

# FAUNA NORVEGICA

No. 1  
1989

SER. B VOL. 36 NO. 1  
Norwegian Journal of Entomology



PUBLISHED BY  
NORSK ZOOLOGISK TIDSSKRIFTSENTRAL  
OSLO

# Fauna norvegica Ser. B

## Norwegian Journal of Entomology

### Norsk Entomologisk Forenings tidsskrift

---

**Appears with one volume (two issues) annually**  
Utkommer med to hefter pr. år.

**Editor-in-Chief (Ansvarlig redaktør)**

John O. Solem, University of Trondheim, The Museum, N-7004 Trondheim.

**Editorial Committee (Redaksjonskomité)**

Arne Nilssen Zoological Dept., Tromsø Museum, N-9000 Tromsø, Ole A. Sæther, Museum of Zoology, Muséplass 3, N-5007 Bergen, Albert Lillehammer, Zoological Museum, Sars gt. 1, N-0562 Oslo 5.

**Subscription**

Members of Norw. Ent. Soc. will receive the journal free. Membership fee N.kr. 110,— should be paid to the Treasurer of NEF: Lise Hofsvang, Brattvollveien 107, N-1164 Oslo 11. Postgiro 5 44 09 20. Questions about membership should be directed to the Secretary of NEF: Trond Hofsvang, P.O. Box 70, N-1432 Ås-NLH. Members of NOF receive the journal by paying N.kr. 60,—, non-members by N.kr. 80,— to: NZT, Zoological Museum, Sarsgt. 1, N-0562 Oslo 5, Postgiro 2 34 83 65. Outside Fennoscandia: additional postage N.kr. 10,— per year (surface mail).

**Abonnement**

Medlemmer av Norsk Entomologisk Forening får tidsskriftet fritt tilsendt. Medlemskontingent kr. 110,— innbetales til kassereren til NEF: Lise Hofsvang, Brattvollveien 107, N-1164 Oslo 11. Postgiro 5 44 09 20. Medlemmer av Norsk Ornitolo-

gisk Forening mottar tidsskriftet ved å betale kr. 60,—. Andre må betale kr. 80,—. Disse innbetalingene sendes til NZT, Zoologisk Museum, Sarsgt. 1, N-0562 Oslo 5. Postgiro 2 34 83 65.

**FAUNA NORVEGICA B** publishes original new information generally relevant to Norwegian entomology. The journal emphasizes papers which are mainly faunistical or zoogeographical in scope or content, including checklists, faunal lists, type catalogues and regional keys. Submissions must not have been previously published or copyrighted and must not be published subsequently except in abstract form or by written consent of the Editor-in-Chief.

**NORSK ENTOMOLOGISK FORENING**

ser sin oppgave i å fremme det entomologiske studium i Norge, og danne et bindeledd mellom de interesserte. Medlemskontingenten er for tiden kr. 110,— pr. år. Henvendelse om medlemskap i NEF sendes sekretæren: Trond Hofsvang, Postboks 70, 1432 Ås-NLH. Medlemmer får tidsskriftet fritt tilsendt og kan abonnere til redusert pris på FAUNA NORVEGICA serie A (generell zoologi, 1 hefte pr. år) for kr. 30,— og på serie C (ornitologi, 2 hefter pr. år) for kr. 55,—. Disse innbetalingene sendes til NZT, Zoologisk museum, Sarsgt. 1, N-0562 Oslo 5. Postgiro 2 34 83 65.

Trykket med bistand fra Norges almenneviten-skapelige forskningsråd. Opplag 700.

**Norsk zoologisk tidsskriftsentral (NZT)** er et felles publiseringsorgan for NEF og NOF i samarbeid med de zoologiske avdelingene ved universitetsmuseene i Oslo, Bergen, Trondheim og Tromsø. Adresse: Zoologisk museum, Sarsgt. 1, 0562 Oslo 5. Postgiro 2 34 83 65.

**Managing Editor (Administrerende redaktør)**  
Edvard K. Barth, Zoologisk museum, Sarsgt. 1, 0562 Oslo 5.

**Editorial Board (Redaksjonsråd)**

Wim Vader, Tromsø, Svein Haftorn and John O. Solem, Trondheim, Rolf Vik, Oslo.

Kristiansen & Wøien, Oslo. ISSN 0332-7698

---

Fauna (Norsk Zoologisk Forening) har gått ut av Norsk Zoologisk Tidsskriftsentral. **Avtalen om gjensidig reduserte abonnementspriser på foreningens tidsskrifter vil for fremtiden derfor bare gjelde mellom Norsk Entomologisk Forening og Norsk Ornitologisk Forening.**

---

# Insektenes tilpasning til høyfjellet

LAURITZ SØMME

Sømme, L. 1989. Adaptations in insects and other terrestrial arthropods to the alpine environment. *Fauna norv. Ser. B* 36, 1—10.

The fauna of the arctic and alpine areas have traditionally attracted the interest of Nordic entomologists. Although parallels to the Arctic may easily be drawn, the present paper concentrates on the adaptations of terrestrial arthropods to the alpine environment. To survive these hostile surroundings, different patterns of adaptations have evolved. The fitness of each species depend on different combinations of abilities in accordance with their special habitats.

Morphological adaptations like reduced body-size, are known from a number of alpine insects, increasing their possibility to seek sheltered microhabitats. Wing atrophy, which is also known from insects in other extreme environments, is widespread. In many species absorption of solar radiation is increased by melanism. Alpine butterflies often orient the dark basis of their wings perpendicular to the rays of the sun. Increased pubescence, protecting against heat loss, is known from alpine butterflies and bumblebees.

As an adaptation to the short and cold alpine summers several species of terrestrial arthropods require more than one year to complete their lifecycle. Special to these species is their adaptation to low temperatures in two or more overwintering stages. In spite of their cold surroundings several species have univoltine lifecycles, frequently combined with highly specialised adaptations. Increased metabolic rates may be widespread in alpine species as a compensation to low temperatures, but few data are available. The adaptive advantage of nocturnal activity as observed in several species, may be to maintain the water balance of to avoid predation.

Cold tolerance is in particular important to temperate and arctic species. Winter survival in alpine Collembola and mites depends on supercooling, while examples of freezing tolerance are known from beetles. At high latitudes alpine species must endure extended periods of low temperatures during hibernation. Anaerobiosis is known from species enclosed in ice, with lactate as the main end product of metabolism.

Tropical alpine, terrestrial arthropods are faced with special problems. The great daily temperature fluctuations requires cold-hardiness during the night, and resistance to heat during the day. Many species seek sheltered microhabitats under rocks or in the vegetation. Resistance to desiccation becomes increasingly important in the tropics, and some alpine species are comparable to desert insects.

Lauritz Sømme, Department of Biology, Division of Zoology, University of Oslo, P.O.Box 1050 Blindern, N 0316 Oslo 3, Norway.

## INNLEDNING

Faunaen i høyfjellet og i arktiske strøk har alltid virket tiltrekkelige på nordiske entomologer. Vi behøver bare tenke på Zetterstedts reiser i det høye nord, eller Siebkes innsamlinger i norske høyfjell. Foruten alpine og arktiske områder i Fennoskandia, har nordiske entomologer naturlig nok interessert seg for mer fjerntliggende ekstreme lokaliteter på Island, Grønland og Svalbard. Faunaen av insekter og andre terrestre arthropoder er allikevel langt fra fullstendig undersøkt, men større innsats, bl.a. ved muligheten til å ar-

beide ved de nye arktiske og alpine forskningsstasjoner, har ført til økte kunnskaper. Foruten faunistiske undersøkelser, har nyere studier av arktiske og alpine insekter lagt større vekt på de økologiske aspekter.

Selv om det kan trekkes mange paralleller til forholdene i arktiske strøk, skal jeg her begrense meg til den alpine fauna av insekter og andre terrestre arthropoder. I forbindelse med at klimaet forandrer seg avtar antallet av arter meget sterkt over den alpine tregrense. Et sentralt problem er hvorledes disse artene er tilpasset til å overleve høyfjellets ekstreme betingelser. I dette foredraget vil jeg prøve å

analysere de egenskaper som skiller alpine arter fra deres slektninger i mer beskyttede lokaliteter.

## HØYFJELLETS KLIMA

Høyfjellets klima er komplisert og varierende, men skiller seg på flere måter fra klimaet i lavlandet. Uregelmessig topografi fører til store, lokale forskjeller, og dertil blir høyfjellets klima sterkt modifisert av breddegrad og med graden av kontinentalitet. Høyfjells klima er bl.a. beskrevet i oversikter av Mani (1968, 1974), Barry & van Wie (1974), Flohn (1974) og Franz (1979).

Til tross for de store variasjonene forandrer klimaet seg gradvis med økende høyde over havet (Tabell 1). Som påpekt av Mani (1968, 1974) skyldes forandringene først og fremst fallet i atmosfærisk trykk. Temperaturen er blant de faktorer som har størst økologisk betydning, og synker i årlig gjennomsnitt med ca. 6.5 °C pr. 1000 m høyde. Typisk for høyfjellet er raskt skiftende temperaturforhold, og store forskjeller mellom temperaturen i solen og skygge.

Både redusert lufttrykk og lave temperaturer bidrar til at vanddamptrykket reduseres. I mange fjellområder er den tørre luften en viktig økologisk faktor. Nedbøren avtar ofte med høyden, men kan også øke, som f.eks. opp til 3000—3500 m i Alpene.

Tabell 1. Klimatiske forandringer i høyfjellet med økende høyde over havet. (Etter Mani 1968, 1974)

Synkende atmosfærisk trykk
Redusert oksygentrykk
Redusert vanddamptrykk
Synkende temperaturer
Hurtig skiftende temperaturer
Økende temperaturforskjell mellom sol og skygge
Klarere luft
Økende innstråling
Økende utstråling
Avtagende nedbørmengder (med unntak)
Økende vindstyrker
Lengere perioder med snedekke

Andre klimafaktorer av stor økologisk betydning er de tiltagende vindene i store høyder, og de lange periodene hvor marken er dekket av sne. Alle klimafaktorer forandrer seg med breddegraden langs en gradient fra store sesongvariasjoner i nord og syd til store dagvariasjoner ved ekvator.

## MORFOLOGI OG ADFERD

Til de vanligste morfologiske tilpasninger hos alpine insekter hører redusert kroppstørrelse, reduserte vinger eller manglende flygeevne, melanistiske farger og øket tykkelse av hårpelsen. Noen av disse egenskapene er ikke enestående for høyfjellsarter, men fins også hos insekter i lavlandet.

### Kroppstørrelse

I mange insektgrupper er det en tendens til redusert kroppstørrelse med økende høyde over havet. Dette er bl.a. tydelig vist av Mani (1968) for carabider av slekten *Bembidion* i Himalaya, mens det ikke foreligger tilsvarende undersøkelser fra skandinaviske høyfjell. Fig. 1 viser at gjennomsnittstørrelsen for *Bembidion* spp. fra 500 m.o.h. er nærmere 10 mm, mens den ligger under 4 mm hos arter fra 4000 m o.h. Redusert størrelse gjør det

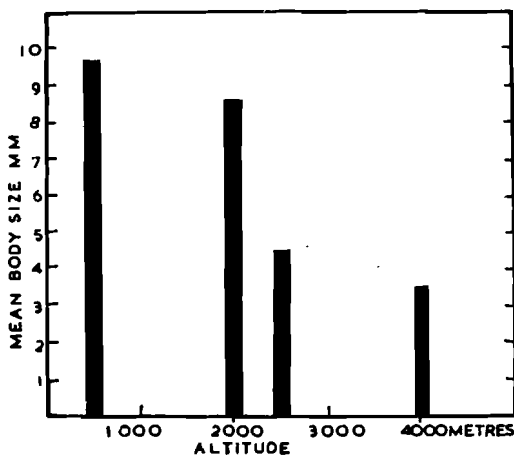


Fig. 1. Reduksjon i kroppstørrelse med økende høyde hos *Bembidion* spp. fra Himalaya. (Etter Mani 1968).

Reduction in body size with increasing altitude in the carabid beetles *Bembidion* spp. from Himalaya. (From Mani 1968.)

lettere å finne skjul i små mikrohabitat, men kan også være en tilpasning til redusert næringstilgang.

Et annet eksempel er dagsommerfugler av slekten *Colias*, som har en meget stor utbredelse. De største artene finner man i subtropiske områder, og de aller minste i arktiske strøk, Andesfjellene og Himalaya. En ytterligere reduksjon av størrelsen fins hos pierine dagsommerfugler av slekten *Phulia* fra høytliggende områder i Andesfjellene. Ifølge Shapiro (1986) er de mindre enn halve størrelsen av normale pieriner, som f.eks. arter av slektene *Pieris* og *Tatochila*.

Lave temperaturer og sterke vinder gjør at de voksne *Phulia*-sommerfuglene søker ly i den lave vegetasjonen det meste av dagen, og kan bare være i aktivitet noen få timer. Ifølge Shapiro (1986) kan behovet for å skjule seg i vegetasjonen ha ført til en seleksjon for redusert vingestørrelse, og dermed også for redusert kroppsstørrelse (Fig. 2). Under de ekstreme klimatiske forholdene er mange av *Phulia*-artenes vertsplanter små og uanselige, og dette kan også føre til seleksjon for redusert størrelse hos sommerfuglene. Et annet eiendommelig trekk ved *Phulia*-artenes biologi er at de legger færre egg enn andre pieriner, men eggene er like store som hos disse. Dette kan også skyldes sommerfuglenes korte aktivitetsperioder under de strenge klimati-

ske forhold. Eggene plasseres ofte på feil plante, og de nyklekte larvene må selv finne den rette vertsplanten. Det er derfor en fordel å være utstyrt med rikelig næring fra egget. Seleksjon for store egg og redusert kroppsstørrelse må nødvendigvis føre til en reduksjon i antallet av egg.

### Melanisme

Mørke farger, eller melanisme, er meget utbredt blant arktiske og alpine insekter. Alleerede i 1836 publiserte sveitseren Heer sine observasjoner om økende antall mørke insektarter med høyden i Alpene. Hos collemboler har Rapoport (1970) vist at antallet mørke arter øker både med breddegrad og med høyden over havet. Ifølge Mani (1968) gir økt pigmentering insektene mulighet for å øke kroppstemperaturen ved absorpsjon av varmestråling fra omgivelsene. Dessuten kan det tenkes at mørke farger beskytter mot skadelige effekter av UV-stråling i store høyder, men dette er et spørsmål som trenger nærmere undersøkelse.

Når det gjelder absorpsjon av varmestråling er det ikke kjent om små arter, som f.eks. collemboler, er i stand til å holde på den energi de absorberer. Det er også interessant å merke seg at insekter med røde eller rufinistiske farger, som man bl.a. finner hos mange løpebiller i høyfjellet (Ottesen 1980) absorberer infrarød varmestråling bedre enn insekter med sorte farger.

Betydningen av melanisme for termoregulering er imidlertid godt dokumentert hos pierine dagsommerfugler. Både arktiske og alpine arter har mørkere kropp og vingebasis enn arter i lavlandet. For å kunne fly må disse sommerfuglene øke sin kroppstemperatur ved å «bask» i solen med en positur som eksponerer de mørke områdene mot solstrålene. Hos fem arter av *Colias* fra 1700—3600 m o.h. i Colorado Rocky Mountains fant Kingsolver (1983) at en kroppstemperatur på 30—40°C var nødvendig for å kunne fly. Ved å plassere sommerfuglene i en fiksert posisjon mot solen kunne han med et tynt termoelement måle hvordan kroppstemperaturen raskt økt under solstråling, og avtok i skygge. Registrerte kroppstemperaturer over 30°C passet nøyaktig med flygeaktiviteten på forsøketstedet hos frittlevende eksemplarer av samme art. Absorpsjon av solenergi hos *Colias*-artene økte med høyde over havet, likeledes

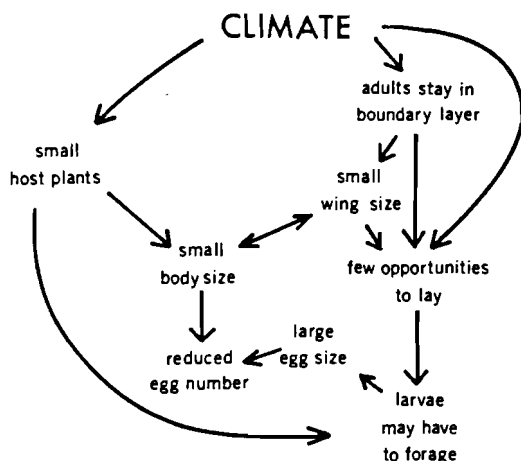


Fig. 2. Seleksjon for liten kroppstørrelse og stor eggstørrelse hos *Phulia* spp. i Andesfjellene. (Etter Shapiro 1986.)

The selection for small body size and large egg size in *Phulia* spp. from the Andes. (From Shapiro 1986.)

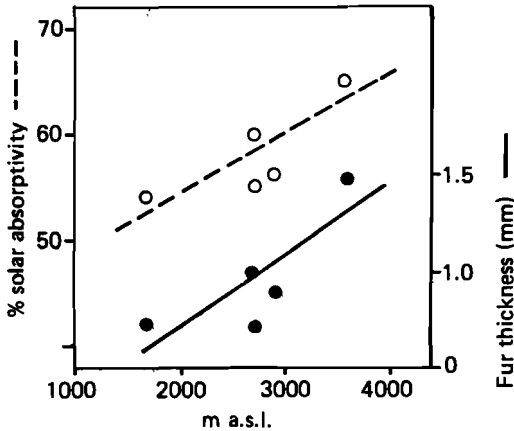


Fig. 3. Absorpsjon av solenergi og øket pelstykke som tilpasning til høyden hos *Colias* spp. fra Rocky Mountains. (Etter Kingsolver 1983.)

Solar absorptivity and fur thickness as adaptations to high altitudes in *Colias* spp. from the Rocky Mountains. (From Kingsolver 1983.)

deres evne til å holde på varmen gjennom øket pelstykke (Fig. 3).

