
concerning the adult beetles will have little influence on the varia-
tion in population sizes. Egg-laying might be density-dependent,
being influenced, for example, by changes in the quantity or quality
of food. But although there is a considerable variation in the num-
bers of eggs laid per oviposition and per female, only minor varia-
tion was found between different populations and between different
seasons (Chapter IV). It is possible that we did not estimate egg
production in situations in which density-dependent egg laying be-
comes important. However, comparing the $(k_1$xsd)-values of egg produc-
tion with those of hibernation (cf Table VIII-3), it is doubtful
whether egg production can have a regulating influence on the popula-
tion size of adult beetles.

3.1.3. Another density-dependent process may be found in larval development. In laboratory experiments with larvae of *Dineutes* (an American whirligig beetle species) cannibalism occured depending upon the available food (Istock 1966, 1967), but it is not clear whether larval cannibalism plays an important role in the field. Moreover, the $k_{\ast}\ast sd$-values of larval and pupal development are at least five times smaller than those of hibernation, so that larval and pupal developments cannot match themselves against hibernation in its influence upon overall fluctuations of population sizes. Like egg production, even if survival of larvae and pupae is density-dependent it is doubtful whether it can have a regulating influence on the population sizes of adults.

3.1.4. Moreover, it seems that, at least in our study area, the chance of extinction is more relevant than the chance of overcrowding. Thus, though a density-dependent egg production or larval mortality might possibly lower high numbers of individuals, it may be doubted whether small populations can be saved from extinction in that way. See also den BOER (1986) for a discussion of density-dependent processes and their effect on population stability.

3.1.5. Southwood (1962) concludes that the amount of dispersal activity is related to the instability of the habitat. Species from instable habitats should show more dispersal than species usually living in more stable habitats. Den Boer (1968) developed the hypothesis of 'spreading of risk'. He supposes, among other things, that the dispersal of individuals between different sites or habitats would decrease the chance of extinction of the populations at the sites concerned and also lead to the (re)colonization of favourable habitats.

3.1.6. Kuno (1981) draws our attention to the fact that exchange between two populations with net reproduction asynchronously varying around R=1 will result in a relative increase of numbers in both populations. Metz et al (1983) and Klinkhamer et al (1984) show in simulations that partial exchange will also lead to a significant improvement of net reproduction ('Kuno'-effect). As the Kuno-effect can only manifest itself in the redistribution of the progeny, we can expect that it will only be traced in following generations, i.e. it occurs when the progeny is dispersing, not when the parents are dispersing (see also de Jong 1979).

3.1.7. In concordance with Southwood's postulation that dispersal is related to the instability of the habitat, we may suppose that the less predictable the conditions in the habitat are the stronger the positive effects of exchange between populations will be. Southwood implicitly assumes that the occurrence of dispersal is related both to mortality in the population and to mortality during dispersal. The worse the prospects for survival and reproduction in the population are or the better these prospects after dispersal activity, the more dispersal activity can occur. Implicitly is accepted that dispersal
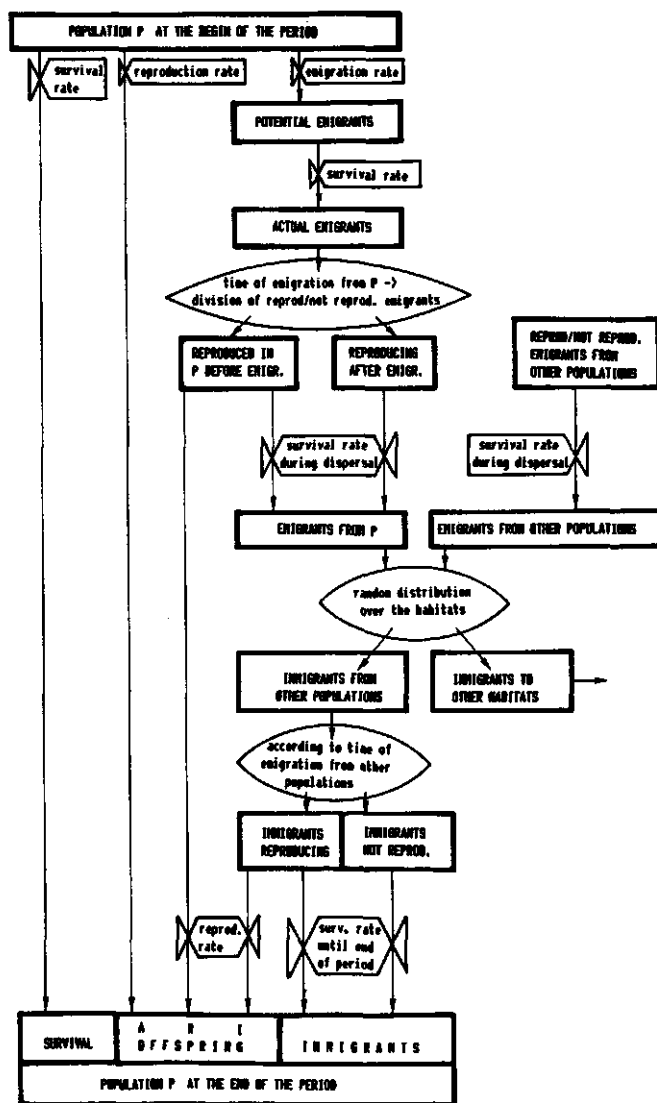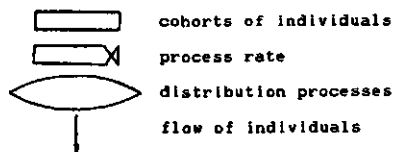
Fig. VIII-3. A flow-diagram of the model used as basis for the stochastic simulations to trace the effects of dispersal activities (see text).

cohorts of individuals

process rate

distribution processes

flow of individuals

activity can occur more randomly when the conditions are more in-
stable and that it will not only occur when conditions are adverse.
Den Boer and Kuno suppose that dispersal not only may have the short
term advantage to an individual of leaving an adverse situation, and
sometimes of escaping overcrowding, but in the long term it will
favour the populations (and thus the individuals or their progeny
concerned) between which exchange occurs.

3.1.8. From this point of view, we can expect that exchange between
Gyrinus-populations may favour persistence of the populations in the
study area. The question is, of course, whether or not the estimated
values for exchange, for reproduction and for survival chances in the
populations as well as during dispersal will allow dispersal to
improve the chance of persistence per population by contributing to a
levelling of population fluctuations. In the following we will try to
investigate this with the help of simulation experiments. The in-
fluence of selection upon dispersal activity will also be simulated.
Apart from the particular situation of the studied populations of
Gyrinus, the effects of dispersal under other conditions will also be
considered.

3.2. Description of the simulation models

3.2.1. Simulation models have to be considered with scepticism. The
results may be greatly influenced by the organization of the model,
the algorithms used, the assumptions, etc. (van der Eijk 1984). To
assess the results of a simulation one must be able to understand the
model, and that is why it is explained rather extensively. A listing
of the model is available on request. A flow-diagram is given in Fig.
VIII-3.

3.2.2. The simulations were run on a 4 MHz personal computer and the
program was writen in MicroSoft Basic. We aimed to construct a model
that simulates the field situation as closely as possible, without
making use of predetermined mathematical functions to describe a
process. As usually in constructing complicated models a number of
versions were developed, from simple to highly complicated. In gene-
ral each process in the more developed versions of the model was
simulated by summation and subtraction. Multiplication was used only
in reproduction procedures. For example, if a number of emigrants
from one habitat had to be distributed randomly over 19 other habi-
tats, we did not use the quick method of dividing the emigrants
randomly into 19 parts, but for each emigrant anew was chosen the
habitat into which it will immigrate, which is how such processes
occur in the field. Only for large numbers of identical emigrants the
quick method was used. The consequence of such a program is that the
simulation takes a great deal of time; a complicated simulation over
100 years took about three days of computer time!

3.2.3. The following features were built into the model:
- Reproduction, survival, hibernation and dispersal were considered separate processes; optionally they could influence each other.
- The initial version of the model concerned two 'species' differing in only one feature: one 'species' (M) shows dispersal, the other one (B) does not (imagine a macropterous and a brachypterous insect species respectively). In more developed versions the two 'species' became two genotypes of the same species, so that the genetic aspects of dispersal could be taken into account.
- In the initial versions no distinction was made between males and females, more developed versions differentiated males and females.
- There was a number of 'habitats' (mostly 20 in initial versions and 10 in more developed versions), between which exchange could occur.
- At the start the population size per habitat could either be deter-mined randomly or set equal for each habitat.
- In a single year two or three generations could occur, the genera-tion in spring always being the hibernated generation from the pre-vious autumn. In early versions there was only one time step per generation, in later versions the model worked with steps of one month. This resulted in significant alterations in the model. For example, the time required for development from egg to teneral was no longer immaterial, because it takes more than one month, i.e. now more than one time step.
- Before the simulation started, for each period (generation or month) mean values and variation coefficients of reproduction, survi-val and dispersal were entered. In the more developed versions both variation in time and variation between habitats were introduced. For each habitat in each period for each process a random value X was taken from a normal distribution with the entered mean and variation coefficient as parameters: $X = m*(a*b*v + 1)$, if m = the mean, v = variation coefficient, $a =\cos(2*rnd)$ (rnd = a random number from a homogeneous distribution between 0 and 1, $b = \sqrt{(-2*\ln(rnd))}$
- Optionally, survival and dispersal could be made density-dependent; dispersal could also be made dependent on the occurrence of adverse conditions.
- Optionally, the variation in some process can be simulated as running synchronously between habitats (for example to simulate an overall influence of weather: if it was cold in one habitat it was more or less cold in all habitats).
- Optionally, the processes could be simulated as being interdepen-dent.
- Optionally, the distribution of dispersing individuals over other habitats could be made dependent on the distance from the source habitat.
- Dispersing females were divided into those reproducing in the new habitat and those that have already reproduced in the old one. In versions with selection females were divided in females that were fertilized before emigration and females that were not. The program noted the genotype of the male that fertilized a dispersing female.
- The amount of eggs laid by an immigrated female was assumed to be influenced by the conditions in its new habitat but not by those in

the previous one.
- To compare the different simulations the random numbers used in a
given process in later versions of the model were the same for each
sequence. In this way in simulations with different starting features
and/or different conditions the population dynamics were considered
as running through the same sequence of years with, for example, the
same weather conditions at the same times.