Foruten hos sommerfugler er termoregulering kjent hos alpine gresshopper fra Rocky Mountains og spyfluer fra 3900 m o.h. i østlige deler av Pamir.

### Nattaktivitet

Ifølge en oversikt av Edwards (1987) er en stor del av predatorne i den alpine sone nattaktive. Noen av dem lever av byttedyr som er ført med vinden fra lavere områder og har landet på sneflekker. På snefrie områder i Colorado Rockies, 3600—4270 m o.h. fant Schmoller (1971) at tyve arter av carabider, tre arter av Opiliones og 14 arter av edderkopper (fam. Gnaphosidae) var mer eller mindre nattaktive. Nattaktive carabider er også kjent fra Alpene, og på Finse fant Ottesen (1985) at 10 av 14 undersøkte billearter fra 1200—1500 m var aktive om natten. I de lysende nettene midt på sommeren omfattet aktivitetsperiodene også skumringstiden.

Fra et tilpassningsmessig synspunkt kan det være flere fordeler ved nattaktivitet. De fleste forfattere mener at nattaktivitet er en beskyttelse mot predasjon. På breer og sneflekker vil insekter lett bli bytte for fugl, og i den åpne, alpine vegetasjonen kan de også være

relativt ubeskyttet. Nattaktivitet er vanligst hos forholdsvis store arter, som lettest vil bli oppdaget om dagen. Nærmere undersøkelser av disse forholdene ville være interessant, bl.a. for å se hva nattaktive insekter og andre terrestre arthropoder egentlig foretar seg om natten. Det kan f.eks. tenkes at nattaktivitet på snefrie områder bare er en form for spredning eller migrasjon, mens næringsopptak, forplantning og andre aktiviteter kan foregå i mer beskyttede mikrohabitater om dagen.

Ifølge Edwards (1987) mener noen forfattere at alpine insekter er nattaktive fordi de ofte er mørke av farge, og lett vil bli overopphetet om dagen. Det virker allikevel usannsynlig at det skulle finne sted en seleksjon for melanisme, hvis det også førte med seg slike negative sider. Mer sannsynlig kan det kanskje være at nattaktivitet kan være en fordel for å unngå uttørking, spesielt i tørre, alpine områder.

### Reduserte vinger

Reduserte vinger eller fullstendig mangel på vinger er vanlig hos insekter med forskjellige former for spesialisert levevis, f.eks. parasitisme. Det er også vanlig hos insekter som lever i ekstreme habitater på øyer, i polare områder eller på høyfjellet. Reduserte vinger er således ikke spesielt for høyfjellet, men den prosentvise andel av slike arter øker med høyden over havet. Mani (1968, 1974) har gitt en oversikt om forekomsten av insekter med reduserte vinger fra forskjellige fjellområder. Han påpeker bl.a. at i Himalaya har 60% av artene over 4000 m reduserte vinger, og at vingete arter ofte mangler evnen til fly. Vingereduksjon hos alpine arter tenkes å være utviklet under seleksjonspress av klimaet. I høyfjellet vil flygende insekter lett føres bort fra sine egentlige habitater av vinden, og den adaptive fordel med reduserte vinger ligger i at risikoen for dette avtar.

### RESISTENS MOT UTTØRNING

Redusert nedbør og den tørre luften i mange alpine områder er av stor økologisk betydning. Fordampningen blir ofte høy, og kan i lengre perioder langt overstige nedbøren, som f.eks. i den høytliggende paramos i Andesfjellene nær ekvator. Under disse forholdene kan insekter og andre terrestre arthropoder bli utsatt for sterk uttørking. Mange

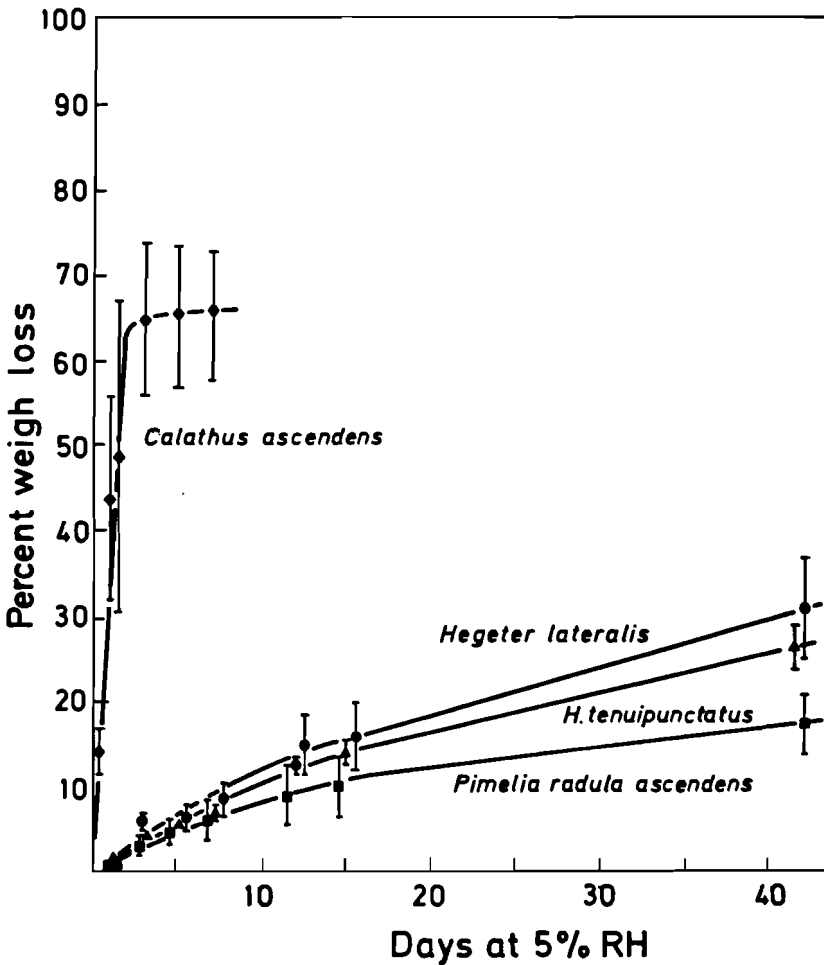


Fig. 4. Resistens mot uttørking hos tre arter av Tenebrionidae og hos carabiden *Calathus ascendens* fra Pico del Teide, Tenerife. (Etter Ottesen & Sømme 1987.)

Resistance to desiccation in three species of Tenebrionidae and the carabid beetle *Calathus ascendens* from Pico del Teide, Tenerife. (From Ottesen & Sømme 1987.)

arter unngår dette ved å søke ly i beskyttede mikrohabitater, f.eks. under sten eller i vegetasjonen. I tropiske høyfjell gir det fuktige, visne løvverket hos rosettplanter som *Espeletia* i Andesfjellene beskyttelse for store antall av terrestre arthropoder. En enkelt plante kan romme mer enn 100 000 individer.

Mange arter i tørre fjellområder har også utviklet stor resistens mot uttørking, i en grad som kan sammenlignes med ørkeninsekter. Tørkeresistente gresshopper er kjent fra Rocky Mountains og Andesfjellene. Enkelte arter av Diplopoda fra store høyder i Alpene tåler mer tørke enn arter fra lavereliggende områder (Meyer & Eisenbeis 1987). Hos tre arter av Tenebrionidae fra 2000–2500 m o.h. på Pico del Teide, Tenerife, fant Ottesen & Sømme (1987) meget stor resistens mot uttørking (Fig. 4). Disse artene levde i mer

enn firti døgn ved 21°C og 5% RH, mens carabiden *Calathus ascendens* fra samme lokalitet tørket ut på under ett døgn. Den siste er avhengig av fuktige planterester under buskvegetasjonen for å overleve.

## LIVSSYKLUS

### Forlenget livssyklus

De korte og kjølige somrene i høyfjellet reduserer hastigheten i vekst og utvikling hos terrestre arthropoder. Mens de fleste tempererte og tropiske arter har en eller flere generasjoner i året, trenger mange alpine arter to eller flere år på å gjennomføre sin livssyklus.

Blant insektene er forlenget livssyklus påvist hos carabider fra Alpene, finsk Lappland og norske høyfjell. Mange arter av ferskvanns-

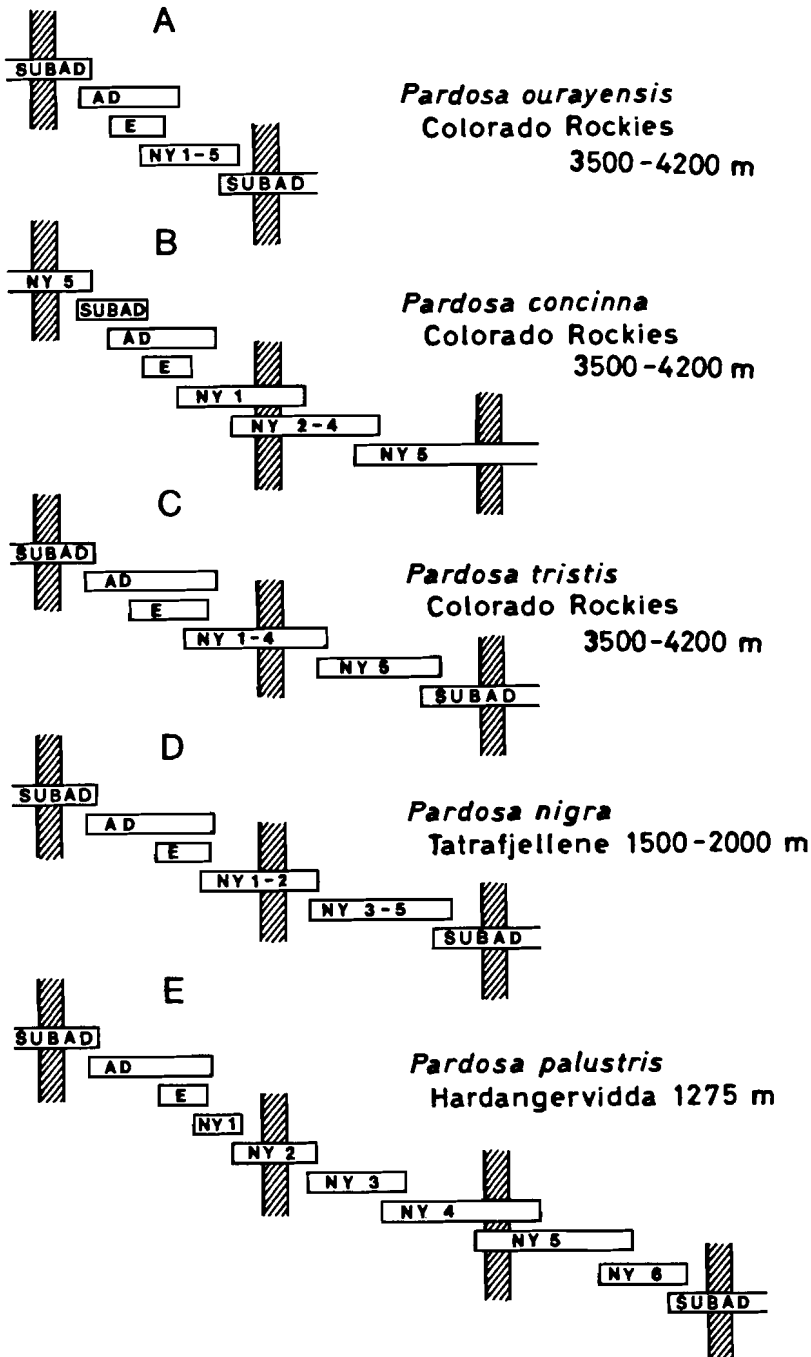


Fig. 5. Livssyklus hos *Pardosa* spp. fra forskjellige fjellområder. Loddrett søyer symboliserer vintrene. E = egg, NY = nymfestadier, AD = voksne. (Se tekst for referanser.)

Lifecycles in wolf spiders (*Pardosa* spp.) from different mountains areas. Vertical bars symbolize winters. E = eggs, NY = nymphal stages, AD = adults. (See text for references.)



insekter, bl.a. Plecoptera, Ephemeroptera og Trichoptera har forlenget livssyklus i høyfjellet. På Finse bruker stankelbenet *Tipula excisa* to år på sin utvikling, mens nærstående arter i lavlandet har ettårig livssyklus.

Blant ulvedderkopper av slekten *Pardosa* fins det en rekke eksempler på forlenget livssyklus (Fig. 5). Mens noen arter nær tregrensen i Rocky Mountains gjennomfører livssyklus på ett år, er *P. concinna* og *P. tristis* fra høyere liggende områder toårige (Schmoller 1970). Toårig livssyklus er også påvist hos *P. nigra* fra Tatrafjellene (Lominicki 1963), mens *P. mixta* fra Alpene (Czermak 1981) og *P. palustris* fra Hardangervidda (Steigen 1975) bruker tre år. Blant de forskjeller artene med forlenget livssyklus er det forskjeller i hvilke stadier som overvintrer. Dette tyder på at seleksjon for forlenget livssyklus har foregått uavhengig i forskjellige fjellområder. Preadaptasjon hos en felles stamform kan ha øket sjansene for at denne form for tilpasning skulle utvikles hos flere beslektede arter.

### Ettårig livssyklus

Ettårig livssyklus er også vanlig blant alpine insekter til tross for at de lever i kalde omgivelser. Både i Rocky Mountains, Tatrafjellene og på Hardangervidda fins det bl.a. arter av Opiliones som gjennomfører sin utvikling på ett år. Tilsvarende forhold er kjent hos alpine Orthoptera, Ephemeroptera, Plecoptera, Trichoptera og Coleoptera. Nærmere undersøkelser av de enkelte artene viser at hver av dem har sine spesielle tilpasninger til miljøet, bl.a. gjennom adferd og bedre utnyttelse av gunstige mikroklimatiske nisjer. Noen utmerker seg ved rask vekst i larvestadiet, slik som arter av Trichoptera fra temporære dammer, som tørker inn i løpet av sommeren (Solem 1983).

Et eiendommelig tilfelle av ettårig livssyklus er funnet hos chironomidene *Diamesia kohshimai* og *D. valavia*, som tilbringer hele sitt liv på isbreer i en høyde på over 5000 m i Himalaya. Ifølge Kohshima (1984) overvintrer disse artene som voksne, hvilket også er uvanlig hos chironomider.

Hos carabiden *Pelophila borealis* fra 1200 m på Finse gjennomføres utviklingen fra egg til voksen i løpet av sommeren, og de voksne billene overvintrer. Tilsynelatende kan hele populasjonen risikere å dø ut hvis den får en sommer med usedvanlig ugunstig værfor-

hold. De voksne billene lever imidlertid to eller tre år, og vil derfor være istand til å kompensere for slike tap det følgende år. I laboratoriet lykkes det å indusere imaginal diapause tre ganger på rad i samme individer av *P. borealis*, med egglegging etter diapauseutviklingens avslutning (unpubliserte data).

### Konklusjon

Fra disse eksemplene kan det konkluderes at både ettårige og flerårige livssyklus er vanlige hos alpine arthropoder. Arter med ettårig livssyklus er antagelig de mest spesialiserte. Hos mange arter er livssyklus fleksibel ett- eller flerårig, avhengig av høyden over havet. Arter med forlenget livssyklus er relativt uavhengige av spesielle tilpasninger i adferd, valg av mikrohabitat eller øket metabolisme. De skiller seg derimot fra andre arter ved at to eller flere stadier må være tilpasset kulde og overvintring. De evolusjonistiske prosesser bak utviklingen av kuldetoleranse i flere stadier kan derfor være en barriere som hindrer mange lavlandsarter i å tilpasse seg den alpine sone.

### METABOLISME

Hastigheten av vekst, utvikling og andre aktiviteter hos poikiloterme dyr er nøye knyttet til temperaturen. Mange dyr, bl.a. flere marine arter, er i stand til å kompensere for lave temperaturer ved øket metabolisme. Et øket oksygenopptak, som uttrykk for metabolismen, er også påvist hos enkelte arktiske og antarktiske terrestre arthropoder. Mange arktiske insekter har allikevel ikke høyere metabolisme enn tilsvarende arter fra tempererte områder, men deres temperaturgrense for vekst og utvikling ligger ofte lavere.

Øket metabolisme er påvist hos enkelte alpine arter av colleboler, gresshopper og biller. Hos gresshopper av slekten *Trimerotropis* er oksygenforbruket høyere hos en art fra Rocky Mountain enn hos en nærbeslektet art fra Somora-ørkenen (Massion 1983). *Aeropedellus clavatus* og *Melanoplus dogei*, som også er gresshopper fra Rocky Mountains, har høyere oksygenforbruk på 4000 m enn i 2500 m o.h. (Alexander & Hilliard 1969).

Bortsett fra disse undersøkelsene fins det få opplysninger om metabolisme hos alpine insekter som er egnet til sammenligning med

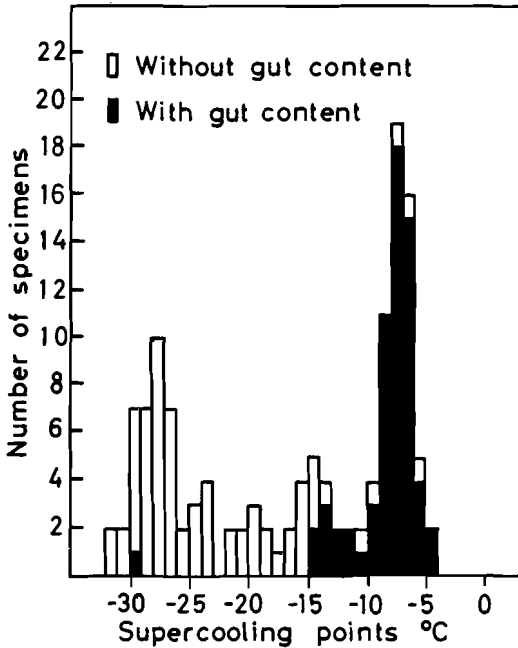


Fig. 6. Fordeling av underkjølingspunktene hos 133 eksemplarer av *Tetracanthella wahlgreni* med og uten matrester i tarmen. (Etter Sømme & Conradi-Larsen 1977.)