3.3. Results

3.3.1. The effects of dispersal in relation to reproduction and survival.

3.3.1.1. In many insect species no flight activities occur during
reproduction (or occur only at a low intensity), see Johnson (1969:
the oogenesis-flight syndrome), den Boer (1977) and van Huizen
(1979)). Both flight activities and the production of eggs are consi-
dered to demand much energy and would thus generally exclude each
other (e.g. Johnson 1969). On the other hand, it could be favourable
for females to distribute their egg-clusters over a number of diffe-
rent patches (de Jong 1979). *Gyrinus* females are able to combine
flight activities with egg production, although they fly at a lower
frequency than after the reproduction period (Chapter VI). Exchange
between populations by swimming is higher during the reproduction
period than afterwards (Chapter VII).
In theoretical analyses of exchange between populations (e.g. Reddin-
gius and den Boer 1970, de Jong 1979, Kuno 1981, Metz et al 1983,
Klinkhamer et al 1984) the conclusions are restricted to annual
species, or at least to species in which the individuals of consecu-
tive generations are strictly separated in time. In S 3.1.7. we
argued that dispersal will be the more important the lower the expec-
tation of life of the individuals. Therefore, it might be expected
that perennial species will show less dispersal than annual species.
On the average 25 per cent of the spring generation of whirligig
beetles is still alive when the summer generation emerges, but only a
low percentage of the summer generation will be alive the next spring
and able to reproduce a second time. It is nearly completely the
autumn generation that reproduces in spring.

To trace the relationship between dispersal activities on the one
hand and reproduction and survival on the other we can use the re-
sults of the simplest version of the simulation model, in which each
year has only two periods, a reproductive season followed by a pre-
reproductive season of the offspring. In this version two 'species'
were simulated, one (M) with, the other (B) without dispersal activi-
ty. The different values of reproduction and survival per habitat and
per period were, however, the same in both species, so that possible
difference in the course of population size could only be due to the
difference in dispersal activity. Though this simple model was in-
spired by the field study on *Gyrinus marinus,* it is not a model of the

population dynamics of *Gyrinus.* None the less, the results obtained appear similar to those of the more complex models that better imitate the field situation of *Gyrinus marinus* (see below).

3.3.1.2. Some results of these simulations over 25 years are shown in Table VIII-4. The simulations distinguish between (1) a low (0.05) or (2) a high (0.50) survival chance in the reproductive season, and between situations with (a) a rather low (0.20) and (b) a rather high (0.50) survival chance in the second season. The mean value for reproduction is adjusted such that the expectation value of net reproduction for the B-population is R = 1 (no decrease or increase of population size expected). Low (about 3 %) and high (about 50 %) dispersal during and/or after the reproduction season is compared with the situation without dispersal. The survival from dispersal is 80 per cent (I/E = 0.8). In the area simulated 20 favourable habitats are available. Each habitat starts with 500 individuals of both species. The population per habitat is considered as a local population of the overall natural population from all habitats together. The situation after 25 years is given by the distribution of local population sizes over six logarithmic classes. The mean net reproduction of the overall population in the total area is given by $R_{g} = (P_{n}/P_{0})^{(1/n)}$, Since, $R = P_{1}/P_{0} * P_{2}/P_{1} * .. * P_{n}/P_{n-1} = P_{n}/P_{0}.^{(1/n)}$ The variation of R is the average of the variation coefficients of R-values over n (n≤25) years. The range between which the total population size has fluctuated is given by the Log-Range, $LR = \log(H) - \log(L)$, if H and L are the highest and lowest total population size respectively (cf den Boer 1981).

3.3.1.3. The following average results were obtained from 10 runs per situation (Table VIII-4):
Simulation (1a). Low survival chances in both seasons (no overlap of generations, annual species).
- Within 25 years species B, without dispersal, diesout in about 50 percent of the habitats. Most of the surviving populations contain less than 100 individuals.
- In all situations with dispersal the chance of extinction per local population is smaller than without dispersal, with almost no extinctions within 25 years. But the size of the dispersal effects depends distinctly on the amount and season of dispersal.
- Dispersal during reproduction has only little or no effect on population size and fluctuation range, but the chance of extinction is significantly diminished, even if only three per cent of the individuals show dispersal activities. With a high dispersal level population sizes decrease, but with less heavy fluctuations (Table VIII-4:v.c.R_{g}, but not LR). However, on the long term this will lead to extinction in all 20 habitats (the deterministic prediction from the average $R_{g} < 1$ is that after 75 years only 3 individuals should still be present in the area).
- Dispersal that only occurs after reproduction, i.e. that is shown mainly by the offspring, has clear positive effects: Both the variation and the range of population size is reduced in comparison with

Table VIII-4. Simulations of dispersal activity during 25 years in an area with 20 habitats, with asynchronously changing conditions of survival and reproduction. A year is divided into two seasons, a reproductive season and a non-reproductive one during which the tenerals enter the population (to reproduce in the next year). Variation coefficient used with all mean values = 0.4. Survival chance from dispersal (I/E) = 0.8. Mean values:

Q_1, Q_2 =survival in first and second season respectively
ten = number of tenerals/adult
d_1, d_2 =percentage of emigrating individuals
0, 10^1,.., $>10^4$ = mean number of populations after 25 years with sizes of 0, $1-10^1$, $10^1 - 10^2$,.., $>10^4$
R_g = geometric mean of net reproduction values = $(P_n/P0)(1/n)$, if P_0 = starting size (= $20 \times 500 = 10000$), and n = last year the species was present in the area ($n \leq 25$)
$v.c.R_g$ = variation coefficient of R_g
LR = log(H)-log(L), if H and L are the highest and the lowest population size observed, respectively.
B = simulation of species B (no dispersal)
M = simulation of species M (with dispersal)

the case without dispersal after reproduction, and also the mean population sizes after 25 years are higher. With a high dispersal level the populations even increase in size (Kuno-effect).
- With dispersal in the pre-reproductive season of the offspring, population sizes below 10 become rare, while population sizes above 1000 (i.e. at least twice the start value) occur more frequently. This can also be seen in Fig VIII-4, showing the fluctuations in the population size of all 20 habitats taken together from one simulation.
- A further stabilization and decrease of both variation and size-range is reached when dispersal occurs during the whole year, i.e. in both seasons. However, a high dispersal level in one season overrules a low dispersal level in the other season. We see that a low dispersal rate during reproduction together with a low or high dispersal rate out of the reproductive season gives the best stabilizing effects: R_g has most approached R = 1, both the variation and the range of population sizes are very low. This situation comes rather close to the field situation in many surface dwelling arthropods.
- In Fig VIII-4 is shown that with low dispersal rates the population sizes follow about the same course as without dispersal activity: downward trend during the first 15 years, then rapidly increasing again. Only with a high dispersal rate outside of the reproductive season is a rather stable pattern at a hardly changing level shown.

Table VIII-4

1a. Q_1 = 0.05, Q_2 = 0.20, ten = 5.00

	d_1	d_2	0	10^1	10^2	10^3	10^4	$>10^4$	R_g	v.c.R_g	LR
B	–	–	9.5	4.5	2.5	2.0	1.5	–	0.958	0.311	1.012
M	3	–	1.0	7.5	7.0	3.0	1.5	–	0.959	0.299	0.939
M	50	–	–	8.5	9.0	2.0	0.5	–	0.898	0.154	1.222
M	–	3	–	0.5	8.5	9.5	2.0	–	0.987	0.246	0.723
M	–	50	–	–	5.5	9.0	5.0	0.5	1.016	0.130	0.356
M	3	3	0	0	3	12	5	0	1.009	0.289	0.615
M	3	50	0	0	0	12	7	1	1.002	0.121	0.183
M	50	3	0	2	14	4	0	0	0.909	0.172	1.097
	0	50	0	0	8	11	1	0	0.923	0.127	0.866

1b. Q_1 = 0.05, Q_2 = 0.50, ten = 2.00

	d_1	d_2	0	10^1	10^2	10^3	10^4	$>10^4$	R_g	v.c.R_g	LR
B	–	–	9.5	4.0	3.0	1.5	2.0	–	0.973	0.308	0.906
M	3	–	–	4.5	8.0	5.0	2.5	–	0.986	0.269	0.770
M	50	–	–	1.0	8.0	10.0	1.0	–	0.952	0.145	0.667
M	–	3	–	1.0	9.5	7.5	2.0	–	0.979	0.259	0.766
M	–	50	19.5	0.5	–	–	–	–	0.687	0.080	4.000
M	3	3	0	0	4	11	5	0	1.002	0.297	0.807
M	3	50	20	0	0	0	0	0	0.653	0.130	4.000
M	50	3	0	0	9	9	2	0	0.942	0.165	0.753
	0	50	20	0	0	0	0	0	0.582	0.140	4.000

2a. Q_1 = 0.50, Q_2 = 0.20, ten = 4.55

	d_1	d_2	0	10^1	10^2	10^3	10^4	$>10^4$	R_g	v.c.R_g	LR
B	–	–	7.0	5.5	4.0	1.5	2.0	–	0.965	0.287	0.929
M	3	–	–	6.0	7.0	5.5	1.5	–	0.972	0.254	0.801
M	50	–	–	10.0	9.5	0.5	–	–	0.899	0.146	1.528
M	–	3	–	–	4.5	9.0	6.5	–	1.009	0.217	0.629
M	–	50	–	–	–	–	–	20.0	1.244	0.128	2.368
M	3	3	0	0	1	11	7	1	1.022	0.250	0.740
M	3	50	0	0	0	0	0	20	1.206	0.119	2.029
M	50	3	0	3	14	3	0	0	0.892	0.162	1.284
	0	50	0	0	0	0	17	3	1.083	0.128	0.850

2b. Q_1 = 0.50, Q_2 = 0.50, ten = 1.50

	d_1	d_2	0	10^1	10^2	10^3	10^4	$>10^4$	R_g	v.c.R_g	LR
B	–	–	6.0	5.5	5.0	1.5	2.0	–	0.964	0.270	0.926
M	3	–	–	6.5	8.5	4.0	1.0	–	0.958	0.224	0.806
M	50	–	–	7.5	12.5	–	–	–	0.893	0.154	1.564
M	–	3	–	1.0	8.5	8.0	2.5	–	0.975	0.211	0.710
M	–	50	–	17.0	2.5	0.5	–	–	0.916	0.122	1.958
M	3	3	0	0	7	10	3	0	0.976	0.231	0.685
M	3	50	0	17	3	0	0	0	0.805	0.109	2.357
M	50	3	0	11	9	0	0	0	0.849	0.148	1.775
M	50	50	20	0	0	0	0	0	0.662	0.134	4.000

Simulation (1b). A low survival chance (0.05) during the reproductive
season and a good survival chance (0.50) in the second season and
during hibernation (annual species, no overlap of generations).
- Without dispersal the results are similar to those given in simula-
tion (1a).
- Low dispersal activities lead to similar effects as in simulation
(1a). However, a high dispersal level during reproduction gives good
results now, whereas it has very negative effects if it occurs out of
the reproductive period; in the latter case all or nearly all popula-
tions become extinct within 25 years.
- The deviating results of the high dispersal activity in both pe-
riods in this situation as compared with that of simulation (1a) may
be due to the already assumed relation between dispersal activity,
with its own survival chance, and the survival chance in the popula-
tions. Appearently, the losses by dispersal in the second period are
too high in relation to the survival chance of the emigrated indivi-
duals if they had stayed in the population.

Simulation (2a). A good survival (0.50) during the reproductive
season and a lower one (0.20) in the second season of the year and
during hibernation (some overlap of generations within a year, annual
species).
- Without any dispersal activity a better result is obtained after 25
years than in the previous cases. The better survival during the
reproductive season probably contributes to the stability of the
numbers of individuals in the second season: if by chance reproduc-
tion is low in some year the surviving adults from the first period
will somewhat level the fluctuations in the numbers of adults that
start reproduction in the next year (on the average 10 per cent will
reproduce a second time).
- Under these conditions of survival and reproduction, differences in
the level of dispersal has less effect than in the cases (1a) and
(1b), though the occurrence of dispersal is in itself still favour-
able. It seems that the effect of a better survival from the first
season is reinforced by dispersal in the second season. A high dis-
persal level can even result in overcrowding.

Simulation (2b). A good survival (0.50) in both seasons (25 % of the
individuals reproduce a second time).
- Without any dispersal the situation equals that in simulation (2a).
- A high level dispersal apparently carries with it too heavy losses
given the low reproductive rate, though the results are somewhat
better than in case (1b). Nevertheless, the conditions of (2b) in
all cases allow the prediction of extinction of the species within 50
- 75 years.
- Low dispersal in the first season decreases the chance of a rapid
extinction but hardly influences mean population size or its fluctua-
tions or range.
- Low dispersal activities in both seasons or only in the second one
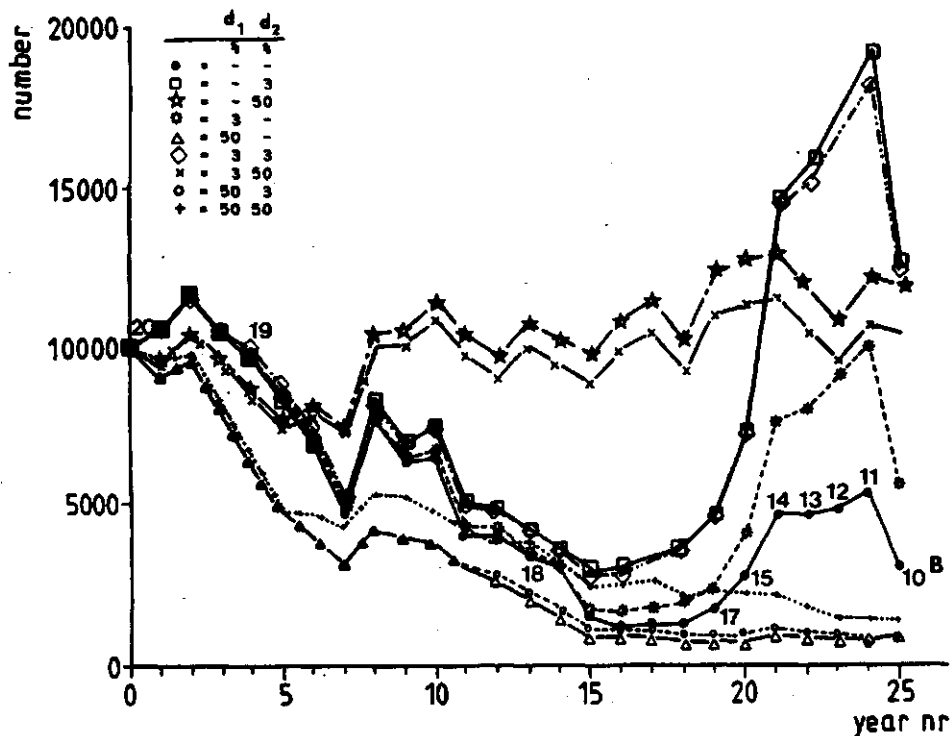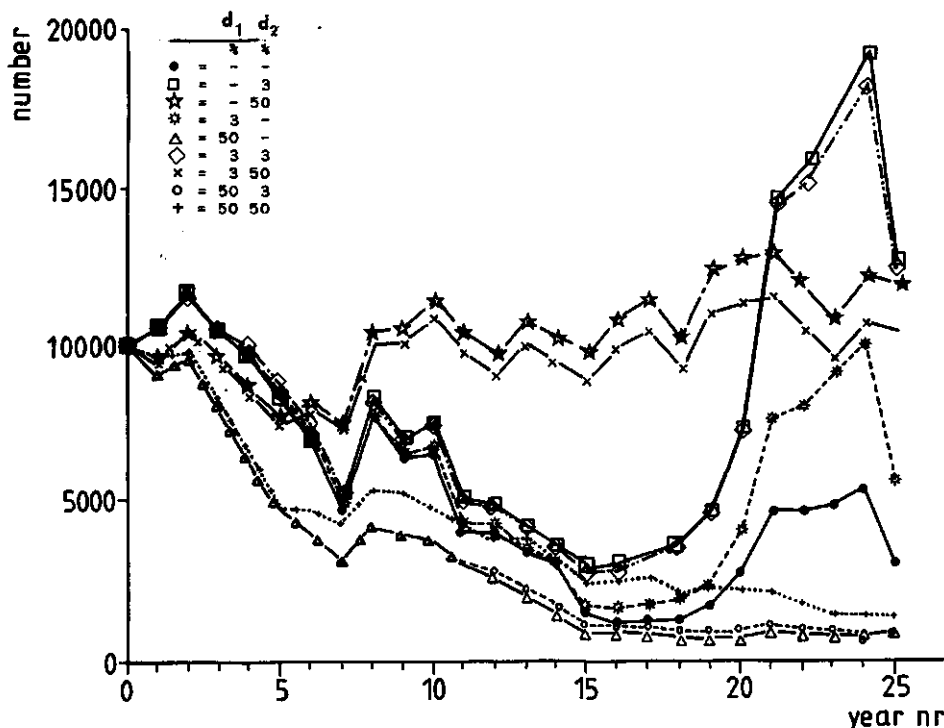entails the best survival possibilities for the species under the
given circumstances.

Fig. VIII-4. The fluctuations during 25 years of population size summed over 20 habitats under different dispersal conditions as described in Table 4a. The numbers along the curve without any dispersal (B) show the numbers of populations still surviving. In all other cases all 20 populations were present each year. d_1, d_2 = mean percentage of beetles that emigrate in the first and in the second generation respectively.

Fig. VIII-4. The fluctuations during 25 years of population size summed over 20 habitats under different dispersal conditions as described in Table 4a. The numbers along the curve without any dispersal (B) show the numbers of populations still surviving. In all other cases all 20 populations were present each year. d_1, d_2 = mean percentage of beetles that emigrate in the first and in the second generation respectively.

3.3.1.4. Our general conclusion thus is that in most situations dispersal activities cause a decrease of the chance of extinction of the populations concerned, in spite of the losses during dispersal. Remarkable is the significant influence of dispersal by only a small fraction of the individuals, comparable to the dispersal activity by flight of whirligig beetles (cf Table VIII-1). The direct numerical effects of such a low dispersal rate are negligible, but the indirect effects of decreasing the chance of extinction and of increasing population size seem to be very important.
An important conclusion may also be that dispersal shown by the offspring out of the reproductive season has more effect than dis-

persal activity during reproduction. Obviously, this is due to the
'Kuno'-effect mentioned before, which works best if exchange between
populations occurs before the reproductive period. The advantages of
dispersal during reproduction mainly result from spreading the risks
for the progeny. Therefore, it becomes comprehensible that some
combinations of dispersal during both the first and second season
appear to be most favourable.

3.3.1.5. To keep the simulations mutually comparable the mean values
for survival and for reproduction were chosen such that the expected
value of net reproduction in each case was R = 1 if there was no
dispersal activity. This means, however, that because of different
survival chances in the cases simulated, a fixed level of dispersal
concerns different numbers of individuals. Because we wanted to
adjust the mean values in the simulations above to different survival
chances we had to change the numbers of tenerals per adult, to keep R
= 1, by which the number of dispersing individuals in the second
season is changed too.

3.3.1.6. The relation between dispersal and reproduction is rather
complicated. During the reproduction season part of the reproducing
females becomes redistributed over the habitats, which results in
spreading of their egg batches over different habitats. This effect
will be the more important the lower the number of reproducing fe-
males in comparison to the number of habitats (de Jong 1979). Another
effect of exchange during the reproductive period is that differences
in progeny between habitats may decrease to the extent that these are
due to differences between individual females.

3.3.2. The importance of variability

In the above simulations a single variation coefficient (v.c. = 0.4)
was used for all processes. This variation coefficient symbolized the
spatial as well as the temporal variation, and thus all the variabi-
lity in the simulated area. Therefore, in the 4 simulations of Table
VIII-4 (1a - 2b) the influence of this level of variability was also
tested for a lower (v.c. = 0.2) and for a higher (v.c. = 0.8) varia-
tion coefficient for both the cases of low dispersal during both
seasons and that of no dispersal at all (Table VIII-5). The lower the
variability the lower appears to be the chance of extinction but also
the smaller the effects of dispersal. Moreover it appears that varia-
bility has less influence if the survival chances increase. The
spatial and temporal variability will be treated separately later
(C.3.4). These results confirm the assumed relationship between dis-
persal and variability, and also illustrate another form of spreading
of risk, which den Boer (1968) and van Dijk (1973) mentioned, viz.
spreading of the risk per individual over different reproduction
seasons or generations. Note that in all cases with high variability
(v.c. = 0.8) the B-populations die out rapidly (compare part 3.3.1)

Table VIII-5. Influence of variability upon the effects of dispersal activity.
The same situations 1a – 2b as in Table VIII-4.
v.c. = variation coefficient of the mean values used in the simulations
B = case without any dispersal
M = case with only 3 % dispersal in both seasons.
For further explanation see Table VIII-4.