Supercooling point distribution histogram of 133 specimens of the collembolan *Tetracanthella wahlgreni* with and without the presence of gut content. (From Sømme & Conradi-Larsen 1977.)

arter i lavlandet. Forholdene kompliseres også ved at metabolisme innen samme art og stadium kan være meget variable, bl.a. avhengig av forutgående akklimatisering, kjønn og forplantningfase. Hos hunner av den alpine bladbillen *Melasoma collaris* blir f.eks. oksygenopptaket tredoblet under vitellogenese, men avtar sterkt etter egglegging.

## KULDETOLERANSE

De lange vintrene i nordlige høyfjell krever spesielle tilpasninger til kulde hos terrestre arthropoder. Alpine arter overvintrer under forhold hvor arter fra varmere strøk raskt ville bli drept. Kuldetoleranse omfatter egentlig både tid og temperatur. I arktiske strøk og nordlige høyfjell kan vinteren være av en varighet på 8—9 måneder eller lenger.

Overvintringsforholdene er allikevel meget forskjellige for insekter og andre arthro-

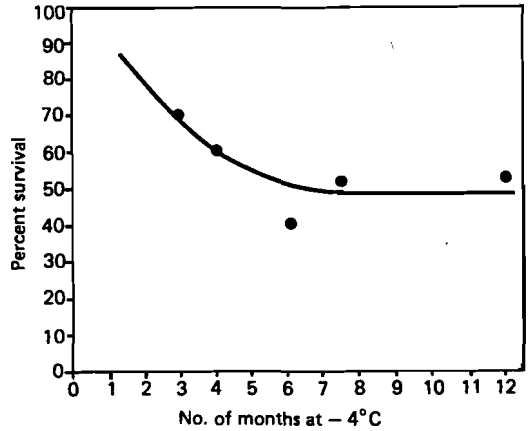


Fig. 7. Langtids overlevelse ved  $-4^{\circ}\text{C}$  hos *Pelophila borealis* fra Finse. Hvert punkt representerer tolv individer.

Long-time survival rates at  $-4^{\circ}\text{C}$  in the alpine, carabid beetle *Pelophila borealis* from Finse, Norway. Each dot represents twelve specimens.

poder. Arter i ferskvann har konstante temperaturer nær  $0^{\circ}\text{C}$  hele vinteren, og i jorden er mange arter beskyttet mot lave temperaturer av et tykt dekke av sne. Derimot er fjellrabber, hvor vinden blåser sneen bort, langt mer utsatt. I det øverste tynne jordsmonnet, hvor mange insekter og midd overvintrer, svinger temperaturen ofte i takt med lufttemperaturen.

Utviklingen har prinsipielt gått i to retninger når det gjelder muligheten til å overleve lave temperaturer. Såkalte frysetolerante insekter kan tåle isdannelser i kroppsvæsken, og overvintrer i frossen tilstand. De fleste terrestre arthropoder er frysefølsomme, og blir drept hvis de fryser. Slike arter er avhengige av sin evne til å underkjøle når omgivelsenes temperatur synker under kroppsvæskens frysepunkt (Sømme 1982).

Blant de alpine arter som hittil er undersøkt er det relativt få som er frysetolerante. Collemboler og midd som overvintrer i de mest utsatte habitater er avhengig av underkjøling. Arter som overvintrer i norske høyfjell og i Alpene tåler ofte nedkjøling til mellom  $-30$  og  $-45^{\circ}\text{C}$  før frysing inntreffer. Underkjølingspunktet, eller den nedre grense for underkjøling, varierer imidlertid sterkt med årstidene. Et typisk eksempel er collembolen *Tetracanthella wahlgreni* fra Finse, som bare kan underkjøles til ca.  $-6^{\circ}\text{C}$  om sommeren,

men til mellom -35 og -40 °C om vinteren (Sømme & Conradi-Larsen 1977).

Slike sesongvariasjoner skyldes flere faktorer. Matrester i tarmen kan ofte inneholde stoffer eller såkalte nukleatorer, som induserer frysing i et underkjølt system, og mange insekter kvitter seg med tarminnholdet om høsten. Hos *Tetracanthella wahlgreni* faller underkjølingspunktene i to grupper avhengig av tilstedeværelsen eller mangel på tarminnhold (Fig. 6). I tillegg til tømning av tarmen akkumulerer mange arter glycerol og andre lavmolekylære, kuldebeskyttende stoffer, som øker evnen til å underkjøle.

Sjansen for frysing i et underkjølt system øker også med tiden, men vi vet ikke nok om hvordan underkjølingen stabiliseres hos insekter og andre terrestre arthropoder. I denne sammenheng knytter det seg stor interesse til de såkalte termisk hysterese proteinene, som kan tenkes å forsinke dannelse av mikroskopiske iskrystaller, eller kim, hos underkjølte insekter (Zachariassen 1985).

Vi vet heller ikke så meget om hvilke fysiologiske eller biokjemiske mekanismer som gjør det mulig å overleve lange perioder ved lave temperaturer. Mens insekter fra varmere strøk blir drept etter kort tid ved temperaturer nær eller over 0 °C, må mange alpine arter leve i måneder ved temperaturer under frysepunktet. Et eksempel er carabiden *Pelophila borealis*, som i laboratoriet kunne leve 13 måneder ved -4 °C (Fig. 7). Mens mange forskere har konsentrert seg om frysetoleranse og underkjøling, har tidsfaktorer i kuldetoleranse blitt et forsømt område.

## ANAEROBIOSE

I mange alpine habitater fryser de øverste lagene av jorden til en kompakt ismasse om vinteren. Det kan f.eks. gjelde visse fuktige habitater, men også avblåste fjellrabber hvor regn og sne, som smelter om høsten, etterhvert skaper et tett isdekke. De dyrene som overvintrer på slike steder blir omsluttet av is, og det oppstår mangel på oksygen. Under slike forhold skifter mange insekter og midd over fra aerob til anaerob metabolisme. Løpebillen *Pelophila borealis* kan f.eks. leve inefrosset i mer enn 6 måneder (Conradi-Larsen & Sømme 1973). Under mangel på oksygen akkumuleres lactat som et anaerobt endeprodukt. Anaerob metabolisme er en meget viktig tilpasning hos alpine insekter, men disse forholdene er foreløpig forholdsvis lite undersøkt.

## KONKLUSJONER

De eksemplene som er gitt viser at tilpasning til alpine områder kan omfatte mange egenskaper. Insekter og andre terrestre arthropoder må kunne gjennomføre forplantning, vekst og utvikling i de korte og kjølige somrene, og ofte tåle lange perioder med lave temperaturer om vinteren. Mange arter blir utsatt for andre stressfaktorer, som f.eks. vind, tørke eller mangel på oksygen. Den enkelte arts totale tilpasning fortøner seg som et mønster av spesialiserte egenskaper i overensstemmelse med de krav som stilles av dens levevis og spesielle habitat. Gjennom en kombinasjon av morfologiske, fysiologiske egenskaper, adferd og valg av mikrohabitat skiller alpine, terrestre arthropoder seg fra sine slektninger i varmere områder. Fremdeles gjenstår mange problemer når det gjelder å forstå disse egenskapene fullt ut, både enkeltvis eller i kombinasjoner. De kombinasjoner som særpreger alpine arter forutsetter at evolusjonen samtidig virker på flere felt. Nettopp her ligger kanskje forklaringen på begrensningene i høyfjellets fauna, og at antallet av arter reduserer så sterkt over tregrensen.

## LITTERATUR

- Alexander, G. & Hilliard, J. R. Jr. 1969. Altitudinal and seasonal distribution of Orthoptera in the Rocky Mountains of northern Colorado. *Ecol. Monogr.* 39, 385—431.
- Barry, G. R. & van Wie, C. C. 1974. Topo- and microclimatology in alpine areas, pp. 73—83 in: Ives, J. D. & Barry, R. G. (eds.) *Arctic and alpine environments*. Methuen, London.
- Conrad-Larsen, E.-M. & Sømme, L. 1973. The overwintering of *Pelophila borealis* Payk. II. Aerobic and anaerobic metabolism. *Norsk ent. Tidsskr.* 20, 325—332.
- Czermak, B. 1981. Autökologie und Populationsdynamik hochalpiner Araneen unter Besonderer Berücksichtigung von Verteilung, Individuendichte und Biomasse in Grassheidebiotopen, pp. 101—152 in: Franz, H. (ed). *Veröff österr. MAB-Hochgebirgsprogr. Hohe Tauern* 4. Wagner, Innsbruck.
- Edwards, J. S. 1987. Arthropods of alpine aeolian ecosystems *Ann. Rev. entomol.* 32, 163—179.
- Flohn, H. 1974. Contribution to a comparative meteorology of mountain areas, pp. 55—71 in: Ives, J. O. & Barry, R. G. (eds.) *Arctic and alpine environments*. Methuen, London.
- Franz, H. 1979 *Ökologie der Hochgebirge*. 495 pp. Ulmer, Stuttgart.

- Kingswolver, J. G. 1983. Thermoregulation and flight in *Colias* butterflies: Elevation patterns and mechanistic limitations. *Ecology* 64, 534—545.
- Kohshina, S. 1984. A novel cold-tolerant insects found in a Himalayan glacier. *Nature* 310, 225—227.
- Lominicki, A. 1963. The distribution and abundance of groundsurface inhabiting arthropods above the timberline in the region of Zolta Turnia in the Tatra Mountains. *Acta Zool. Cracoviensia* 8, 183—249.
- Mani, M. S. 1968. *Ecology and biogeography of high altitude insects*. 527 pp. W. Junk, The Hague.
- Mani, M. S. 1974. *Fundamentals of high altitude biology*. 196 pp. Oxford and IBH Publ. Co., New Dehli.
- Massion, D. D. 1983. An altitudinal comparison of water and metabolic relations in two acridid grasshoppers (Orthoptera). *Comp. Biochem. Physiol.* 74 A, 101—105.
- Meyer, E. & Eienbeis, G. 1985. Water relations in millipedes from some alpine habitat types (Central Alps, Tyrol) (Diplopoda). *Bijdr. Dierk.* 55, 131—142.
- Ottesen, P. 1980. Evolusjon av rufinisme hos løpebiller (Coleoptera: Carabidae). 75 pp. Cand.scient. oppgave ved Zoologisk institutt, Universitetet i Oslo.
- Ottesen, P. 1985. Diel activity pattern of South Scandinavian high mountain ground beetles (Coleoptera, Carabidae). *Holarctic Ecol.* 8, 191—203.
- Ottesen, P. & Sømme, L. 1987. Adaptations to high altitudes in beetles from Tenerife. *Vieraea* 17, 217—226.
- Rapoport, E. H. 1969. Gloger's rule and pigmentation of Collembola. *Evolution* 23, 622—626.
- Schmoller, R. 1970. Life histories of alpine tundra Arachnida in Colorado. *Amer. Midl. Natur.* 83, 119—133.
- Schmoller, R. 1971. Nocturnal arthropods in the alpine tundra of Colorado. *Arct. Alp. Res.* 3, 345—352.
- Shapiro, A. M. 1986. r-k selection at various taxonomic levels in the pierine butterflies of North and South America, pp. 135—152 in: Taylor, F. & Karban, R. (eds.) *Evolution of insect life histories*. Springer, Berlin.
- Solem, J. O. 1983. Temporary pools in the Dovre mountains Norway, and their fauna of Trichoptera. *Acta Entomol. Fennica* 42, 82—85.
- Sømme, L. 1982. Supercooling and winter survival in terrestrial arthropods. *Comp. Biochem. Physiol.* 73 A, 519—543.
- Sømme, L. & Conradi-Larsen, E.-M. 1977. Cold-hardiness of collembolans and oribatid mites from windswept mountain riges. *Oikos* 29, 118—126.
- Steigen, A. L. 1975. Energetics in a population of *Pardosa palustris* (L.) (Aranea, Lycosidae) on Hardangervidda. pp. 129—144 in: Wielgoaski, F. E. (ed.) *Fennoscandian tundra ecosystems, Part 2*. Springer, Berlin.
- Zachariassen, K. E. 1985. Physiology of cold tolerance in insects. *Physiol. Rev.* 65, 799—832.

Received 5 July 1988

# Entomology in Iceland

GISLI MAR GISLASON AND ERLING OLAFSSON

Gislason G. M. & Olafsson, E. 1989. Entomology in Iceland. *Fauna norv. Ser. B* 36, 11—16.

Entomological studies in Iceland can be dated back to 1638. From early writings on insects and terrestrial arthropods, only a few species can be identified. By the end of the 18th century, 80 insect species had been recorded. The number of species recorded from Iceland increased during the 19th century, being 311 in 1857. It was not until 1931 a comprehensive knowledge was obtained about the zoogeography of insects in Iceland and their faunistics with 700 insect species identified from Iceland. Their present number is now about 1200.

Only a few papers were published about terrestrial arthropods in Iceland before 1900. In the beginning of the 20th century, the number of publications increased to over one per year. There was an exponential increase in number of publications to 1940 (5.6 publications a year), when the numbers fell to about 3 a year. An increase was again observed after 1970, with now about 8—9 publications on terrestrial arthropods per year. Papers only dealing with other arthropod groups than insects are 12.5% of the total numbers.

Entomological research in Iceland was dominated by Danish and Swedish scientists until after 1930, when Icelandic scientists increased their share in entomological publications. Now Icelandic scientists are about 60% of authors writing about terrestrial arthropods in Iceland. Most papers dealing with Icelandic entomology are on faunistics, but after 1970, increasing number of papers deals with other subjects.

Gisli Mar Gislason, Institute of Biology, University of Iceland, Grensasvegur 12, IS-108 Reykjavik, Iceland.

Erling Olafsson, Icelandic Museum of Natural History, Laugavegur 105, IS-105 Reykjavik, Iceland.

## INTRODUCTION

Most entomological studies in Iceland have been conducted as a result of academic interests rather than as applied research. Until recently, applied studies have been concentrated on the few pest species found in Iceland (Gigja 1944), but now, entomology plays a major role in environmental studies. Iceland has attracted several scientists from other countries to study insects. They have mainly examined faunistics, island zoogeography and the problem of colonization (e.g. Lindroth 1931, Buckland et al. 1986, Downes 1988). In this paper we will look at the development of research on terrestrial arthropods, especially insects, in Iceland till 1987.

## METHODS

Literature on terrestrial arthropods in Iceland was searched in all major libraries in

Iceland and in Lund, Sweden. Also, the reference lists in the publications we got hold of were searched, especially the references in the series *The Zoology of Iceland*, published by Munksgaard in Copenhagen. These references were classified according to their year of publication, content and nationality of authors (first author of multi-author papers).

A complete list of publications on terrestrial arthropods in Iceland is available from the authors.

## RESULTS AND DISCUSSION

Altogether 359 publications were found dealing with terrestrial arthropods in Iceland. Insects were dealt with in 314 publications, often with other aspects of natural sciences and 45 with other terrestrial arthropods than insects (Fig. 1). The earliest works mentioning insects were manuscripts from 1638 (Oddsson 1917) and about 1640 (Hermansson 1924). Only 3 species of insects could be

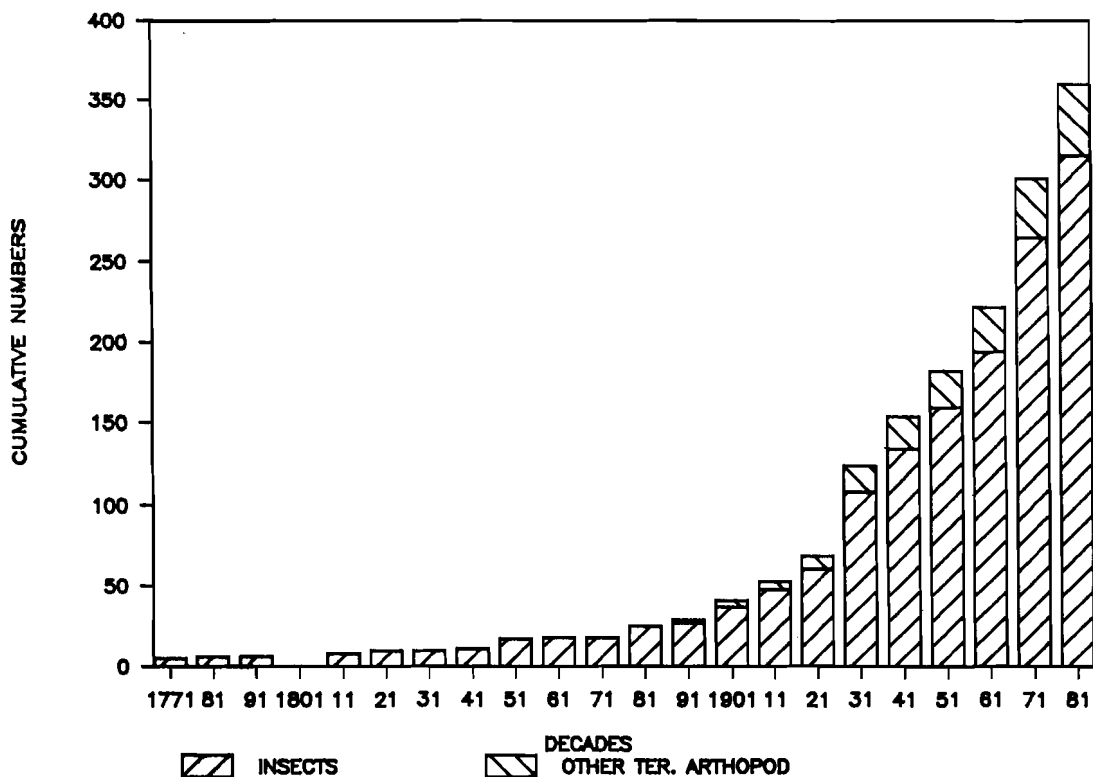


Fig. 1. Number of publications dealing with Icelandic terrestrial arthropods from 1771—1987. Other subjects of natural sciences were often in-

cluded in publications with insects in the early publications, e.g. geology, geography and records of other animal groups.

identified from their descriptions. Authors writing about insects in Iceland in the following century (Anderson 1746, Horrebow 1752) did not describe species well enough for their identification. It was not until Olafsen and Povelsen (1772) wrote their book *Travel in Iceland*, that the number of insect species rose to 50. In the 19th century several authors, mainly German and English, travelled in Iceland and collected insects. The number of recorded species was 311 in 1857 (Staudinger 1857). The insect collections made in the 19th century were sporadic. It was not until Carl H. Lindroth began his systematic collection in the lowlands of Iceland, that a general picture was obtained of insect life in Iceland. He started his sampling in 1926 which lead to several publications (Lindroth ed. 1928). He returned to Iceland in 1929 for further studies, which lead to his doctoral thesis (Lindroth 1931) on the dis-

tribution of insects in Iceland. He recorded 700 species in his studies. The number of known species did not rise markedly during the next 14 years and had only reached 750 species in 1945 (Gigja 1945) in spite of increased effort with the publication of the series *The Zoology of Iceland*, the first issue of which appeared in 1937. With increased studies after 1970, the number of species had risen to 1.220 (Fig. 2, Table 1).

The number of publications dealing with terrestrial arthropods was around 1—2 every 10 years until the late 19th century. Then a phase of exponential growth started resulting in 5—6 publications in 1931—40 (Fig. 3). Most of these studies were made by Danish and Swedish scientists (Fig. 3), with an increasing number of Icelandic scientists after 1931. Entomological research suffered a setback during the next 3 decades, in 1941—60 the number of publications was less than 3

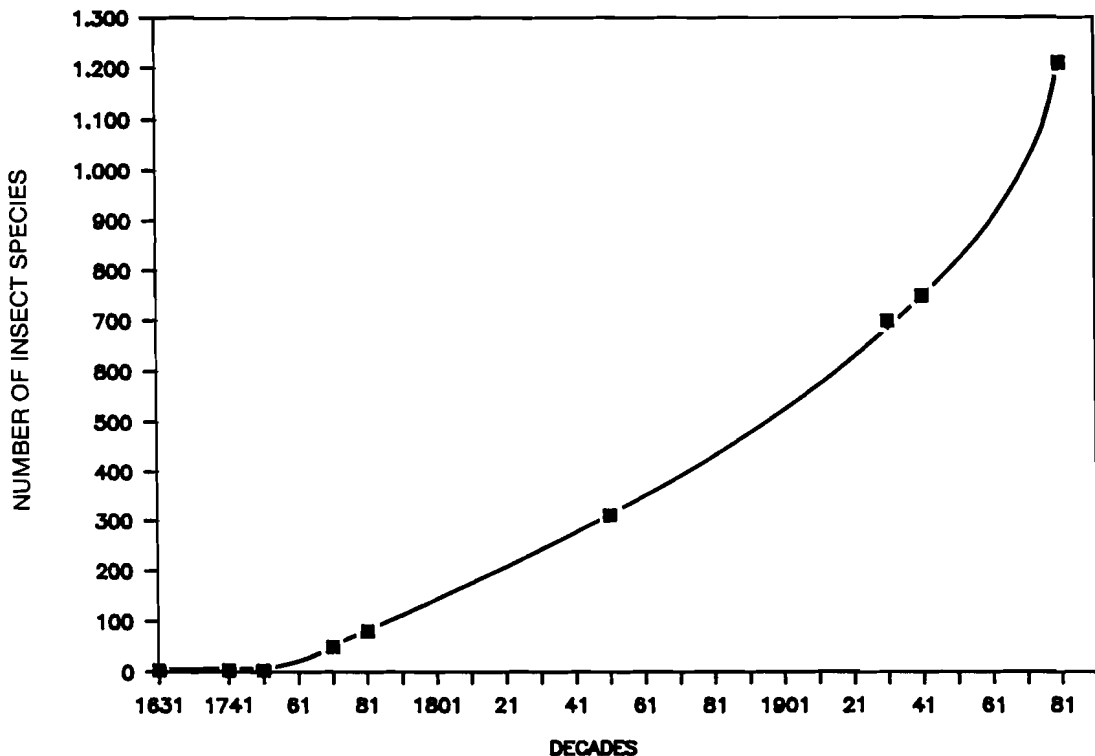


Table 1. Number of insect species found in Iceland.

Order	Number
<b>APTERYGOTA</b>	
Archeognatha	1
Thysanura	1
Protura	3
Collembola	73
<b>PTERYGOTA</b>	
Ephemeroptera	1
Odonata*	1
Plecoptera	1
Orthoptera*	2
Dermoptera	1
Dictyoptera*	5
Psocoptera	10
Phthiraptera	69
Hemiptera*	73
Thysanoptera	7
Neuroptera*	3
Coleoptera*	235
Siphonaptera	8
Diptera*	367
Lepidoptera*	97
Trichoptera	11
Hymenoptera*	251
<b>TOTAL</b>	<b>1,220</b>

\*Casual introductions included in these orders.

Fig. 2. Number of insect species recorded in Iceland from 1638—1987. Line fitted by eye.

per year (Fig. 3). Swedish scientists became more active in Iceland after 1960. Most of this activity was connected with the Surtsey eruption which started in 1963 (see Lindroth et al. 1973). Also, environmental conflict about proposed hydroelectric development of the River Laxá, the outflow of Lake Myvatn, N-Iceland, lead to ecosystem studies involving insects and other arthropods (Jónsson ed. 1979). Icelandic scientists increased their share in research in the 1970s, especially after the establishment of the Department of Biology at the University of Iceland in 1968. After 1970 more than half of all publications were by Icelanders (Fig. 3, Tables 2 and 3) and the number of publications rose to 8—9 per year (Fig. 3).

Most of the publications on terrestrial arthropods are on faunistics (Fig. 4). These are records of occurrence of species and their distribution. With the establishment of the University Research Institute in 1937, which later gave rise to 5 separate research institutes in applied sciences, research on pests has increased to about 20% of all papers on terre-

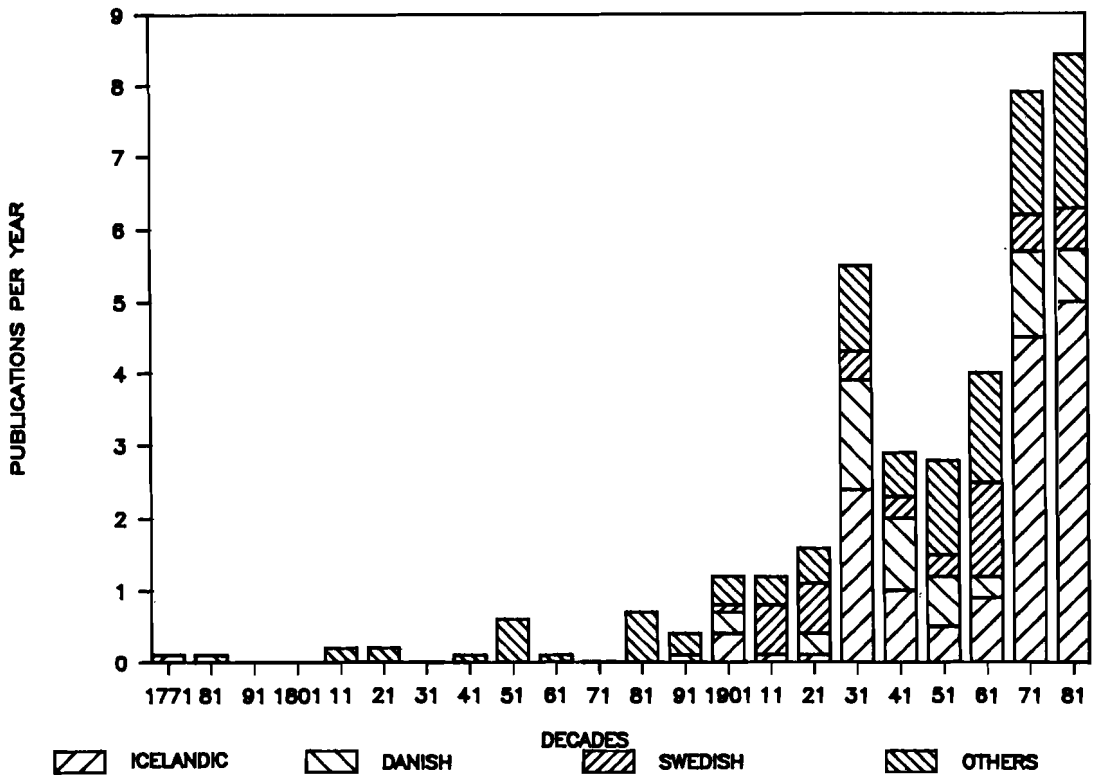


Fig. 3. The number of publications per year dealing with terrestrial arthropods in Iceland 1771—1987, divided according to the nationality of authors

(first author of publications with more than one author).

terrestrial arthropods. Ecological studies began with the studies on animal communities in hot springs in the 1930s (Schwabe 1936, Tuxen 1944). Their share has increased, mainly after 1970 and is now about 30% of the publications (Fig. 4, tables 2 and 3). Most of the ecology work is on aquatic insects (see references in Gislason 1985, Gislason and Gardarsson 1988). Studies have also been made

in palaeoentomology (Buckland et al. 1986, Einarsson and Hafliðason 1988) (Tables 2 and 3). However, studies in terrestrial ecology of insects have declined from the period 1968—77 to 1978—87, from 17% of published material to 2%.

At present, the Icelandic Natural History Museum in Reykjavik is working on faunistics and zoogeography of insects and other

Table 2. Number of publications in 1968—1977 classified according to subjects and nationality of authors.

	Faunistics	Taxonomy	Terrestrial ecology	Aquatic ecology	Pests	Palaeo-entomology	Miscellaneous	Total
Icelandic	13		8	6	2		4	33
Danish	3	1		2		2		8
Swedish	5	3	3					11
Finnish	1	1						2
German	3			1				4
English	4	1						5
Others	1	2						3
<b>Total</b>	<b>30</b>	<b>8</b>	<b>11</b>	<b>9</b>	<b>2</b>	<b>2</b>	<b>4</b>	<b>66</b>



Table 3. Number of publications in 1978—1987 classified according to subjects and nationality of authors.

	Faunistics	Taxonomy	Terrestrial ecology	Aquatic ecology	Pests	Palaeo-entomology	Miscellaneous	Total
Icelandic	8	1	2	22	10	4	2	49
Danish	2	1		2	4		1	10
Swedish	1	4						5
Finnish	2	2		2			1	7
Norwegian	1							1
German		1		1				2
English	5					3	3	11
Others	2	2						4
<b>Total</b>	<b>21</b>	<b>11</b>	<b>2</b>	<b>27</b>	<b>14</b>	<b>7</b>	<b>7</b>	<b>89</b>

terrestrial arthropods in Iceland. However, most Icelandic entomologists are working on freshwater insects and doing faunistic work as a secondary subject. Aquatic entomology is concentrated around Lake Myvatn.

**ACKNOWLEDGEMENT**

We thank Ms Eva Thordardottir for compiling the list of Icelandic references into D base III, which made all analyses much easier. Thanks are also due to Prof. Arnthor Gardarsson and Dr. Arni Einarsson for reading the manuscript and making corrections and valuable comments on it.

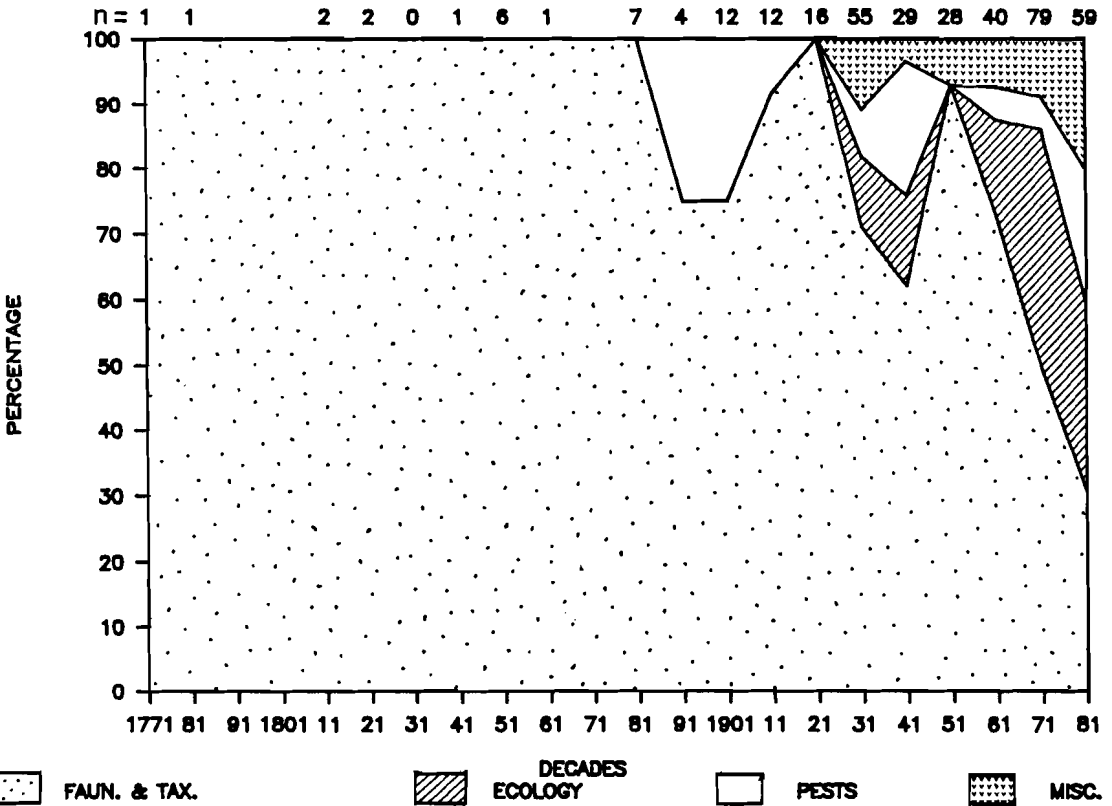


Fig. 4. The subjects covered by publications on Icelandic terrestrial arthropods in 1771—1987, showing percentage for each decade: Faunistics

and taxonomy, ecology, pest species and miscellaneous. n = number of publications per decade.

## REFERENCES

- Anderson, J. 1746. *Nachrichten von Island, Grünland und der Strasse Davis*. Georg Christian Grund. Hamburg. 558 pp + 5 tabs + 1 plate.
- Buckland, P. C., D. W. Perry, G. M. Gislason & A. J. Dugmore 1986. The pre-Landnám fauna of Iceland: a palaeontological contribution. *Boreas* 15: 173—184.
- Downes, J. A. 1988. The post-glacial colonization of the North Atlantic Islands. In *Origins of the North American insect fauna* (eds J. A. Downes and D. H. Kavanaugh). Memoirs of the Entomological Society of Canada 144: 55—92.
- Einarsson, Á. and H. Haflidason 1988. Predictive paleolimnology: effects of sediment dredging in Lake Myvatn, Iceland. *Verh. int. Verein. Limnol.* 23: 860—869.
- Gigja, G. 1944. *Meindýr i húsum og gróðri og varnir gegn þeim*. Jens Gudbjörnsson, Reykjavík. 235 pp.
- Gigja, G. 1945. Íslenskt skordýratil. Suppl. to *Skýrsla um Hid isl. náttúrufræðifélag 1943*. Hid íslenska náttúrufræðifélag, Reykjavík.
- Gislason, G. M. & A. Gardarsson 1988. Long term studies on *Simulium vittatum* Zett. (Diptera: Simuliidae) in the River Laxa, North Iceland, with particular reference to different methods used in assessing population changes. *Verh. int. Verein. Limnol.* 23: (in press).
- Hermannsson, H. 1924. Jón Gudmundsson and his natural history of Iceland. *Islandica* 15: 40 pp + 9 plates. Cornell, New York.
- Horrebow, N. 1752. *Tilforladelige Efterretninger om Island*. København. 512 pp.
- Jonasson, P. M. (ed.) 1979. Ecology of eutrophic, subarctic Lake Mývatn and the River Laxá. *Oikos* 32: 1—308.
- Lindroth, C. H. (ed.) 1928. Zur Land-Vertebratenfauna Islands I. *K. Vet. Vitt. Samh. Handl.* 5. *följden (B)* 1, No. 4: 1—52. Göteborg.
- Lindroth, C. H. 1931. Die Insektenfauna Islands und ihre Probleme. *Zool. Bidr.* 13: 105—589.
- Lindroth, C. H., H. Andersson, H. Bódvarsson & S. H. Richter. 1973. Surtsey, Iceland. The development of a new fauna, 1963—1970. Terrestrial invertebrates. *Ent. scand. Suppl.* 5: 1—280.
- Oddsson, G. 1917. De mirabilis Islandiae. *Islandica* 10: 84 pp. Cornell, London.
- Olafsen, E. & B. Povelsen 1772. *Reise igiennem Island foranstaltet af Videnskabernes Selskab i Kjöbenhavn*. Sorøe, 1042 pp.
- Staudinger, O. 1857. Reise nach Island zu entomologischen Zwecken unternommen. *Stett. ent. Z.* 18: 209—289.
- Schwabe, G. H. 1936. Beiträge zur Kenntnis Isländischer Thermalbiotope. *Arch. f. Hydrobiol. Suppl.* 6: 161—352.
- Tuxen, S. L. 1944. The hot springs of Iceland. Their animal communities and their zoogeographical significance. *Zool. Icel.* 1, 11: 1—216. Munksgaard, Copenhagen.