		0	10^1	10^2	10^3	10^4	$>10^4$	R_g	$v.c.R_g$	LR
1a.										
v.c.=0.2	B	0	0	4	12	3	1	1.004	0.104	0.266
	V	0	0	0	12	7	1	1.009	0.088	0.200
v.c.=0.4	B	10	3	4	1	2	0	0.952	0.322	1.018
	V	0	0	3	12	5	0	1.009	0.289	0.615
v.c.=0.8	B	20	0	0	0	0	0	0.468	0.943	4.000
	V	20	0	0	0	0	0	0.830	0.523	4.000
1b.										
v.c.=0.2	B	0	0	2	14	3	1	1.019	0.103	0.269
	V	0	0	0	13	7	0	1.007	0.091	0.196
v.c.=0.4	B	10	2	4	2	2	0	0.968	0.315	0.908
	V	0	0	4	11	5	0	1.002	0.297	0.807
v.c.=0.8	B	20	0	0	0	0	0	0.528	0.966	4.000
	V	0	11	4	3	2	0	0.947	0.703	1.995
2a.										
v.c.=0.2	B	0	0	3	13	4	0	1.003	0.095	0.189
	V	0	0	0	10	9	1	1.021	0.080	0.275
v.c.=0.4	B	7	4	5	2	2	0	0.959	0.281	0.881
	V	0	0	1	11	7	1	1.022	0.250	0.740
v.c.=0.8	B	20	0	0	0	0	0	0.601	1.113	4.000
	V	0	0	2	9	6	3	1.044	0.622	1.664
2b.										
v.c.=0.2	B	0	0	3	13	4	0	0.990	0.089	0.799
	V	0	0	0	16	4	0	0.981	0.079	0.275
v.c.=0.4	B	5	7	5	1	2	0	0.955	0.264	0.799
	V	0	0	11	8	1	0	0.947	0.230	0.881
v.c.=0.8	B	20	0	0	0	0	0	0.582	1.055	4.000
	V	0	16	2	1	1	0	0.930	0.644	2.082

3.3.3. Dispersal in relation to different spatial conditions.

3.3.3.1. Since the effects of dispersal depend both on the amount of exchange between the populations in a certain area and on the variation between populations, it is obvious that the number of habitats and populations will influence the effects of dispersal. The distances between two populations or habitats may also be important. Both aspects were studied by 10 simulations over 25 years. We again simulated a situation with low dispersal activity (1.5 % emigrated, of which the chance to immigrate elsewhere = 0.5), and with high dispersal activity (30 % emigrated, with a chance to immigrate somewhere else of 0.7). The results are summarized in Table VIII-6. See Table VIII-4 for explanation of the parameters and variables used.

3.3.3.2. As far as the chance of extinction, mean population size, and the ratio between the highest and the lowest population size are considered, exchange between a low number of habitats has less favourable effects on population sizes after 25 years than exchange between a higher number of habitats (Table VIII-6). Dispersal at a high level gives better results in comparison with dispersal at a low level In the case of 5 habitats than in the simulations with 20 habitats.

3.3.3.3. Exchange between populations by swimming appears to be related to the distance between the habitats (Chapter VII). If exchange between populations is made dependent on mutual distances, the simulations give a better result if dispersal is low than if it occurs at a high level; at low dispersal levels population sizes after 25 years are higher (R_r > 1) and the ratio between highest and lowest population size is smaller than at high dispersal levels, which moreover lead to R_r < 1 (Table VIII-6).

3.3.3.4. Both Southwood and den Boer (cf part 3.1.5-7) attribute considerable importance to variability in environmental factors in regard to dispersal activity. Variability can be considered in time (fluctuations at one site) and in space (differences between different sites at the same time). In 3.3.2. (Table VIII-5) the influence of different levels of variability in time was analysed. Whereas a lower variation in time gives both a decrease of the chance of extinction, of mean population sizes, and in the fluctuations and range of population sizes (compare Table VIII-6.e with VIII-6.a), a decrease in variation in space leads without any exception leads to extinction of the species in the entire area. The synchronisation between the habitats (Table VIII-6d) may have been too complete, however, so that in fact the habitats behaved as a single habitat. Nevertheless, the influence of somewhat less synchronisation is in the same direction, as is convincingly shown by den Boer (1981) by comparing two carabid beetles that react to a different degree to spatial heterogeneity. Decreasing heterogeneity in an area leads to unfavourable population dynamics because neither overcrowding nor extinction can be prevented by exchange between habitats.

Table VIII-6. Simulation of exchange between habitats under different spatial conditions; the influence of the number of habitats, the variability between habitats and the distance between habitats upon the population-dynamic effects of dispersal. The table gives the mean results of 10 simulations per situation.
(a):20 habitats, exchange between habitats random, variation coefficient v.c.=0.5
(b): as (a), but only 5 habitats
(c): as (a), but exchange between habitats related to the distances between them
(d): as (a), but values for reproduction, survival and dispersal synchronized between the habitats (see text)
(e): as (a), low variability v.c= 0.3 (see text)
dispersal:
- = no dispersal activity
1.5 = 1.5 % emigration, I/E = 0.5
30 = 30 % emigration, I/E = 0.70.
For further explanation, see Table VIII-4.
Numbers of populations per size group are given as percentages.

disp	pop. sizes after 25 years								
	0	101	102	103	104	>104	Rq	v.c.Rq	LR
(a) 20 habitats									
-	79.00	7.00	4.00	4.00	5.00	1.00	0.974	0.621	1.385
1.5	0.00	2.50	35.00	40.00	19.00	3.50	1.018	0.439	1.237
30.0	0.00	0.00	25.00	70.50	4.50	0.00	0.970	0.199	0.608
(b) 5 habitats									
-	90.00	0.00	4.00	4.00	2.00	0.00	0.695	0.711	2.436
1.5	16.00	22.00	30.00	24.00	8.00	0.00	0.901	0.563	1.597
30.0	0.00	22.00	26.00	50.00	2.00	0.00	0.921	0.365	0.966
(c) distance									
-	80.00	8.75	4.58	2.50	2.92	1.67	0.950	0.639	2.314
1.5	0.00	7.50	28.75	38.75	16.25	8.75	1.047	0.456	2.902
30.0	0.00	19.50	68.00	12.50	0.00	0.00	0.898	0.253	1.202
(d) synchr.									
-	100.00	0.00	0.00	0.00	0.00	0.00	0.260	1.435	4.997
1.5	100.00	0.00	0.00	0.00	0.00	0.00	0.293	1.509	5.203
30.0	100.00	0.00	0.00	0.00	0.00	0.00	0.308	1.493	5.207
(e) low var.									
-	5.50	8.50	20.50	33.00	18.50	14.00	1.109	0.299	1.399
1.5	0.00	0.00	0.00	24.50	61.50	14.00	1.097	0.207	1.222
30.0	0.00	0.00	4.50	66.00	29.50	0.00	1.010	0.166	0.412

3.3.4. The causes of dispersal activity.

3.3.4.1. Dispersal of whirligig beetles by swimming can be considered a consequence of the daily swimming activities connected with looking for food, etc. In Chapter VI arguments were given for the hypothesis that these beetles can only show flight activities when the weather is favourable for flight. In the above simulations we have shown that even the small exchange between populations as a result of flight activities may considerably decrease the chance of extinction of the populations.
This does not fit the current view (e.g. Johnson 1969) that emigration mainly occurs when conditions in the habitat become adverse, whether this be due to abiotic (e.g. drying up of wet habitats) or to biotic factors (e.g. overcrowding). If the beetles react to density with dispersal activities the exchange between populations would be density-dependent. In comparison with the above simulations in which dispersal activities occur randomly, dispersal activities would occur more contagiously distributed both over the habitats and over time. We tested by simulation whether dispersal activities that are more concentrated in space and in time (because they occur as a reaction to adverse conditions or to density) would have similar effects on the course of population size as random dispersal. These simulations are carried out according to the same procedures as above and the results are given in Table VIII-7.

3.3.4.2. Density-dependent dispersal entails the best reduction of variation in population size, and after 25 years population sizes mostly occur between 1000 and 10000. However, if dispersal were strictly density-dependent no dispersal would occur at low population sizes. This means that with population densities far below the carrying capacity a rapid extinction of all populations will occur (see also den Boer 1968, 1986). On the long term such a dispersal will result in a higher chance of extinction than if dispersal were to occur randomly.

3.3.4.3. To make dispersal a reaction to adverse conditions, a chance of 0.1, 0.2 or 0.5 respectively of the occurrence of adverse conditions is introduced into the model, together with a mean percentage of individuals that will emigrate when such conditions occur. In this way one case of low dispersal activities is obtained (on the average 1.5 percent of all individuals will emigrate from about 10 per cent of the populations per season), and two cases with high dispersal activities (almost all individuals emigrate from 20 per cent of the populations and about 50 per cent of the individuals emigrate from about 50 per cent of the populations per season).
With low dispersal activities extinctions occur, and the range of population sizes is not reduced. If nearly all individuals emigrate per season from 20 per cent of the habitats a general overcrowding is the result, i.e. the range of sizes is not at all reduced. If only 50 per cent emigrate from 50 per cent of the habitats the results are in between the cases in which a high dispersal level is either due to

Table VIII-7. The effects of dispersal (b) occuring randomly, (c) as
            density-dependent reaction (carrying capacity), and (d)
            as a reaction to adverse conditions.
            (d) adverse conditions: 1.5 % emigr: emigration from 10
            % of the habitats, 100 % emigr: from 20 % of the habi-
            tats, 50 % emigration from 50 % of the habitats.
            See text and Tables 4 and 6 for further explanations.

dispersal	pop. sizes after 25 years (% of number of populations)						R_e	v.c.R_e	LR
	0	10^1	10^2	10^3	10^4	$>10^4$	R_e	v.c.R_e	LR
(a) no dispersal	79.00	7.00	4.00	4.00	5.00	1.00	0.974	0.621	1.385
(b) random disp.									
1.5 % emigr	0.00	2.50	35.00	40.00	19.00	3.50	1.018	0.439	1.237
30.0 % emigr	0.00	0.00	25.00	70.50	4.50	0.00	0.970	0.199	0.608
(c) carr. cap.									
1.5 % emigr	0.00	1.00	11.00	43.50	44.50	0.00	1.043	0.306	0.766
30.0 % emigr	0.00	0.00	0.00	22.00	78.00	0.00	1.050	0.205	0.783
(d) adverse cond.									
1.5 % emigr	6.00	27.00	32.50	23.00	8.50	3.00	0.998	0.486	1.381
100.0 % emigr	0.00	2.00	11.00	29.00	41.50	16.50	1.072	0.324	1.525
50.0 % emigr	0.00	0.00	25.00	63.00	12.00	0.00	0.983	0.255	0.708

random or to density-dependent conditions. In general, it seems that
dispersal due to adverse conditions will entail more instable situa-
tions than when dispersal is due to density-dependent reactions or
when it occurs randomly.
The results of the above simulations show that there are no apriori
disadvantages connected with the hypothesis of randomly occurring
dispersal.