Received 10 July 1988

# Seasonality and effects of forestry practices on forest floor arthropods in The Kibale Forest, Uganda

MATTI NUMMELIN

Nummelin, M. 1989. Seasonality and effects of forestry practices on forest floor arthropods in the Kibale Forest, Uganda. *Fauna norv. Ser. B* 36, 17–25

Comparisons of arthropod numbers in forest floor vegetation in natural forests, selectively felled forests and exotic pine plantations were made at five different sites over a 23 month period in the Kibale Forest of western Uganda. Study method was monthly sweepnet sampling (800 sweeps).

The number of arthropods in a sample varied from 250 to 1900. Arthropod numbers were positively correlated with rainfall. There was a time lag between cumulative 30 days rainfall and the number of arthropods varied depending on the site. In selectively felled areas the time lag was roughly one month and in natural forest and pine plantation the time lag was roughly three months. In selectively felled areas arthropod numbers were positively correlated with the percentage of ground vegetation cover. No correlations between vegetation cover and arthropod densities were found in the natural forest or pine plantation.

Matti Nummelin, Dept. Zoology, University of Helsinki, P-Rautatiekn. 13, SF-00100 Helsinki, Finland.

## INTRODUCTION

There are few studies of the long term ecological effects of forestry practices in East Africa, especially in Uganda (Hamilton 1984). Even on a world scale the ecology of tropical forests is poorly understood with regard to forestry practices (e.g. Myers 1984).

A long term study of the effects of forestry practices in the Kibale Forest in western Uganda has provided results on primates (Struhsaker 1975, Skorupa 1986), on tree-falls (Skorupa & Kasenene 1984), and on small rodents (Kasenene 1984, Basulta & Kasenene 1987). This study compares arthropod numbers in the forest floor vegetation of two selectively felled areas, an exotic pine forest, and of two natural mature forest areas. The sampling was done by monthly sweepnetting over 23 months.

## STUDY SITES

The Kibale Forest is a medium altitude moist evergreen forest in western Uganda ( $0^{\circ}13'$  to  $0^{\circ}41'N$  and  $30^{\circ}19'$  to  $30^{\circ}32'E$ ) (Fig. 1). Average elevation is ca. 1500 m a.s.l., and the yearly rainfall is roughly 1500 mm (Fig. 2). Kibale differs from lowland tropical rainfo-

rest in having higher altitude, lower temperature, and lower rainfall, but otherwise it possesses most of the same typical features as

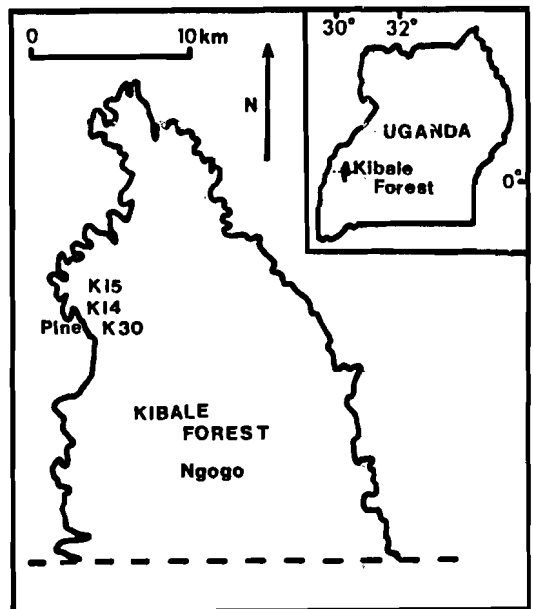


Figure 1. The location of the Kibale Forest and the study sites.

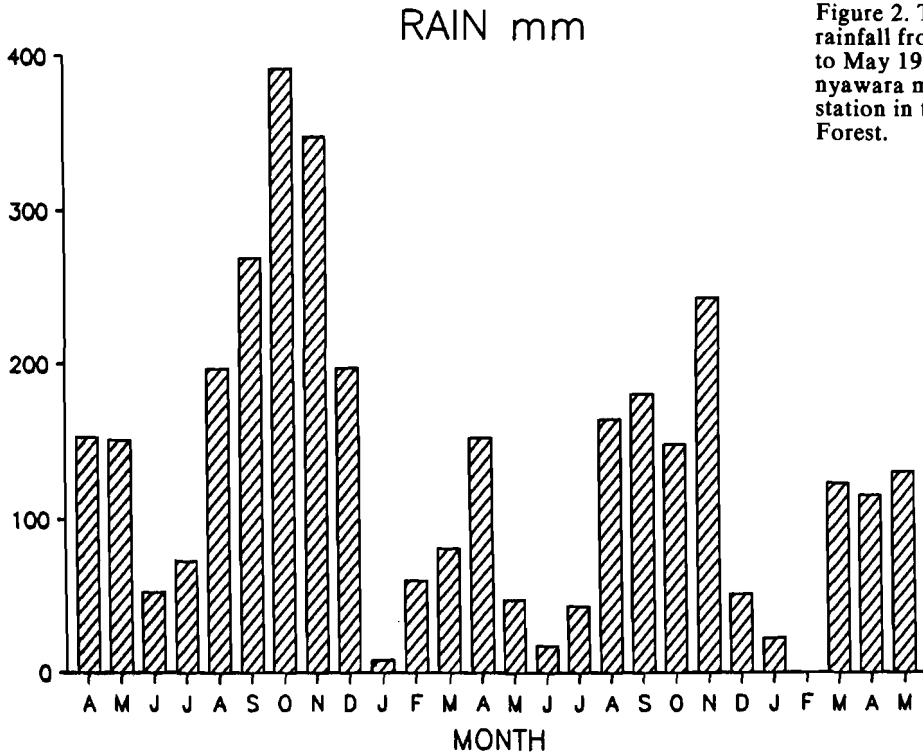


Figure 2. The monthly rainfall from April 1983 to May 1985 at the Kanyawara meteorological station in the Kibale Forest.

lowland forests (Langdale-Brown et al. 1964). The topography is gently undulating with forest in some instances replaced by swamps in low-lying areas and by grasslands on hilltops. The study sites of sweepnetting are described in more detail below.

#### Study Area: K30 (Natural forest)

The K30 study site was in mature natural and almost undisturbed forest. The sampling site for sweepnetting was situated in the Kibale Forest Project trail system along trail E between trails 26 and 34. There had been some pit-sawing before 1970, but this had relatively little impact on the forest (Skorupa & Kasenene 1984). There were no cut tree stumps in the area sampled for arthropods.

The most common plant species on the forest ground were *Palisota scweinfurthii* and *Mimulopsis solmsii* (The scientific names of grasses are according to Lind & Tallantire (1965), and of trees according to Hamilton (1981)). The mean coverage of forest ground vegetation varied from 40% (March 85) to 59% (January 85). The most common tree species in the sweepnetting area were *Panco-*

*via turbinata*, *Newtonia buchananii*, *Olea welwitschii*, *Parinari excelsa*, *Chrysophyllum gorungosanum*, *Celtis africana*, *Strombosia scheffleri*, *Teclea nobilis* and *Uvariopsis congensis*. K30 is described in more detail by Struhsaker (1975).

#### Study Area: Ngogo (Natural forest)

This study site was in mature natural forest. The sweepnetting site was situated along trail 4.5 between trails D and E. The most common plant species at the site on the ground vegetation were *Leptaspis cochleata* and *Aframomum* sp. The forest ground coverage was 46% (March 85). The most common tree species in the sampling area were *Celtis durandii*, *Olea welwitschii*, *Funtumia latifolia*, *Strombosia scheffleri*, *Monodora myristica*, *Chrysophyllum albidum*, *Pterygota mildbraedii*, *Uvariopsis congensis*, and *Conopharyngia holstii*. Ngogo area is described in more detail by Ghiglieri (1984).

#### Study Area: K14 (Selectively felled)

This area was in selectively felled forest. Harvesting took place in 1969. The total har-

vest averaged 14 m<sup>3</sup>/ha (Skorupa & Kasene 1984). The sweepnetting site was along trail 13 between trails R and T, and it was quite heavily affected by felling.

The most common plant species at the site on the forest floor were *Brillantaisia nitens*, *Achyranthes aspera*, and *Cyathula uncinulata*. The vegetation cover of the forest ground varied from 45% (March 85) to 79% (January 85). The most common tree species were *Trema orientalis*, *Celtis durandii*, *Monodora myristica*, *Diospyros abyssinica*, *Markhamia platycalyx*, *Aphania senegalensis*, *Ficus exasperata*, *Cordia millenii*, and *Olea welwitschii*. A large shrub *Vernonia amygdalina* was also common.

#### Study Area: K15 (Selectively felled)

In this study area the forest was selectively felled in 1968–69. Total harvest averaged 21 m<sup>3</sup>/ha (Skorupa & Kasene 1984). The area was heavily disturbed by the felling. The sweepnetting site was along trail 1E between trails WB and 25. The most common plant species at the site in the forest floor were *Brillantaisia nitens*, *Mimulopsis solmsii*, *Palisota scheinfurtii*, and *Acanthus pubescens*. The forest ground coverage varied from 47% (March 85) to 82% (January 85). The most common tree species in the sampling site were *Olea welwitschii*, *Celtis durandii*, *C. africana*, *Milettia dura*, *Parinari excelsa*, *Diospyros abyssinica*, *Fagaropsis angolensis*, *Newtonia buchananii*, *Gabunia odoratissima*, *Funtumia latifolia*, *Teclea nobilis*, and *Uvariopsis congensis*.

#### Study Area: Pine (Exotic plantation)

The sweepnetting site was near K30 along trail 49 from the road to trail W (1/4 of the sample) and along trail WB from the road to trail 51. The pine forest was formerly abandoned gardens which reverted to elephant grass. About 16 years prior to sampling it was cleared and planted with *Pinus caribbaea*. The height of the pines was ca. 25 m, and the crown cover was ca. 50%. The most common plant species at the sampling site on the forest floor were *Achyranthes aspera*, *Pollia condensata*, and *Pteridium aquilinum*. The mean forest ground coverage varied from 23% (March 85) to 53% (January 85). Indigenous tree species have invaded the area and *Celtis durandii*, *Funtumia latifolia*, *Albizia grandi-*

*bracteata*, *Milettia dura*, *Uvariopsis congensis*, and *Fagaropsis angolensis* were quite common in the sampling area. Some have grown up to 5 m.

## MATERIAL AND METHODS

Sweepnet samples were taken in every habitat on a monthly basis from July 1983 to May 1985 in K14, K15, K30, and Pine. Samples were not collected in Aug. 84 from Pine; Aug. & Sep. 84 and May 85 from K14. Sweepnet samples from Ngogo were taken monthly from Jan. 1984 to May 1985, except in Mar., Sep. & Dec. 84, and Feb. 85.

The rainfall data were collected from the Kibale Forest Project meteorological stations at Kanyawara (near K14, K15, K30, Pine) and at Ngogo. The numbers of arthropods in the samples were correlated to the 30 days cumulative rainfall that began 45, 60,

Table 1. The number of arthropods in 800 sweep samples in different forest areas in the Kibale Forest between June 1983 and May 1985.

	Pine	K30	K15	K14	Ngogo
1983					
Jun	959	822	403	602	-
Aug	1399	414	437	515	-
Sep	1701	816	584	1095	-
Oct	660	260	558	501	-
Nov	962	678	1737	907	-
Dec	1864	585	1875	1528	-
1984					
Jan	1928	1570	1629	1892	1213
Feb	1522	1535	1008	831	944
Mar	1544	1007	1551	928	-
Apr	1521	768	1376	1190	702
May	683	684	935	1178	741
Jun	1362	858	951	800	1142
Jul	1144	780	483	916	1011
Aug	-	721	583	-	426
Sep	1086	804	330	-	-
Oct	866	366	974	1516	508
Nov	834	331	887	1259	837
Dec	594	1083	1369	843	-
1985					
Jan	1012	1009	1587	846	717
Feb	700	592	1040	900	-
Mar	472	841	430	570	1016
Apr	1007	606	834	896	595
May	801	862	850	-	525

90, and 120 days before the sweepnet sampling date.

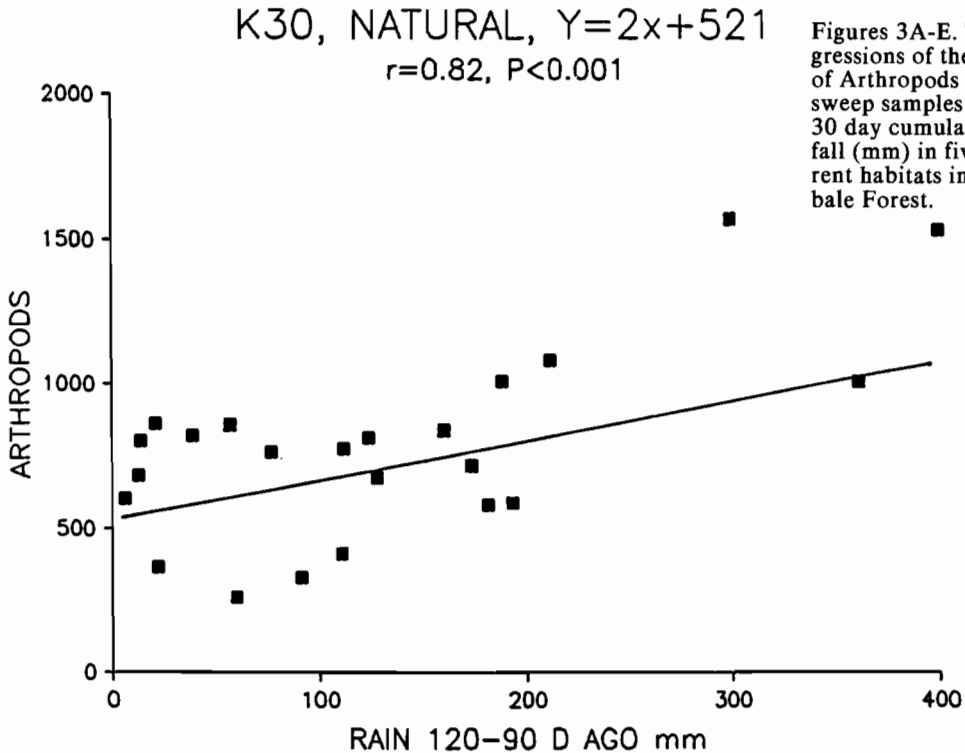
Each sample consisted of 800 sweeps. The diameter of the mouth of the net was 37 cm, and the depth of the net was 60 cm. The length of the net handle was 60 cm. One half of the sweeps was taken from the trail sides, and the other half was taken further away from the trails. However, all the samples from Ngogo were taken inside the trail grid squares. Sweeping off the trails did not follow a straight line. Sweeps were made in places where the net could hit forest ground vegetation. Thus open gaps in vegetation were not sampled. Depending on the height of the forest ground vegetation the minimum sweeping height varied from 20 to 80 cm. For more details on the sweeping method see Janzen (1973).

The percent coverage of the forest ground vegetation up to 1.3 m height from all study sites was estimated from 1 x 1 m<sup>2</sup> squares chosen at random locations (e.g. Janetschek 1982: 84). The open areas were not omitted from these estimates. Thirteen squares were sampled in selectively felled forest ten in Pine, and six in natural forest.

## RESULTS

The numbers of arthropods in 800 sweep samples varied seasonally from under 300 to nearly 2000. (Table 1). This variation correlated with the rainfall in the months prior to sampling. The time lag between 30 days rainfall and arthropod numbers varied among the different habitats. In the natural forest arthropod numbers were most strongly correlated with the 30 days cumulative rainfall from 120 to 90 days before the sampling. In the selectively felled forest arthropod numbers were most strongly correlated with rainfall from 60 to 30 days before the sampling. In Pone the strongest correlation was with rainfall 120 to 90 days before the sampling, although this correlation was not statistically significant (Figs. 3A-E).

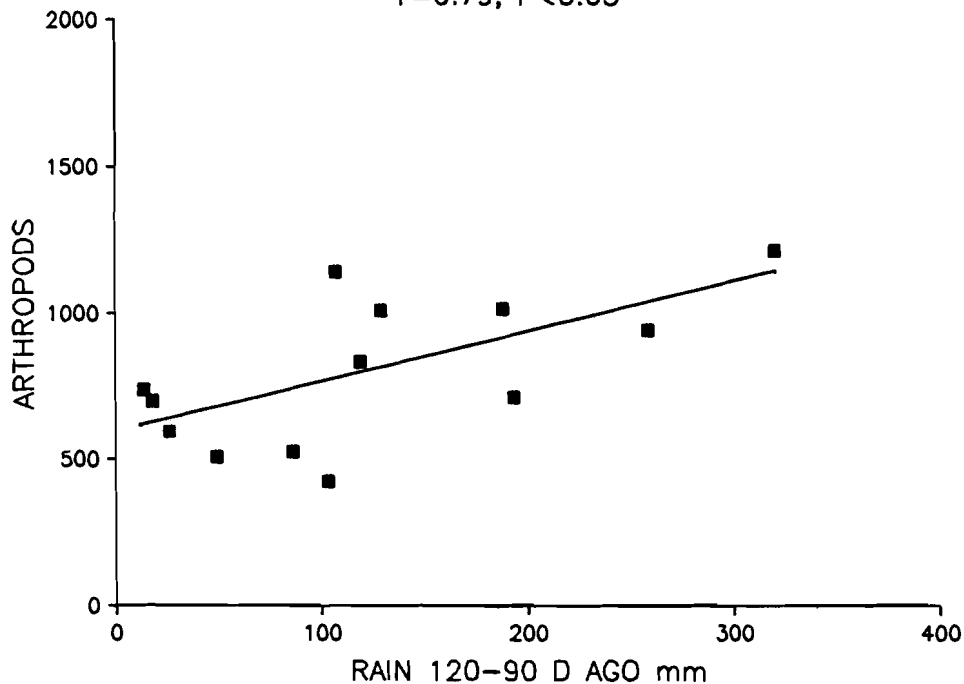
In the selectively felled forest arthropod numbers were positively correlated with the percent coverage of the forest ground vegetation in the sampling area (Fig. 4). When the residuals of this correlation analysis were analyzed further, and when the effect of vegetation was removed in the further analysis there was no correlation with rainfall. In con-



Figures 3A-E. The regressions of the number of Arthropods in 800 sweep samples against 30 day cumulative rainfall (mm) in five different habitats in the Kibale Forest.