3.3.5. The role of dispersal by flight.

3.3.5.1. So far the simulations concern species of which the entire
progeny emerges at the same moment and is thus present at the begin-
ning of the next season. These simple models show some interesting
consequences of dispersal activities, but what may we expect in the
more complex situation described by our field studies?

3.3.5.2. From the field studies we know that flight activities of
Gyrinus marinus occur at a low level of less than 5 per cent of the
beetles, and that flight is restricted to days with good weather
conditions. During the reproduction season females show less flight
activity than males. The sexes also differ in chance of survival,

activity decreases the chance of extinction of a population. We will now try to trace the population-dynamic effects of a low dispersal activity comparable with the flight activity of whirligig beetles. First of all males and females will be handled separately using the mean values found in the field. As the estimates of the mean numbers of tenerals per oviposition and those of survival from hibernation are the least reliable field estimates, these are adjusted such that in the model no overall increase or decrease of population sizes could be expected if no dispersal occured and all variation was neglected (deterministic net reproduction, R = 1). The length of a period of observation will be one month, so that a year will have eight periods: seven months from April to October and one winter period. A consequence of periods of one month is that the model has to follow the development from egg to teneral. Unfortunately, the RAM-memory of the personal computer used does not allow a more complicated structure in the model than simply simulating the number of tenerals per female in month j that developed from eggs in month i. Nevertheless, we think that we approached the reality of the field situation sufficiently closely with the separate monthly simulation of the processes of emigration and immigration, survival and production of tenerals, but also with the interactions between these processes. In Table VIII-8 a review is given of the mean values and variation coefficients used in this simulation model.

Table VIII-8. Mean values and variation coefficients of field variables used in the simula tions concering the effects of flight activities of whirligig beetles. Given are mean values and variation coefficients (between brackets) per month.
ten/fem = number of tenerals per female
surv f., surv m. = survival chance of females and males respectively
flight f., flight m. = fraction of females resp. males that fly away
I/E = fraction of emigrants that immigrate elsewhere in the area.

| month	ten/fem	surv m.	surv f.	flight f.	flight m.	I/E
1 April	9.0 (0.54)	0.66 (0.04)	0.60 (0.05)	0.009 (1.40)	0.015 (0.70)	0.40 (0.70)
2 May	9.0 (0.54)	0.66 (0.04)	0.60 (0.05)	0.058 (1.40)	0.100 (0.70)	0.40 (0.70)
3 June	9.0 (0.54)	0.66 (0.04)	0.60 (0.05)	0.100 (1.40)	0.160 (0.70)	0.40 (0.70)
4 July	7.5 (0.32)	0.57 (0.05)	0.52 (0.06)	0.100 (1.40)	0.160 (0.70)	0.40 (0.70)
5 August	5.0 (0.32)	0.57 (0.05)	0.52 (0.06)	0.058 (1.40)	0.100 (0.70)	0.40 (0.70)
6 Sept.	-	0.34 (0.09)	0.32 (0.07)	0.058 (1.40)	0.100 (0.70)	0.40 (0.70)
7 Oct.	-	0.34 (0.09)	0.32 (0.07)	0.058 (1.40)	0.100 (0.70)	0.40 (0.70)
8 winter	-	0.32 (0.73)	0.35 (0.82)	-	-	-
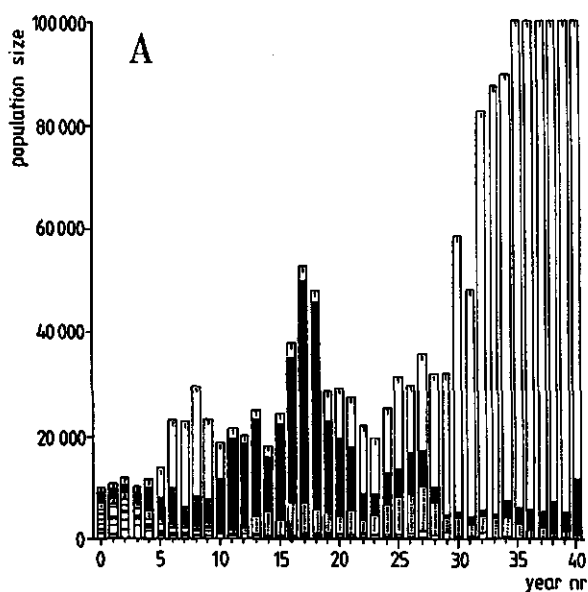
Fig. VIII-5.

Simulation of *Gyrinus* field data.
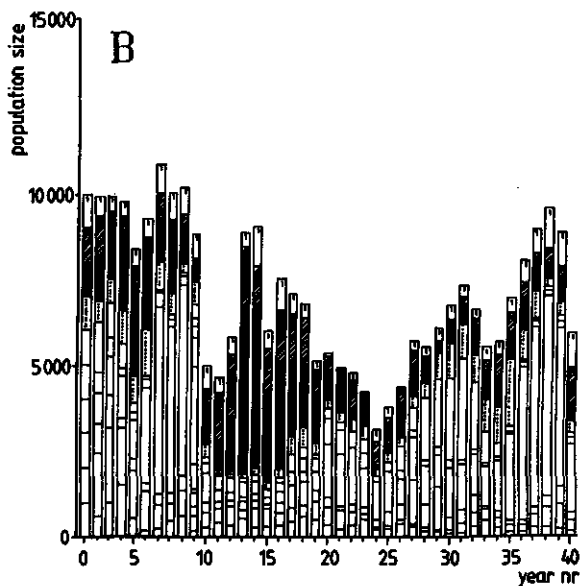
Summed population size in 10 habitats during 40 years.

(A) without flight activity
(B) with flight activity.
Scale Y-axis (A) = 6.67 x scale Y-axis (B)
Each bar fraction corresponds with one population

population 1, 2, 3, 4 resp.

An important consequence of time steps of one month is, that the
periods of reproduction and non-reproduction are no longer strictly
separated. Egg-production occurs from April through August, but tene-
rals emerge from June through October. The results of the simulations
with and without dispersal activity are shown in Fig VIII-5.
Without dispersal population size of all habitats together increases
after 30 years to more than 8 times the starting size, which is
caused by only one single, very large population. In the first 25
years the summed population size fluctuates between 10,000 and
60,000. However, after 40 years, only five of the 10 populations at
the start are still present with sizes of 12, 112, 677, 10,919 and
214,394 (this last population had reached a peak of 557,399 in the
39th year). The total number of individuals is thus mainly determined
by a few populations; the others were small or rapidly went extinct
(Fig VIII-5A).
With low dispersal activities the fluctuations in population size and
the range of variation are relatively small. In the first 25 years
the summed population size varies between 12,000 and 4000. The indi-
vidual populations fluctuate between 25 and 4908 individuals. After
40 years all 10 populations still exist. Instead of the trend toward
increasing population sizes - as found in the case without dispersal
- a slow decrease in population size appears (Fig VIII-5B). It is
possible that the values for reproduction (tenerals/female) or survi-
val during hibernation should be somewhat better than we assumed (as
noted, these estimates were not as reliable as they should be (Chap-
ters IV and V).

3.3.5.3. This simulation with a more complicated model confirms the
general conclusions we reached above with simple models, which indi-
cates that these general conclusions are also valid in the specific
case of *Gyrinus marinus*. Dispersal by flight of these beetles has a
stabilizing effect upon population size, decreasing both the fluctua-
tions of numbers and the chance of extinction. When discussing the
field data about flight, we concluded that flight activities could
not be of importance because we focussed only upon the absolute
numbers of individuals that show flight activities (cf Chapter VI).
We must now correct this earlier conclusion since it appears that
even minor flight activities highly favour the permanent occurrence
of *Gyrinus* in an area with separate populations that cannot exchange
by swimming.

3.3.6. Selection of dispersal features.

3.3.6.1. Given the survival chances and reproduction values, numbers
of habitats and survival chances during dispersal, as found in the
field, there is an optimal level of dispersal. We consider dispersal
to be optimal when the progeny (possibly after some generations) of
the dispersing individuals is about equal to or greater than the
progeny of the not-dispersing individuals. This implies that also
random dispersal is subject to selection and will change to an opti-

mal level. The chance of survival from dispersal activity (i.e. the net exchange between populations, or the (re)founding of populations) is crucial in this context. It is useless to consider emigration from a single population if arrival in other suitable habitats is not taken into account. Carlquist (1966), for example, shows that seeds of species of *Compositae* plants lose their ability to spread over long distances if no settlements occur (island situations). Similar data are given by Darlington (1943) for carabid beetles in Alpine mountains and on islands.

3.3.6.2. Flight activity of *Gyrinus marinus* is apparently pure dispersal activity with no other apparent function than leaving the present site. Flight ability of carabid beetles is related with wing size and development of flight muscles (den Boer et al 1980, van Huizen 1979), so let us assume for convenience that the wing-size of whirligig beetles determines the occurrence of flight activity by an individual beetle (but you may imagine another feature if you like). Assume further that wing size depends on a single recessive gene. The homozygotic genotype that can fly will be called macropterous (MM-type), the homozygotic genotype that cannot fly brachypterous (BB-type). Only the MM-type is supposed to be able to fly (the feature to fly is recessive). The choice of recessiveness is not only made for computing reasons, but also because there are reliable indications that macroptery is often recessive, at least in a number of beetle species (Jackson 1928, Lindroth 1946, Stein 1973, den Boer et al. 1980, Aukema 1986).

3.3.6.3. The genetic situation described above is built into the complicated simulation model. For emigrating females we note whether they were fertilized and if so, by what genotype of male.
The results of the simulations are shown in Figures VIII-6 and VIII-7. Without dispersal activity (Fig VIII-6) there is no selection at all and the frequencies of BM, BB and MM conform the Mendelean distribution segregation (2:1:1). When dispersal activities occur the relative frequencies of the genotypes change. The BB-type makes up an increasing fraction of the population. From Fig VIII-6 it appears that the MM-type is more stable than the other two types and that the MM-type numbers are much lower than those of BB and BM. With increasing population size the relative frequency of the MM-type decreases and vice-versa.

3.3.6.4. Dispersal activity is shown in this model by only one of the three genotypes so that dispersal activity of the population as a whole is lower than in previous simulations with only one genotype. Nevertheless, the same effects of dispersal are found, see Fig VIII-7. Such limited dispersal activity cannot sufficiently eliminate the exceptional growth of one of the ten populations, although it is more restricted than in the case without dispersal.

3.3.6.5. Since we assumed that dispersal activity is a recessive feature the heterozygotic individuals preserve the feature, without
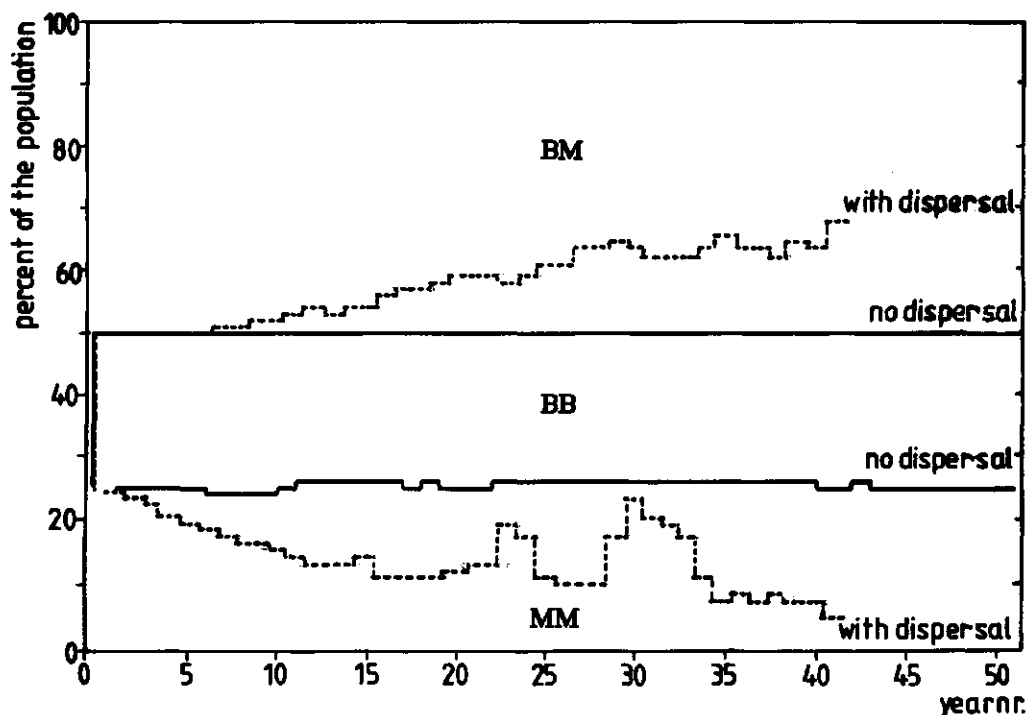
Fig. VIII-6. Simulation of *Gyrinus* field data with the assumption of natural selection on flight activity.

Course during 40 years of the relative composition of genotypes in the summed populations of 10 habitats.

——— = no flight activity of genotypes MM occurs

- - - - - - = flight activity of genotypes MM occurs

being able to express it. When dispersal occurs a part of the genes responsible for dispersal activity will leave the population with the emigrating individuals. Without compensating immigration the relative frequency of these genes will decrease (cf also Carlquist 1966). However, since the feature is also hidden in the not-dispersing heterozygotic individuals, the 'dispersal'-genes can hardly be completely eliminated from the population, because no direct selection occurs on these 'hidden' genes, and there are no special reasons to
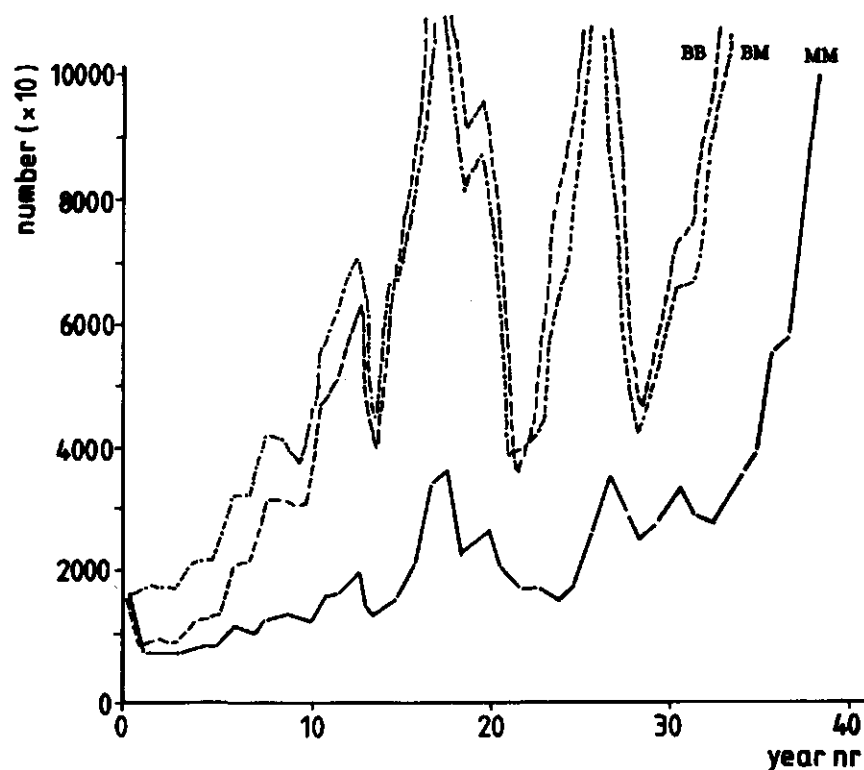
Fig. VIII-7. Simulation of *Gyrinus* field data with the assumption of selection on flight activity.
Summed population sizes in 10 habitats during 40 years.
With flight activity of genotype MM.

- - - - = course in numbers of genotype BB

—·—·—· = course in numbers of genotype BM

———— = course in numbers of genotype MM

suppose that indirectly there will occur some positive or negative selection of heterozygotes (e.g. via pleiotropic effects). The heterozygotic genotype will thus function as a buffer for the feature 'dispersal activity'.

3.3.6.6. In the cases described above only dispersal by flight is considered, exchange between populations by swimming being considered to be a consequence of the daily swimming activities. In fact, the

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situation is more complicated. In the field we generally find clus-
ters of populations. Between the populations of the same cluster
exchange by swimming frequently occurs; properly speaking, we delt
with subpopulations then. Between these clusters of subpopulations
only little exchange by flight is possible. In the first simulations
above (Table 4) it has been shown that a high level of exchange will
have impressive stabilizing effects upon the subpopulation sizes. We
may thus assume that each cluster of a number of subpopulations is
already stabilized because of exchange by swimming, and that the
complex of clusters in the whole area will be stabilized by the
flight activities. When the simulation program can be run on a more
powerful computer this situation of clusters of subpopulations can be
built into the model and tested.

4. SOME FINAL CONCLUSIONS.

The simulations lead to the following conclusions and hypotheses:

- According to the key-factor analysis population size and its fluc-
tuations are principally determined by survival from hibernation.
None of the other processes or stages - either alone or in combina-
tion - seem to be able to compensate the high and variable losses
from hibernation.
- However, by spreading the risk over a number of habitats it appears
to be possible to counterbalance the losses from hibernation in a
particular habitat by the differing fluctuations in numbers in other
habitats, which are actualized by means of exchange of individuals
between the habitats.
- Dispersal, even when it occurs at a low frequency, appears to be
crucial for the survival of a species in a group of different habi-
tats. Low frequency dispersal may suffice to prevent extinction of
populations and/or lead to refounding at sites where extinction has
taken place. Emigration from and immigration into habitats has a
strong stabilizing influence on population size, thus decreasing the
chance of extinction of the populations considered.
- If dispersal activities are connected with only one recessive
genotype the numbers of the 'non-dispersing' genotypes may vary
considerably, whereas the fluctuations in numbers of the 'dispersing'
genotype are much smaller. The 'dispersing' genotype decreases the
chance of extinction for the entire population, also for the hete-
rozygote and homozygote fractions of the population. The relative
frequency of the 'dispersing' genotype may become very low as a
result of dispersal activities, but the chance that it disappears
altogether is small because of the buffering effect of the heterozy-
gote.
- The influence of dispersal activities upon the course of population
size depends on the difference between the rates of emigration and
immigration, i.e. on survival (s) during dispersal, and on the survi-
val chance (θ) in the habitats. Also of importance will be the va-
riability (v) of the processes that are responsible for the spatial
and temporal fluctuations in population size, the number (n) of

habitats in the area, and the distances (d) between these habitats. As we saw, it also matters whether dispersal occurs during or out of reproduction (r). Therefore, it may be expected that natural selection will stabilize the level of dispersal (e) of a species in a certain area such that the balance between the risks and the advantages of dispersal activity will be about optimal according to the above definition. These relations can be expressed by the formula:

$$F(e) = \frac{F(s).F(v).F(n)}{F(Q).D(d).F(r)}$$

where each F(x), if x = s,v,..r, respectively, stands for some function between dispersal activity and the parameter concerned.

- For the field populations of *Gyrinus marinus* studied the hypothesis cannot be rejected that the flight activities of some of the beetles depend only on favourable weather conditions, even when local conditions are favourable for survival.