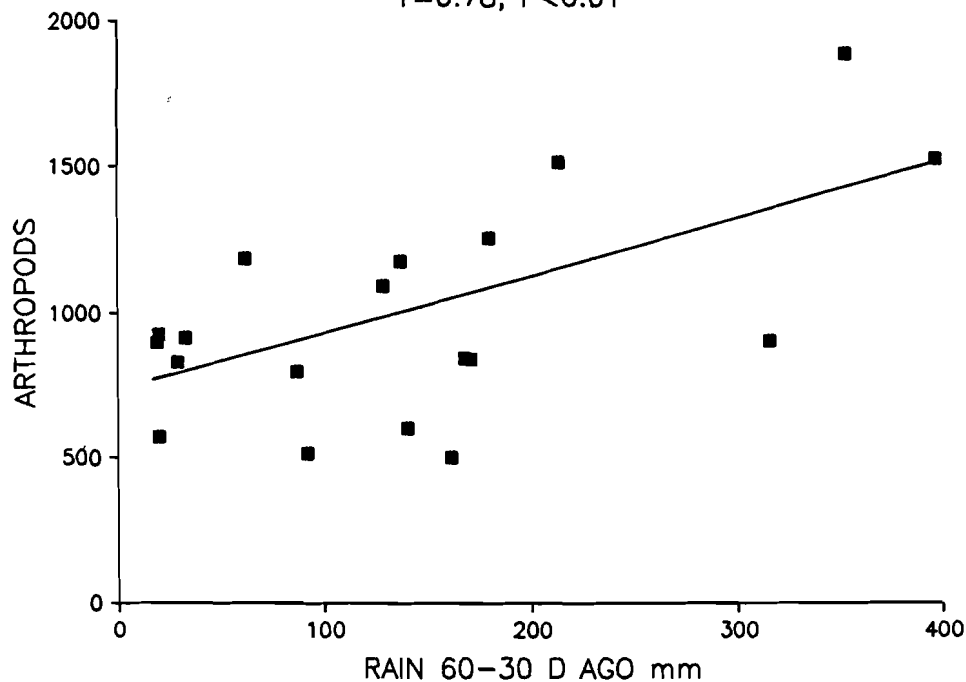
NGOGO, NATURAL,  $Y=1.7x+587$

$r=0.79, P<0.05$



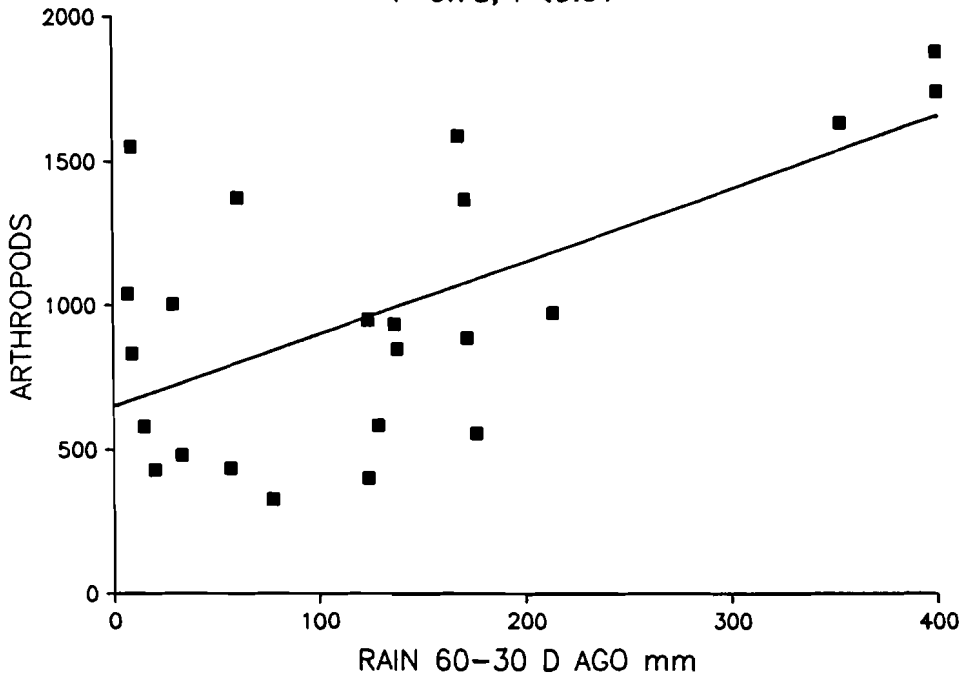
K14, FELLED,  $1.9x+729$

$r=0.78, P<0.01$



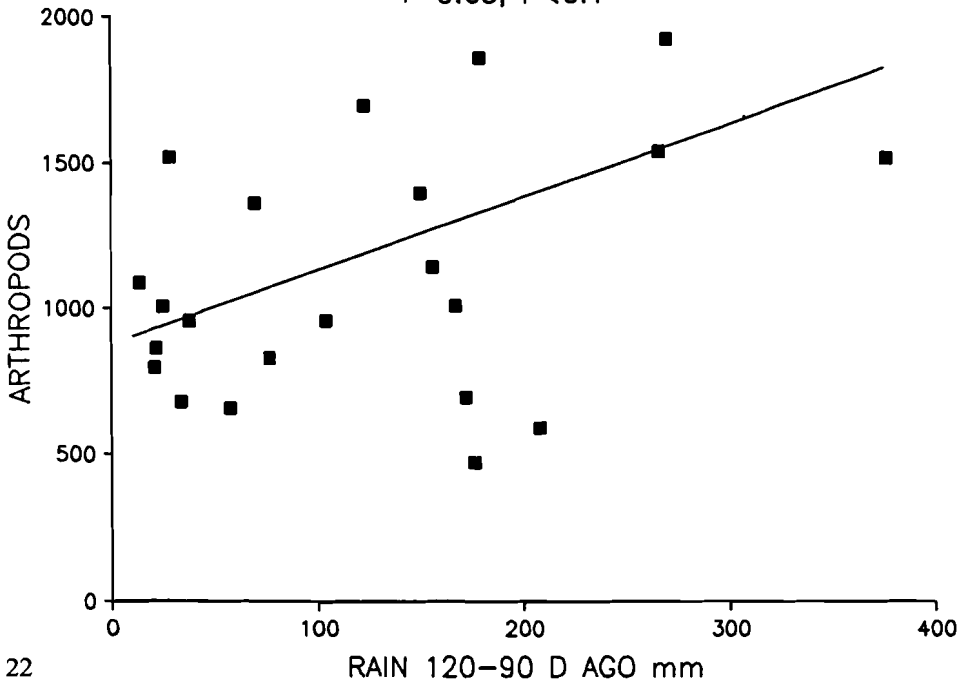
K15, FELLED,  $Y=2.3x+667$

$r=0.78, P<0.01$



PINE,  $Y=1.7x+904$

$r=0.63, P<0.1$

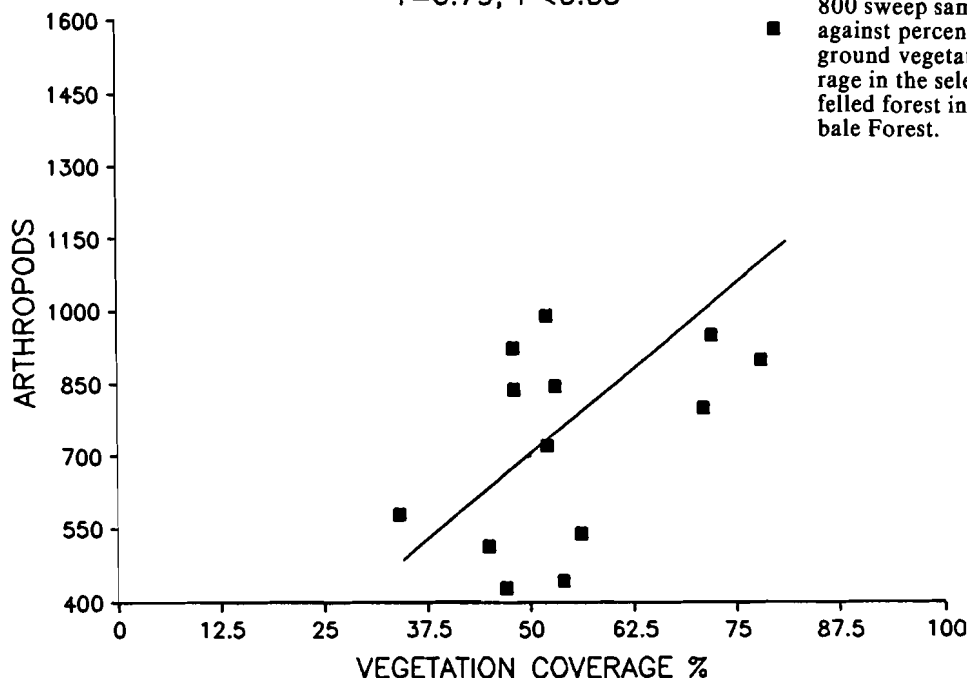




$$\text{FELLED } Y=14x+1.5$$

$$r=0.79, P<0.05$$

Figure 4. The regression of arthropod numbers in 800 sweep samples against percent forest ground vegetation coverage in the selectively felled forest in the Kibale Forest.



trast, in the natural and pine forest the number of arthropods was uncorrelated with the percent vegetation coverage (Figs. 5A, B). Combined data for all habitat showed no correlation between vegetation coverage and arthropod numbers.

Pairwise comparisons of arthropod numbers in different forest types reveal a significant difference in two instances. The pine forest had significantly more arthropods than the natural forest K30 ( $P=0.003$ , Wilcoxon signed rank test) and Ngogo ( $P=0.04$ ). The results of pairwise comparisons of all other habitats were not statistically significant.

## DISCUSSION

Forest ground vegetation coverage increases during the rainy season, this may explain the increases in arthropod numbers in selectively felled forest. In the large canopy gaps of the selectively felled forest the seasonal fluctuation in the ground vegetation coverage is clear and easy to detect by direct observations. When the effect of the vegetation is removed from the analysis, the residuals are not explained by the rainfall. Thus the rain-

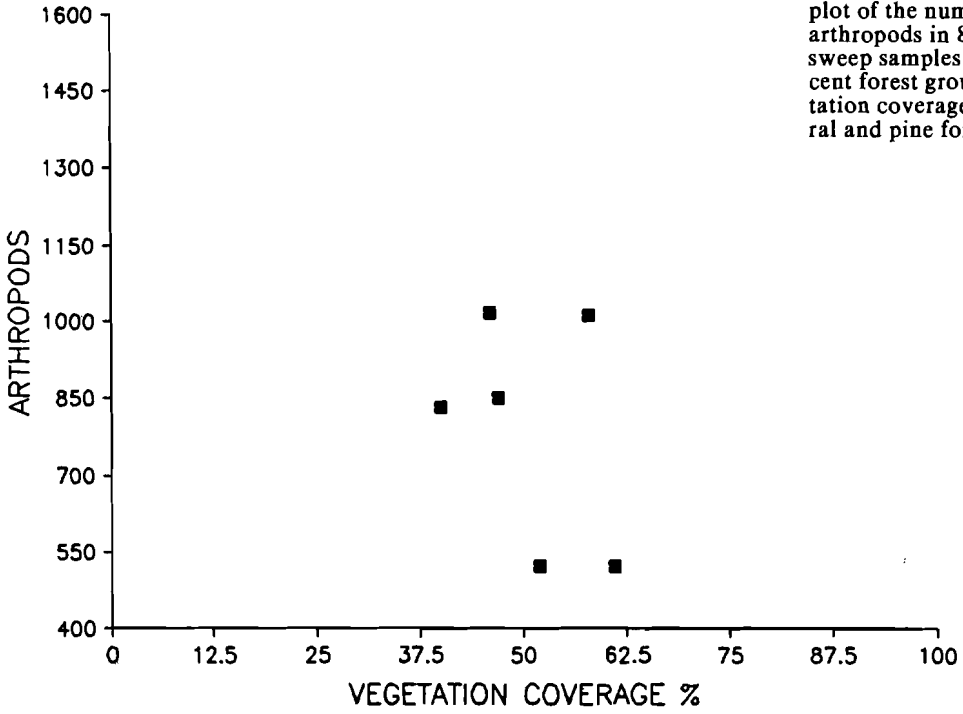
fall does not affect directly the arthropod numbers. The increase in vegetation may simply reflect a larger sample area in sweeping. The net hits larger amount of leaves in dense vegetation, and even though the arthropod numbers per leaf area may be the same, the results for the same amount of sweeps will become higher.

However, the relation between the vegetation cover and arthropod numbers is not obvious in all habitats. In the natural forest and pine forest the increase in arthropod numbers cannot be explained by the increase in ground vegetation coverage. Also when the data for all sites are pooled the arthropod numbers in the samples cannot be explained by the vegetation cover. Thus the results for natural and pine forests are probably not due to small sample sizes. These results also indicates that the significant positive correlation between percent vegetation coverage and the number of arthropods is not a general pattern in the Kibale Forest.

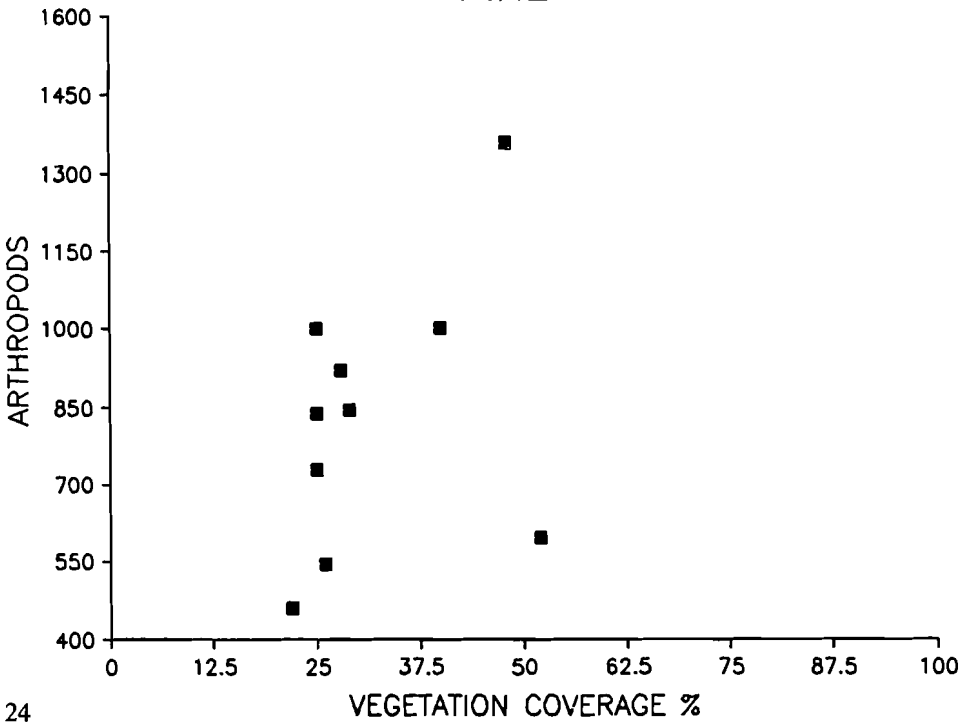
The increase in arthropod numbers during the rainy season therefore must be explained by other factors. One possible explanation is the seasonal life cycles of arthropods. Most

# NATURAL

Figures 5A, B. The X-Y plot of the number of arthropods in 800 sweep samples and percent forest ground vegetation coverage in natural and pine forest.



# PINE



arthropods collected by sweeping are adults. In natural and pine forests the peak densities of adult arthropods seems to come roughly three months after the start of the rainy season. In the selectively felled forest the peak density is roughly one month after the beginning of the rains. This might indicate differences in life history patterns of the arthropod communities in different forest areas. More detailed analysis on arthropods in the samples will be published elsewhere. (See also results of pitfall trapping of dung beetles at the same sites (Nummelin & Hanski 1989)).

The seasonal fluctuations in selectively felled forest are so wide that even though the peak catches during the rainy season are higher than in the natural forest, the late dry season catches are lower than in natural forest. However, the habitats do not differ significantly when they are compared pairwise in monthly samples. On the other hand, in the pine forest the catches remained significantly higher than in natural forest during the entire study period. The studied pine plantation is an exceptional one. It has dense ground vegetation, and the recruitment of indigenous forest trees is reasonably good. Thus it differs from the more typical «clear floor» pine plantations which are a common sight throughout East Africa. These generally lack any substantial ground cover.

The general seasonal pattern in the arthropod numbers with a peak during the late rainy season resembles the results obtained about tettigoniid light trapping at Kwanda, Uganda (Bailey & McCrae 1978) and arthropod sweepnetting in the savanne in Kenya (Lack 1986). In Kibale no increase in arthropod numbers were detected during the late dry season as in a Costa Rican and an Australian rainforests (Buskirk & Buskirk 1976, Frith & Frith 1985).

#### ACKNOWLEDGEMENTS

I wish to thank National Research Council of Uganda, Forest Department, and President's Office for permission to conduct research in Uganda. J. Kasenene helped in plant identification. The Kibale Forest Project and New York Zoological Society provided logistic support and funding in Uganda, Academy of Finland funded the analysing of the data. Comments by T. Jones, J. Kasenene and T. Struhsaker improved the manuscript.

#### REFERENCES

- Basuta, I. & Kasenene, J. M. 1987. Small rodent populations in mature and selectively felled tracts of Kibale Forest, Uganda. *Biotropica* 19: 260—266.
- Bailey, W. J. & McCrae, A. W. R. 1978. The general biology of swarming in the East African tettigoniid *Ruspolia differens* (Serville) (Orthoptera). *J. nat. Hist.* 12: 259—288.
- Buskirk, R. E. & Buskirk, W. H. 1976. Changes in arthropod abundance in a highland Costa Rica forest. *Am. Midland Nat.* 95, 288—298.
- Frith, C. B. & Frith, D. W. 1985. Seasonality of insects abundance in an Australian upland tropical rainforest. *Austr. J. Ecol.* 10, 237—248.
- Ghiglieri, M. P. 1984. *The chimpanzees of Kibale Forest*. Columbia Univ. Press, N.Y.
- Hamilton, C. A. 1981. *A field guide to Uganda forest trees*. A. Hamilton, Belfast.
- Hamilton, C. A. 1984. *Deforestation in Uganda*. Oxford Univ. Press, Nairobi.
- Janetschek, H. (ed.) 1982. *Ökologische Feldmethoden*. Ulmer, Stuttgart.
- Janzen, D. H. 1973. Sweep samples of tropical foliage insects: Description of study sites, with data on species abundances and size distribution. *Ecology* 54, 661—686.
- Kasenene, J. M. 1984. The influence of selective logging on rodent populations and the regeneration of selected tree species in the Kibale Forest, Uganda. *Trop. Ecol.* 25, 179—195.
- Lack, P. C. 1986. Diurnal and seasonal variation in biomass of arthropods in Tsavo East National Park, Kenya. *Afr. J. Ecol.* 24, 47—51.
- Langdale-Brown, I., Osmaston, H. A. & Wilson, J. G. 1964. *The vegetation of Uganda*. Government Printing Office, Entebbe.
- Lind, E. M. & Tallantire, A. C. 1965. *Some Common Flowering Plants of Uganda*. Oxford Univ. Press, Nairobi.
- Myers, N. 1984. *The Primary Source, Tropical Forests and Our Future*. W. W. Norton & Comp., N.Y.
- Nummelin, M. & Hanski, I. 1989. Dung beetles of the Kibale Forest, Uganda: Comparison between virgin and managed forests. *J. Trop. Ecol.* (in print)
- Skorupa, J. P. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. In: Benirschke, K. (ed.), *Primates, the road to self-sustaining populations*, 57—70. Springer-Verlag, N.Y.
- Skorupa, J. P. & Kasenene, J. M. 1984. Tropical forest management: can rates of natural tree-falls help guide us? *Oryx* 18, 96—101.
- Struhsaker, T. T. 1975. *The Red Colobus Monkey*. Univ. Chicago Press, Chicago.

Received 10 July 1988.



# Water balance of beetles as an indicator of environmental humidity

KARL ERIK ZACHARIASSEN & GEOFFREY M. O. MALOIY

Zachariassen, K. E. & Maloiy, G. M. O. 1989. Water balance of beetles as an indicator of environmental humidity. *Fauna norv. Ser. B* 36, 27—31

Investigations on the evaporative water loss of dry habitat insects are reviewed, and new data on the paths of evaporative water loss are presented. It is concluded that in dry habitat beetles of the families Carabidae, Curculionidae and Tenebrionidae spiracular water loss makes up the main component of evaporative water loss.

Rates of water loss and metabolism of beetles from areas with different humidities are presented, and these data are used to establish a biologically based index for environmental humidity.

Karl Erik Zachariassen, Department of Animal Physiology, University of Nairobi, P.O. Box 30197, Nairobi, Kenya and Department of Zoology, The University of Trondheim, AVH, N-7055 Dragvoll, Norway. Geoffrey M. O. Maloiy, Department of Animal Physiology, University of Nairobi, P. O. Box 30197, Nairobi, Kenya.

## INTRODUCTION

The dry savanna in East Africa supports a great number of insect species. The prevailing high temperatures and dry conditions in these areas have caused the development of species with a very restrictive water balance (Edney 1977).

Evaporative water loss makes up a major component of water loss in these beetles. In general, evaporative water loss takes place in part across the exoskeleton and in part through the spiracles, where it accompanies the exchange of respiratory gases. In a number of species the elytra and the abdomen have fused, so that they form a so-called subelytral cavity (Fig. 1), in which the gas exchange over the abdominal spiracles takes place. The air inside this cavity is assumed to be almost saturated with vapour, thus reducing the spiracular or respiratory water loss. It is commonly assumed that in resting insects the respiratory water loss is insignificant compared to the trans-cuticular component (Edney 1977), and many investigators prefer to express rates of water loss in relation to body surface area, thus using cuticular water permeability (the inverse value of rate of water loss per unit surface area) as a measure of the degree of restrictivity of water balance of insects (Edney 1977).

The view that trans-cuticular water loss is

the main component of water loss in all insects has recently been challenged by Zachariassen *et al.* (1987), who found evidence indicating that the respiratory water loss is the main component of water loss in beetles from dry habitats in East Africa. However, since their conclusion was based only on indirect evidence, more data are needed to draw firm conclusions regarding the nature of the evaporative water loss of dry habitat beetles.

The present paper gives a review of the experimental data on the nature of the evaporative water loss in insects, and provides more direct experimental evidence on the paths of evaporative water loss in dry habitat beetles. Data on water loss of beetles from environments with high humidities are also

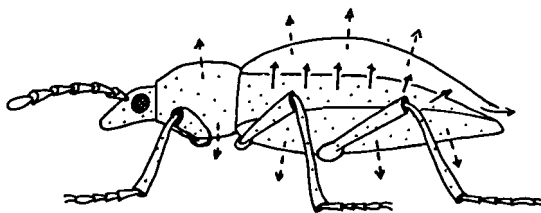


Fig. 1. Paths of transpiratory water loss in a dry habitat beetle. Broken arrows: Transcuticular water loss. Solid arrows: Respiratory water loss. S: Subelytral cavity; SP: Spiracles.

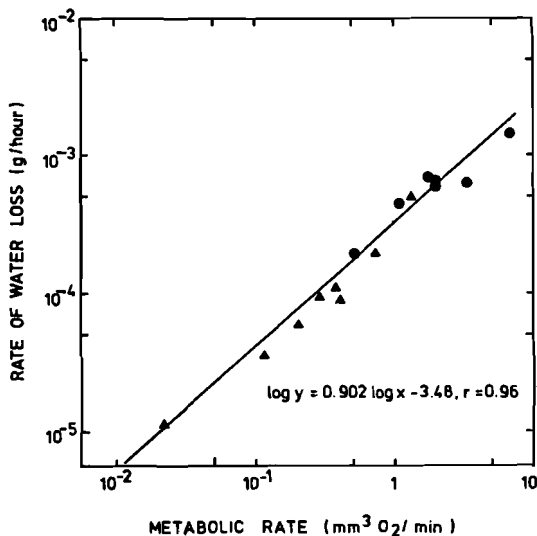


Fig. 2. Rate of transpiratory water loss of East African dry habitat carabids (○) and tenebrionids (●), plotted as a function of their metabolic rate. Solid line: Calculated linear regression line. (From Zachariassen *et al.* (1987)).

presented, and these data are used to establish a biological index to characterize the humidity conditions of different biotops.

### Previous studies on water loss of dry habitat insects

The water balance of dry habitat insects has been the object of a great number of investigations (Edney 1977). Great differences exist between the rates of water loss of insects from different habitats, i.e. insects from humid habitats may have rates of water loss which are more than a 100-fold higher than those of insects from dry habitats. These differences have been ascribed mainly to differences in cuticular water permeability (Edney 1977).

Zachariassen *et al.* (1987) measured rates of water loss and metabolic rates of beetles from dry areas in East Africa. Their results revealed that carabids had rates of water loss which were almost ten-fold higher than the rates of tenebrionids, but also metabolic rates that differed in the same way. When the rates of water loss were plotted on a log — log basis as a function of metabolic rates (Fig. 2), it turned out that the values of all dry habitat beetles (carabids and tenebrionids) were si-

tuated along the same straight line. Although carabids and tenebrionids have very different rates of water loss, the rates varied as a linear function of the respiratory rate. They figured that the most plausible explanation for this is that in both groups the water loss is in some way associated with respiration, and that this would be the case if the water loss were associated mainly with the exchange of respiratory gases in the spiracles. This view implies that the cuticular water permeability in these beetles is reduced so much that the beetles are left with the respiratory water loss as the dominating component.

This may appear plausible from an adaptational point of view, but it is contrary to the established view, i.e. that respiratory water loss makes up only a minor part of the total transpiratory water loss in resting insects. However, serious objections have been raised against the experiments that form the basis of the established view.

As pointed out above, the view that transcuticular water loss makes up the dominating part of water loss in insects is based on experiments with dead insects, the spiracles of which had been sealed with wax. The experiments with the greatest relevance to the present study were those of Ahearn (1970), who used the tenebrionid beetle *Cryptoglossa verrucosa* in his studies. This species inhabits the desert areas in the southwestern United States, and has rates of water loss of the same magnitude as those of East African tenebrionids of the same size. The results revealed that sealing the spiracles did not significantly reduce the rates of water loss. This was interpreted as indicating that spiracular water loss in intact beetles is very low compared to the total water loss. This interpretation is based on the assumption that killing the animals does not affect the cuticular water loss of the beetles. However, this assumption is not necessarily correct. In a number of cases the rates of water loss of dead beetles with sealed spiracles turned out to be considerably higher than those of live specimens. Thus, there is no doubt that killing the animals and sealing the spiracles affect the water balance beyond elimination of spiracular water loss. An increase in total water loss following the killing of the animals and sealing their spiracles has also been observed in experiments with other insects and arachnids (Davies & Edney 1952, Winston & Nelson 1965, Noble-Nesbitt 1969). As pointed out

by Winston & Nelson (1965) and Hadley (1970), the cuticular water permeability of live insects appears to be maintained at a low level due to active, energy-requiring processes within the cuticle. These processes will be blocked when the animals die, and cuticular water permeability will subsequently increase. On this background, the contention that trans-cuticular water loss is the main component of water loss in all resting insects appears to lack a platform of experimental support.

### Further experiments on insect water loss

In order to provide further evidence on the nature of the evaporative water loss in dry habitat beetles a series of experiments with covering the cuticulum with a water proof layer of vaseline was conducted. The experiments were carried out with tenebrionids of the species *Phrynocolus petrosus* and carabids of the species *Thermophilum babaulti*, which both inhabit dry savanna in East Africa.

The rates of water loss of the beetles were measured before and after covering the abdomen of the animals with vaseline. The rates of water loss were determined as rates of weight loss of beetles kept inside a desiccator, in which the relative air humidity was kept low (less than 5% r.h.) by means of silica gel. In order to prevent the vaseline from sticking to the substrate and thus disturbing the weighing, the beetles were suspended inside the desiccator by means of thin metal wires, each attached to the beetle with a loop around thorax. The wires were weighed together with the beetles.

In order to test the water-proofing capacity of the vaseline, a series of experiments was conducted in which four grapes were suspended inside the desiccator. Two of the grapes were covered with a thin layer of vaseline, and the rate of weight loss of all four grapes measured. The results of these experiments are shown in Fig. 3. It appears from the figure that covering the grapes with vaseline reduces the water loss to almost nil. Thus, vaseline appears to have the water-proofing capacity that is required for the experiments.

The beetles were removed from the desiccator and weighed at different intervals, and the rates of weight loss calculated in relation to the time elapsed since the preceding weighing. The rates before and after covering

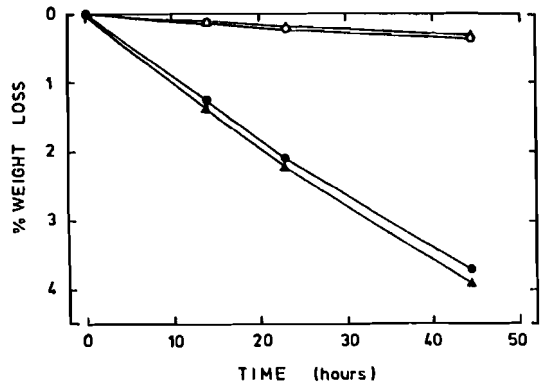


Fig. 3. Weight of normal (open symbols) and vaseline-covered (closed symbols) grapes suspended in dry air at room temperature, plotted as a function of time.

the abdomen of the beetles with a layer of vaseline are shown in Fig. 4. The area covered with vaseline constitutes about 50% of the total surface area, and thus, if trans-cuticular water loss is the only important component of water loss, one should expect the water loss to be reduced by about 50%. The results in Fig. 4 shows that for both species of beetles

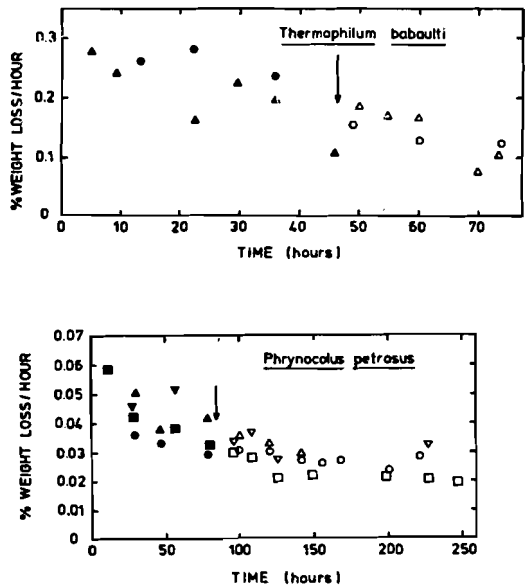


Fig. 4. Rate of weight loss of the East African carabid *Thermophilum babaulti* and the tenebrionid *Phrynocolus petrosus* before (closed symbols) and after (open symbols) sealing the abdomen with vaseline. Values are plotted as a function of time in dry air.

there was a gradual decline in the rates of water loss as the dehydration proceeded. However, sealing the abdomen does not seem to affect the rates of water loss to any noticeable extent. This must imply that trans-cuticular water loss does not constitute a significant fraction of the total evaporative water loss of the beetles. Thus, the results provide support to the hypothesis put forward by Zachariassen *et al.* (1987), i.e. that the respiratory water loss is the major component of evaporative water loss in these beetles.

## CONCLUSION

1. The experiments with African dry habitat beetles show a clear correlation between evaporative water loss and respiratory rate, and no change in water loss when the cuticulum is made impermeable to water. This is in agreement with the idea that respiratory water loss through the spiracles is the only important component of water loss in carabids and tenebrionids in dry areas in East Africa.

2. If the evaporative water loss in dry habitat beetles does not take place through the cuticulum, calculation of water loss in relation to surface area will imply a strong overestimate of the cuticular water permeability. If the aim is to provide a precise value of the water permeability of the cuticulum, the practice of calculating the values from measurements of total water loss is inoperative. For comparative purposes it appears to be more appropriate to relate water loss to body weight. Rates of physiological processes are generally expressed in relation to body weight, and this is also common for water loss of animals other than insects (Schmidt-Nielsen 1972).

## Evaporative water loss of insects from various regions

The conclusions above imply that that in dry habitat carabids and tenebrionids cuticular water permeability is reduced so much that the trans-cuticular water loss is negligible, and that the beetles are left mainly with the obligatory, unavoidable water loss associated with the exchange of respiratory gases. This loss is likely to represent the lowest possible rate of evaporative water loss. The validity of this contention can be tested by comparing the rates of water loss and respiration

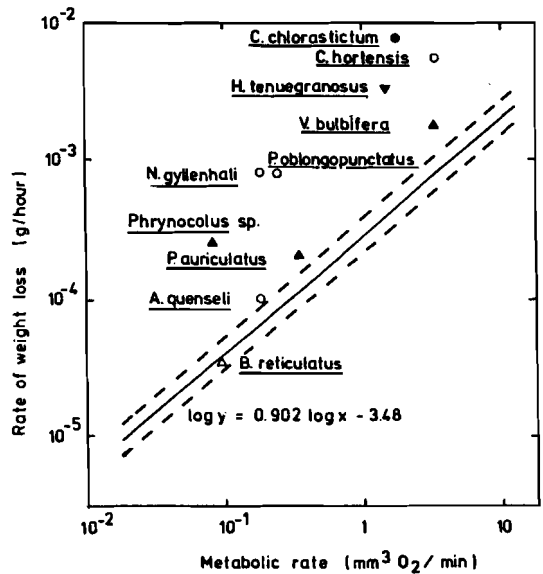


Fig. 5. Rates of water loss of carabid, curculionid and tenebrionid beetles from tropical and temperate regions with different humidity conditions. Solid line: Linear regression line from Fig. 2. Broken lines: Standard deviation around the regression line.

of other notorious dry habitat adapted insects with the regression line in Fig. 2. As shown by Zachariassen *et al.* (1988), the values for dry habitat curculionids, which also have a very restrictive water balance, fit well to the line. Values for species of carabids and tenebrionids from the temperate region are plotted in Fig. 5 together with the regression line from Fig. 2.

The results in Fig. 5 show that even the values of the temperate dry habitat species *Amara quenseli* and *Bolitophagus reticulatus* fit well to the regression line. *A. quenseli* inhabits dry and sandy moraine (Lindroth 1961), whereas *B. reticulatus* hibernates inside dry tree brackets on birch. So far, no insect species is known which has rates of water loss that fall below the values of the regression line, indicating that the line indeed represents the lowest rates of water loss than can be attained by adult insects. The line can consequently serve as a reference line, with which the values of other insects can be compared to evaluate the restrictivity of their water balance. It is implied that in beetles, which have their water loss/metabolism values on the regression line, the evaporative



water loss is largely restricted to the spiracles, whereas increasing deviation from this line reflects an increasing component of transcuticular water loss.