- The simulations confirm both the hypothesis of 'spreading of risk' of den Boer (1968, also Reddingius and den Boer 1970) and the effects noticed by Kuno (1981). The simulations make clear that 'Kuno' effects will only occur when offspring migrate between clusters or sites, and much less or not at all when reproducing females change sites. The principal effect of spreading the risk is the significant decrease of the chance of extinction of populations.

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APPENDIX A

Estimation of the number of emerging tenerals (Chapter IV).

The number of emerged tenerals per week (Y_i) can be estimated from the percentage of tenerals per sample (z_i) when the total number of beetles (A_i) is known, as $Y_i = A_i \times z_i /100$.
However, direct estimates of the total numbers of beetles are not reliable enough to give reliable values for Y_i (chapter V). Estimates of Y_i will therefore be derived from a population of 1000 beetles at week 14 (end of hibernation), i.e. $A_{14} = 1000$. From each population and from each generation (g) the survival chance Q_g is estimated by means of capture-recapture methods (Chapter V, Appendix B). The number of beetles which have survived until week i is estimated then as: $A_i = Q_g \times A_{i-1}$. From the first week that tenerals emerge the number of weekly emerged tenerals Y_i that survive until the next week are added to A_{i+1}. The survival chance of soft tenerals is assumed to be somewhat lower than that of older beetles.
This method needs weekly estimates of the proportion of soft tenerals in the population, but estimates are only available for weeks in which sampling was carried out. For weeks without sampling data the z_i-values are estimated provisionally by extrapolation of the available z_i-values from sampling weeks, by means of the freehandfitted curves of mean z_i-values over all po-pulations in a year (Fig IV-4). With the estimated values of Q_g and z_i a provisional estimate of the number Y_i of emerged tenerals per week (per 1000 beetles in week 14) can be made. Since it is known, from experience, that newly-emerged beetles can be recognized by their soft elytra until they are 5 - 7 days (h) old, Y has to be corrected as $Y_i' = Y_i \times (7/h)$. In general 5 days of hardening is assumed in summer and 7 days in autumn. However, in 1977 h=6 in summer gave better results. Longer periods of hardening in 1977 were very plausible as summer temperatures were low then. Together with the estimates of Y estimates of the population size per week are obtained. These estimates can be compared with the rough estimates of population size by different capture-recapture methods, when these are also calibrated at 1000 beetles in week 14. When the two methods contradict each other their general trends over time (i.e. time of maxima or minima, periods of increase and decrease and the ratio between the generations) the less reliable values of either z_i or Q_g are adjusted somewhat. Then the estimates are repeated, and so on. Sometimes an extra loss of individuals in a particular week has to be assumed. An example of this way of iterative estimation is given below.

Example of the estimation of the rate of recruitment of a population.

Procedure: Fit the numbers estimated from field data concerning survival and recruitment to capture-recapture estimates of the population size, by adjusting either the values of survival or that of recruitment (depending on their reliability).

General assumptions (apart from those mentioned in text, Chapter IV, B.3.1.):
- Emergence is sufficiently regular to be represented by a mathematical function.
- The survival of tenerals may be lower than that of beetles older than 2 weeks (importance of fouraging in the first week).
- Dispersal activities are too low to affect the numbers or the composition of the population.

Example with population: Ks-74 (Fig. A-1).
Data estimated from the field:
Population size estimated by capture-recapture, callibrated at 1000 beetles in week 14 (see Fig. A-1d):

survival chances Q_e and proportion of tenerals per sample:

survival θ:	θ_1	θ_2	θ_3		% tenerals per sample																				
generation	spring	summer	autumn	week number	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44 45
males	0.94	0.92	0.80	mean 1974	0	2	35	41	47	38	30	25	19	12	16	23	32	36	32	24	19	13	10	5	2 0
females	0.93	0.92	0.80	Ks-74 field	0			35		8	5		7	7					17		12				
Capture chance indicating reliability of % tenerals:					58			30		35	13		13	57					47		57				

Adjusted runs (θ_y = survival tenerals/survival other beetles):

survival θ:	θ_1	θ_2	θ_3	θ_y	week nr	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
run 1 (Fig A-1a)	0.94	0.90	0.85	1.00	gives:	0	2	35	41	35	30	8	5	6	7	7	23	32	36	32	24	17	13	12	12	2	0
run 2 (Fig A-1b)	0.94	0.90	0.80	0.90	gives:	0	2	45	35	33	10	5	5	0	4	7	20	30	30	30	30	17	12	12	12	3	0
run 3 (Fig A-1c)	0.94	0.90/0.85	0.80	0.90	gives:	0	2	45	35	33	10	5	5	0	4	7	20	30	31	33	35	17	12	12	12	2	0

Comments:
In the first run the proportion of tenerals in the not sampled weeks is interpolated according to the trends in the mean values of all populations in 1974. In the second run survival values are decreased, tenerals have got a worse survival chance that other beetles, and the proportion of tenerals has been changed to achieve lower numbers and to bring the point of maximum population size forward in time. In the third run survival in summer is divided into a survival chance of 0.9 before week 30 and a survival chance of 0.85 from week 30 onwards. The proportion of tenerals in weeks 36-39 has also been changed. Numbers estimated with these data agree with the estimated capture-recapture data of Fig. A-1d.
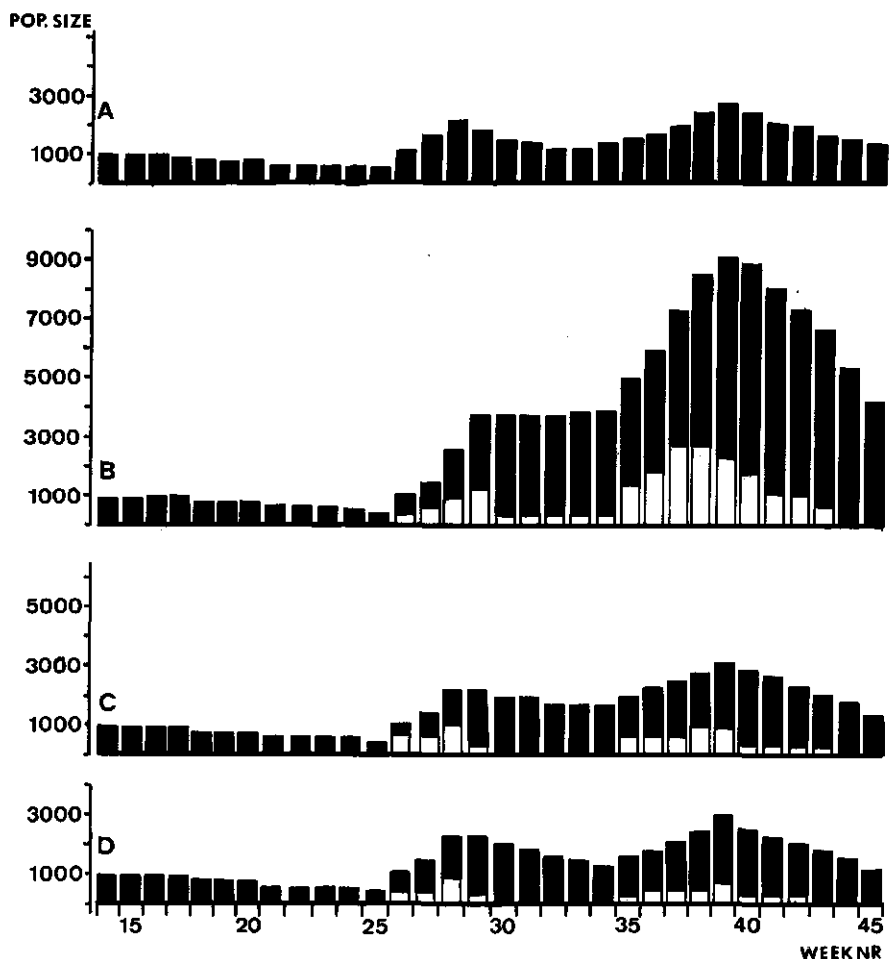
Fig. A-1. Estimated course in population size of population Ks in 1974

a/c: estimated, assuming a survival chance and a size of
       offspring per week, based on estimations in the field.

   d: estimation of the population size according to a modi-
       fied capture-recapture method of Fisher & Ford. The
       estimation is converted to a start number of 1000 in
       week 14.

   ■   = adult beetles

   □   = newly emerged tenerals

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APPENDIX B

Comparison of three methods for estimating survival chance: Chapter V

1. When frequent recaptures of marked individuals are available
several methods can be used to estimate the survival chance and/or
population size during the period of sampling. In some methods survi-
val chance is assumed to be constant (Lack 1943, Fisher and Ford
1947, Bailey 1951). The identical methods of Jolly (1965) and Seber
(1965, 1973) only assume equal capture chances of all individuals
throughout the sample period. For the method of Manly and Parr (1968)
it is sufficient when individuals have an equal capture chance per
sample. We tested the Jolly-Seber method, but it appeared not to be
reliable, particularly for open populations, probably because in our
case the survival chance between two sampling events is small (Bishop
and Sheppard 1973), so that too few data were available to estimate
reliably the necessary Z- and R-values.

2. More accurate estimates of the survival rate and population size
can be obtained with the Fisher & Ford method (explained by Sheppard
et.al. 1969, Begon 1979, see also Southwood 1978). The strength of
the Fisher and Ford estimation is that the data from a number of
samples can be taken together, so that small sample effects are
averaged (Begon 1979). But the method assumes a constant survival
chance. Separate estimates must therefore be made for spring, summer
and autumn, i.e. per generation. The Manly-Parr method is used in
addition to the Fisher & Ford method because the Manly-Parr method is
even not affected by age-dependent mortality. A third method is based
on estimating the average period that a beetle has been present in
the population. This mean time of presence corresponds with a mean
survival chance per individual of 0.5 over that period. This is the
most direct method of estimation and also the most detailed, because
the survival chances are given per date of release. A disadvantage is
that the method gives a minimum estimate since an individual will
usually survive for some time after the last recapture.

3. The three methods for estimating survival chance (Fisher & Ford
(FF), Manly & Parr (MP), and by means of the time spent in the
population (TS)) differ in the way capture-recapture data are
treated. The FF and TS methods both use the time individuals are
available in the population for capture. FF by using the age of the
marked individuals, TS by estimating the time individuals are present
in the population. In other words, FF looks backwards to the history
of a marked individual, whereas TS looks forward to what will happen
to a marked beetle. The MP method uses the decrease in the number of
marked beetles between the day of release and that of recapture.

4. The three methods are compared in Table B-1 for the total season,
and per generation in spring, summer, and autumn. The methods give
significantly different values. In general TS gives higher survival
values than FF, and FF higher than MP. On the average the variation

coefficients of the FF-estimates (per generation and per sex) are about 1.5 times those of the MP-estimates, and the latter are about twice those of the TS-estimates (0.1258, 0.0885, 0.0384 resp.). This may mean that FF estimates less accurately than MP, and MP less accurately than TS. Since TS give minimum estimates of the survival chance (see Chapter VI,2.6.) and TS in fact provides the highest values for survival chance, it is the most reliable of the three methods. The TS method will be used further in this study. Although the three methods give significantly different values, their estimates appear to be correlated, that is, the methods estimate relative differences in the survival of different populations about equally (product-moment correlation tests per generation: P<0.05 (3x), P<0.02 (2x), P<0.002 (4x)).

Table B-1. Comparison of three methods of estimating survival chance.
Significance (2-tailed): z>1.96: P<0.05, z>2.33: P<0.02, z>3.10: P<0.002

METHOD	SURVIVAL CHANCE PER WEEK			WILCOXON TEST (n, z-values)						CORRELATION TEST (n, z-values)					
	FF	MP	TS	FF-MP		FF-TS		MP-TS		FF-MP		FF-TS		MP-TS	
TOTAL PERIOD	0.8640	0.8075	0.8394	53	4.38	57	2.46	52	6.00	54	9.48	58	8.76	53	9.40
SPRING	0.9145	0.8135	0.8666	37	4.16	39	3.07	40	4.54	38	2.12	41	7.24	42	2.38
SUMMER	0.6784	0.7471	0.8526	38	3.40	43	5.41	42	4.85	43	5.43	44	4.21	43	5.43
AUTUMN	0.6704	0.7251	0.7595	8	1.54	15	1.70	9	1.36	11	3.52	17	3.70	11	3.52

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APPENDIX C

Estimation of the emigration rate by swimming activities (Chapter VII)

In chapter VII.3.2.2. the emigration rates by swimming activity were estimated by an iterative computer-model. This model is made with the help of a spreadsheet program (SuperCalc 3). A spreadsheet-model is a computer-model, that (re)calculates the values of all dependent variables when the value of one of the data or of an independent variable is changed. In this way it is possible via sensitivity analyses to achieve optimal estimates. The model is organized in a grid, columns are designated by letters, rows are designated by numbers. Each cel of the grid can be indicated by its column-letter and its row-number and to each cel we can award a value, a variable, a function or a formula, by which relations with other cels can be made. In our model we introduced per population the number of effectively released marked beetles, the number of beetles found elsewhere as immigrant, the number of beetles still available in the population after the last day an immigration elsewhere was recorded and the number of weeks that exchange was recorded. Introducing some survival chance (Q) and an emigration rate (E) as independent variables the model calculates as dependent variables the number of beetles that was expected to be still available in the population (P_e), the number of beetles that should have died (V) and the number of beetles that should have been emigrated (E_e), cf. Table C-1. Assuming that by the daily counts of the beetles in the field approximately all beetles present at some place should have been noticed, the number of beetles expected to be still present in the population (cel A08, Table C-1) has to be equal or one or two specimens higher than was actually observed (cel A09), whereas the number of emigrants (cel A14) should be at least equal to (but usually will be more than) the number of beetles observed elsewhere as immigrants (cel A29). By iteration, adapting the value of the emigration rate, and if necessary also that of the survival rate, those estimates for the emigration (cel A06) and the survival in the population (cel A07) are found that fit best the expected numbers of the still present (P_f) and of the emigrated beetles (E_e) as compared with the numbers observed in the field (P_f and E_f respectively). The value for the survival chance was only altered when the value for the emigration rate would otherwise deviate considerably from the estimate in Table VII-2, pag 99. From the expected total number of emigrants (E_e in cel A14) and the expected number of these beetles elsewhere immigrated (I_e in cel A29) the survival chance during swimming-dispersal can be estimated as $Q_{ee} = I_e /E_e$ (cel A30). Also the dispersal-ratio (Db, cel A34), which is the ratio between the number of immigrated beetles in a population and the number of emigrants from the same population, can be estimated from E_e (cel A14) and the number of beetles immigrated (I, cel A33) from elsewhere in the population. The results are produced in Table VII-4, pag 102.

Two examples of iteration excercises are given in Fig. C-1.

Table C-1. Structure of the spreadsheet-model used for estimating
the emigration rate, the survival chance during swim-
dispersal activity and the dispersal-ratio
The values per population are noted in columns B - K

| Row	Column A	B - K
01	variables	values
02	period number	per
03	population name	popu-
04	R : number of beetles released	lation
05	W : number of weeks with exchange	
06	E : emigration rate/week introduced into the model	
07	Q : introduced survival rate/week in the population	
08	P_e : $P_e = R*(Q-E)^W$, expected number of beetles in the population after W weeks	
09	P_f : number of beetles observed in the population after W weeks	
10	L_e : $L_e = R - P$, expected number of beetles lost from the population after W weeks	
11	L_f : $L_f = R - P$, observed number of beetles lost	
12	from the population after W weeks	
13	V : $V = L_f*(1-Q)/(1-Q+E)$, number of beetles died	
14	E_e : $E_e = L_e - V$, expected number of beetles that have emigrated	
15	E_f : $E_f = L_f - V$, observed number of beetles that have emigrated	
16		
17	I_{fx} : observed numbers of beetles immigrated in population x	
.		
.		
27		
28		
29	I_f : total number of beetles observed as immigrant elsewhere (SUM(cel A17 - A27))	
30	Q_{ee} : Q_{ee} = I_e /E_e, expected survival rate during dispersal	
31	Q_{ef} : Q_{ef} = I_e /E_f , observed survival rate during dispersal	
32		
33	I : number of beetles immigrated from other populations	
34	Db_e : $Db_e = I/E_e$, expected dispersal-balance	
35	Db_f : $Db_f = I/E_f$, observed dispersal-balance	
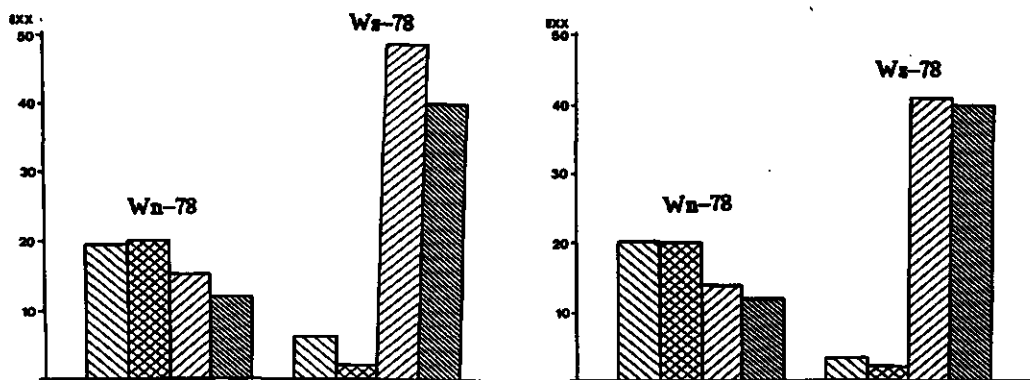
Fig. C-1. Estimation of the emigration rate by swimming from population Wn-78 and Wz-78.

⬚ = estimated number of beetles present in the population (P_e)

⧉ = observed number of beetles present in the population (P_f)

▨ = estimated number of beetles emigrated from the population (E_e)

▨ = observed number of beetles from the population that has immigrated elsewhere (I_f)

a. Q_{wn} = 0.89, Q_{wz} = 0.89; E_{wn} = 0.14, E_{wz} = 0.20.
For Wn-78 $P_e < P_f$, for Wz-78 $P_e >> P_f$, thus for both population the values for E has to be made somewhat lower, and because of the difference of about 3 individuals between P_e and P_f and 6 between E_e and I_f for Wz we also chose a lower value for Q_{wz}

b. Q_{wn} = 0.89, Q_{wz} = 0.82; E_{wn} = 0.13, E_{wz} = 0.19.
For Wn-78 $P_e = P_f$, and for Wz-78 the differences between P_e and P_f, E_e and I_f respectively, are decreased for both to one specimen only.

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CURRICULUM VITAE

Robbert van der Eijk is geboren op 16 april 1946 te Ede. Na de
middelbare school (HBS-B) te Zwolle is hij in 1965 biologie gaan
studeren in Groningen. Al op de middelbare school was hij vooral
geinteresseerd in de limnologie, in het bijzonder de macrofauna. In
1974 studeerde hij af met als hoofdrichtingen dieroecologie en etho-
logie en als bijvak dierfysiologie. Zijn aktieve periode bij de
Nederlandse Jeugdbond voor Natuurstudie mag hier niet onvermeld blij-
ven; met name binnen de NJN heeft hij die veldkennis opgedaan die
geen onderdeel vormt van de biologiestudie.

Aansluitend op de studie is hij werkzaam geweest op het Biologisch
Station van de Landbouwuniversiteit te Wijster. Eerst met assisteren
bij het loopkeveronderzoek en van 1976 tot 1980 met het onderzoek aan
schrijvertjes, waarvan dit proefschrift het resultaat is. In de jaren
erna tot 1985 heeft hij, tussen de huishoudelijke werkzaamheden in
gezin door, nog aanvullende gegevens verzameld en de computersimula-
ties ontwikkeld en uitgevoerd, zoals die zijn terug te vinden in het
laatste hoofdstuk van dit proefschrift.

Naast de artikelen over het schrijvertjesonderzoek zijn van zijn hand
determinatietabellen verschenen voor zoetwaterbloedzuigers en water-
mijten, een artikel over een veldonderzoek naar de betrouwbaarheid
van netmonsters van macrofauna en een sillabus en artikel over schat-
tingsmethoden met behulp van merk-terugvang gegevens

Vanaf 1985 is hij begonnen met het opbouwen van een eigen instituut,
met het oogmerk met de verdiensten, die verkregen worden uit het
verlenen van computerdiensten uiteindelijk eigen onderzoek te finan-
ciëren. Nu dit proefschrift af is, kan hij zich eindelijk volledig
aan de wezenlijking van dat doel wijden.