The relationship between the rates of water loss of a given species *s* and the minimum rate of beetles with the same metabolic rate as expressed by the regression line in Fig. 5, can be expressed by the formula

$$H_s = \frac{B_s}{B_{ref}} \quad (1)$$

where  $B_s$  is the rate of water loss of the species *s* and  $B_{ref}$  is the ordinate value of the regression line when the abscissa value equals the metabolic rate of the species *s*. Values of  $H_s$  of a number of tropical and temperate beetle species are given in Table 1.

The data in Table 1 reveal that the  $H_s$  values vary from 0.86, i.e. close to the regression line value, to 11.7. Beetles from xeric areas have values up to about 2, whereas beetles from hygric habitats have values around 10. Beetles from mesic areas have values between these two extremes. On the basis of these results, the biologically based climatic indexes of biotops with different humidities are as presented in Table 2.

The humidity index is based only on values from beetles of the families Carabidae, Curculionidae and Tenebrionidae. As pointed

Table 1. Quotient of rates of water loss ( $H_s$ ) of tropical and temperate beetles and the minimum rate of beetles with the same metabolic rate. N: Beetles collected in Norway. K: Beetles collected in Kenya.  $H_s$  values are calculated from formula (1).

Species	$H_s$	Climate
<b>Carabidae:</b>		
<i>Carabus hortensis</i> (N)	7.1	Mesic
<i>Nebria ovilienhalli</i> (N)	11.5	Hygric
<i>Pterostichus oblongopunctatus</i> (N)	9.1	Hygric
<i>Anara gueneeli</i> (N)	1.5	Xeric
<i>Camphilis chlorostictus</i> (K)	11.7	Hygric
<b>Tenebrionidae:</b>		
<i>Rollitophagus reticulatus</i> (N)	0.86	Xeric
<i>Vieta bulbifera</i> (K)	2.2	Mesic/Hygric
<i>Phrynocolus auriculatus</i> (K)	1.7	Mesic/Hygric
<i>Phrynocolus</i> sp. (K)	7.4	Mesic
<b>Curculionidae:</b>		
<i>Hipporhinus tenuigranatus</i> (K)	8.3	Mesic

Table 2. Humidity indexes ( $H_s$ ) for biotops based on water loss and metabolic rate of beetles from areas with different degrees of aridity.

Humidity index	Biotop type
$H_s < 2$	Xeric
$2 < H_s < 8$	Mesic
$H_s > 8$	Humid

out by Zachariassen *et al.* (1988), insects of other groups, which live as adults only for short periods during the rainy season or feed on humid food, have rates of water loss that are substantially higher than those of the beetles mentioned above. In the case of the tenebrionid *B. reticulatus*, which inhabits dry tree brackets in boreal forests, the value is indicative only of the conditions in the micro habitat. Thus, the application of the index values requires insight into the life conditions of the respective species.

## REFERENCES

- Ahearn, G. A. 1970. The control of water loss in desert tenebrionid beetles. *J. exp. Biol.* 53, 573—595.
- Davies, M. E. & Edney, E. T. 1952. The evaporation of water from spiders. *J. exp. Biol.* 29, 571—582.
- Edney, E. T. 1977. Water balance in land arthropods. *Zoophysiology and Ecology* 9. Springer, Berlin.
- Lindroth, C.H. 1961. *Sandjägare och Jordlöpare. Fam. Carabidae*. 2nd. edition. Svensk Insektfauna 35, Stockholm.
- Noble-Nesbitt, J. 1969. Water balance in the firebrat, *Termobia domestica* (Packard). Exchange of water with the atmosphere. *J. exp. Biol.* 50, 745—769.
- Schmidt-Nielsen, K. 1972. *How animals work*. Cambridge University Press, London.
- Winston, P. W. & Nelson, V. E. 1965. Regulation of transpiration in the clover mite *Bryobia praetiosa* Koch (Acarina: Tetranychidae). *J. exp. Biol.* 43, 257—269.
- Zachariassen, K. E., Andersen, J., Maloiy, G. M. O. & Kamau, J. M. Z. 1987. Transpiratory water loss and metabolism of beetles from arid areas in East Africa. *Comp. Biochem. Physiol.* 86A, 403—408.
- Zachariassen, K. E., Andersen, J., Kamau, J. M. Z. & Maloiy, G. M. O. 1988. Water loss in insects from arid and humid habitats in East Africa. *Acta Entomol. Bohemoslov.* 85, 81—93.



# Water balance and osmotic regulation of the East African scorpion *Lychas burdoi* (Simon)

RAGNAR BJERKE, ROLV LUNDHEIM, JAN OVE REIN,  
JOHN ALEXANDER STRØMME & KARL ERIK ZACHARIASSEN

Bjerke, R., Lundheim, R., Rein, J. O., Strømme, J. A. & Zachariassen. 1989. Water balance and osmotic regulation of the East African scorpion *Lychas burdoi* (Simon). *Fauna norv. Ser. B* 36, 33—36.

The water balance and osmotic regulation of the scorpion *Lychas burdoi* from dry areas in Kenya were investigated. The scorpion had rates of water loss which were higher than those reported for desert scorpions from Southwest United States. Metabolic production of water gave only a very moderate contribution to the water balance (less than 1% of the transpiratory water loss). During experimental dehydration the scorpions displayed no osmotic regulation. Sodium was the dominating extracellular cation. The concentration of free amino acids was low (below 10 mm) compared to values reported from insects.

Ragnar Bjerke, Rolv Lundheim, Jan Ove Rein, John Alexander Strømme & Karl Erik Zachariassen. Department of Zoology, University of Trondheim, N-7055 Dragvoll, Norway.

## INTRODUCTION

Dry tropical areas support numerous species of scorpions. The adaptations making scorpions able to survive in these areas have been the object of a number of investigations (Edney 1977). Scorpions are reported to have a relatively restrictive water balance (Hadley 1970), about as restrictive as that of dry habitat tenebrionids, which are notorious for their success in arid areas (Zachariassen *et al.* 1988). Most scorpions lack the ability to osmoregulate when undergoing dehydration (Riddle *et al.* 1976, Warburg *et al.* 1980). Only one scorpion species is reported to osmoregulate (Robertson *et al.* 1982).

## MATERIALS AND METHODS

Scorpions of the species *Lychas burdoi* (Simon) were collected from their natural habitats under stones in a semi arid area in the vicinity of Thika, Kenya in January 1987. They were kept inside plastic boxes and transported directly to the laboratory in Nairobi, where they were kept at 20°C for two days before the experiments started. During this period the specimens were not fed, but given water.

The dehydration experiments were carried

out with the scorpions kept at 20°C inside a desiccator, in which the relative air humidity was kept low (5—10%) by means of silica gel. The scorpions were taken out and weighed each day, and the rate of weight loss was used as a measure of rate of water loss. Each day groups of scorpions were removed from the dehydration experiment for determination of metabolic rates, haemolymph solute concentrations and relative water content.

The metabolic rates of the scorpions were determined as rates of oxygen consumption, which were measured by the use of Engelmann constant pressure respirometers (Engelmann 1963) as described by Røskaft *et al.* (1986). The measurements were made at 20°C, and the values were recalculated to dry air and STP.

Samples of haemolymph were obtained by making a hole on the ventral side in the animals, the exuding haemolymph being drawn in to a capillary tube by means of capillary forces. To prevent evaporation the samples were treated as described by Zachariassen *et al.* (1982). The haemolymph was stored inside the capillary tubes at -20°C, and transported inside an ice-filled thermo box to the laboratory in Trondheim, where the samples were analysed after about 3 weeks.

The haemolymph osmolality was determi-

ned by measuring the melting point of 20 nl samples on a Clifton nanoliter osmometer. The temperature at which the last tiny ice crystal disappeared during slow heating of frozen samples was taken as the melting point. The osmolality was calculated from the melting points by means of the osmolal melting point depression ( $1.86^{\circ}\text{C}/\text{Osm}$ ).

The sodium concentration of the haemolymph was measured on a Perkin Elmer atomic absorption spectrophotometer in relation to standard solutions with known sodium concentration.

The free amino acids in the haemolymph were measured as free ninhydrin positive substances (NPS) according to a method described by Moore & Stein (1948). The measurements were made on  $1\ \mu\text{l}$  samples of haemolymph, which were transferred to  $50\ \mu\text{l}$  70% ethanol inside a thin glass tube. The protein precipitate was removed by centrifugation in a Compur M-1000 micro centrifuge, washed twice and recentrifuged, and the combined supernatants transferred to a plastic tube where the samples were stored for up to 3 weeks before they were analyzed. The content of NPS was determined as taurine equivalents at 570 nm on a Bausch & Lomb micro spectrophotometer. The relative water content of the scorpions was determined by weighing them before and after drying to constant weight at  $105^{\circ}\text{C}$ .

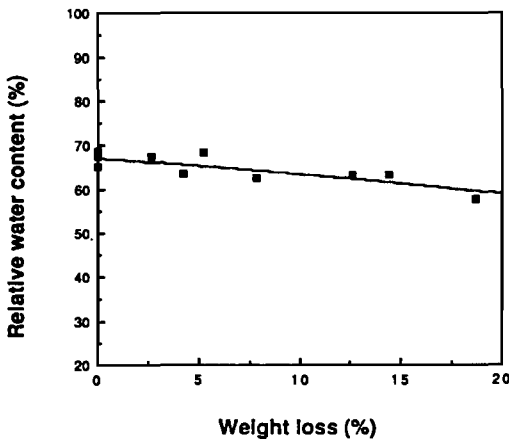


Fig. 1. Relative water content of *Lychas burdoi* scorpions plotted as a function of evaporative weight loss. Solid line: Estimated change assuming that all weight loss is water loss and that the dry weight remains constant.

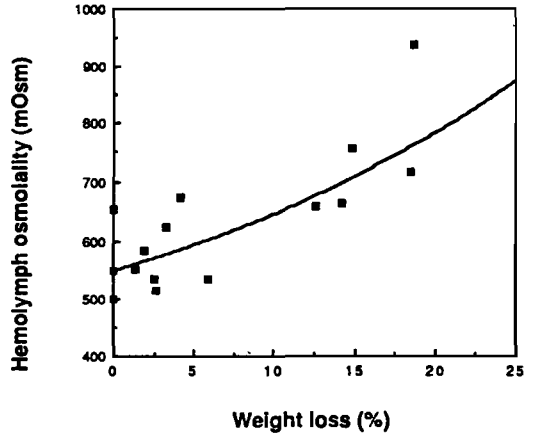


Fig. 2. Haemolymph osmolality of *Lychas burdoi* scorpions plotted as a function of evaporative weight loss. Solid line: Change assuming no osmotic regulation as the dehydration proceeds.

## RESULTS

A group of six scorpions having an average body weight of  $0,1216 \pm 0,047\ \text{g}$  (M.V.  $\pm$  S.D.) had a rate of water loss of  $0,25 \pm 0,05\%$  of body weight per hour. The metabolic rate was  $5,5 \pm 2,5\ \mu\text{l}$  oxygen/(hour  $\times$  g body weight).

The relative water content of the scorpions at different degrees of dehydration is shown in Fig. 1. The figure also shows the estimated change assuming that the entire weight loss is water loss, and that there is no change in dry weight, estimated as described by Zachariassen *et al.* (1987 b). The results reveal that the relative water content drops in agreement with the estimated curve.

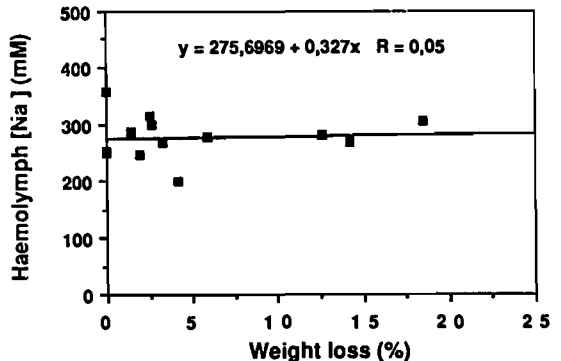


Fig. 3. Haemolymph sodium concentration of *Lychas burdoi* scorpions plotted as a function of evaporative weight loss.

Fig. 2 shows the haemolymph osmolality of the scorpions at different degrees of dehydration. The data show that the haemolymph osmolality of hydrated scorpions was about 550 mOsm, and that dehydration is accompanied by a substantial increase in osmolality. At the end of the dehydration period the osmolality had increased to about 900 mOsm. Fig. 2 also shows a curve describing the expected change in osmolality assuming that the solutes simply become concentrated in a gradually smaller volume of solvent water as the dehydration proceeds, estimated as described by Zachariassen *et al.* (1987 b). The data show that during dehydration the haemolymph osmolality increases in agreement with the estimated curve.

The haemolymph concentration of sodium at different degrees of dehydration is plotted in Fig. 3. The data show that the sodium concentration was about 270 mm, and that it remained constant throughout the observation period.

The concentration of free amino acids in the haemolymph was  $8,34 \pm 3,7$  mm. Due to the wide dispersion of the data it is not possible to say whether this parameter changed as the scorpions became dehydrated.

Due to shortage of haemolymph, no values of extracellular free amino acids from the most dehydrated scorpions were obtained, and the role of free amino acids as osmolytes therefore remains unclear.

## DISCUSSION

Fig. 4 shows the rate of water loss — body weight relationship of the *L. burdoi* scorpions of the present study plotted together with corresponding data for other scorpions and for different families of beetles. The data in Fig. 4 reveal that when body weight is taken into consideration, the African *L. burdoi* scorpions of the present study have high rates of water loss compared to other scorpions. *L. burdoi* scorpions have rates comparable to those of dry habitat carabid beetles of the same body size, and considerably higher than the rates of dry habitat tenebrionids and curculionids.

The high rate of water loss of *L. burdoi* scorpions is also reflected in the fact that the relative water content changes as expected, assuming that all weight loss is water loss and that the dry weight does not change during the dehydration period. Apparently, the de-

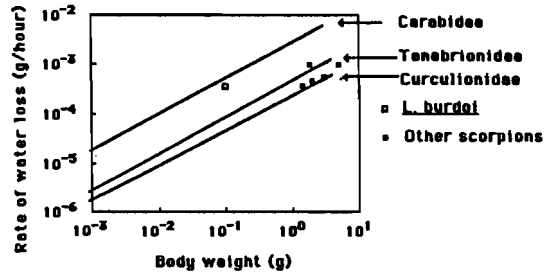


Fig. 4. Double logarithmic plot of rates of water loss of dry habitat scorpions and beetles as a function of body weight. Data for *L. burdoi* scorpions are taken from the present study and data for other scorpions are taken from Hadley (1970) and from Warburg *et al.* (1980). Data for carabid, tenebrionid and curculionid beetles are from Zachariassen *et al.* (1988).

hydration proceeds so rapidly that the metabolic oxidation of dry substance does not cause a significant reduction in dry weight, and no substantial production of metabolic water.

The metabolic rate of the scorpions was approximately  $5,5 \mu\text{l oxygen} / (\text{hour} \times \text{g body weight})$  which is considerably lower than the metabolic rates of desert beetles (Zachariassen *et al.* 1987 a). The low production of metabolic water is not only due to the high rate of water loss and the subsequent short time to reach lethal degree of dehydration, but also to the relatively low metabolic rate. Low metabolic rates in scorpions are also reported by Robertson *et al.* (1982). The low metabolic rate in combination with comparatively high rates of water loss leads to a very moderate contribution from metabolic water to the general pool of body water. Assuming that scorpions, like tenebrionid beetles (Zachariassen *et al.* 1987 b) metabolize fat as they undergo dehydration, the metabolic production of water can be estimated from the oxygen consumption by using the constant applying to fat metabolism, i.e. 1,89 l of oxygen per g water produced. By using this constant in combination with the rate of oxygen consumption of the scorpions, the rate of metabolic water production will be about  $0,0000029 \text{ g water} / (\text{hour} \times \text{g body weight})$ , i.e. below 1% of the rate of transpiratory water loss.

The relatively high rate of water loss is also reflected in the fact that the *L. burdoi* scorpions became lethally dehydrated in about

one week. Dry habitat tenebrionid beetles of the same body size survive for more than two months (unpubl. data)

The osmolality of hydrated scorpions was slightly higher than the values obtained from previous studies of other scorpions (Burton 1984). The agreement between the increase in haemolymph osmolality during dehydration and the curve representing passive concentration of the solutes indicates that the scorpions have no osmotic regulation as they undergo evaporative dehydration. This is in agreement with most previous studies of scorpion osmoregulation (Hadley 1974; Riddle *et al.* 1976; Yokota 1978; Warburg 1980; Robertson *et al.* 1982). Lack of ability to osmoregulate during dehydration has also been demonstrated in two species of dry habitat curculionid beetles from Kenya (Zachariassen, unpubl. data).

The results show that in *L. burdoi* scorpions sodium is the dominating extracellular cation. This appears to be common for all scorpion species, see Burton (1984) for review. In this respect the scorpions are more similar to crustaceans and non arthropod animals, which, in contrast to insects, always have sodium as the dominating extracellular cation.

The sodium concentration remains constant during the dehydration period, indicating that although they do not regulate their total concentration of extracellular solutes, the scorpions regulate their extracellular sodium concentration. This implies that the contribution of sodium to the total solute concentration is diminishing as the dehydration proceeds. This discrepancy must be made up for by some other solutes, but the identity of these solutes is not known.

The concentration of extracellular free amino acids in the scorpions of the present study (8,7 mm) is low compared to values reported for insects. Most insects may have extracellular concentrations of free amino acids in the range from 30 to 80 mm, whereas vertebrates and non-arthropod invertebrates have values below 1 mm. Thus, the scorpions seem to have values in the range between insects and other animals.

#### ACKNOWLEDGEMENTS

We would like to thank Alex McKay, National Museum of Kenya, for help in identifying the scorpions.

#### REFERENCES

- Burton, R. F. 1984. Haemolymph composition in spiders and scorpions *Comp. Biochem. Physiol.* 78A, 613—616.
- Edney, E. T. 1977. Water balance in land arthropods. *Zoophysiology and Ecology* 9, Springer, Berlin.
- Engelmann, M. D. 1963. A constant pressure respirometer for small arthropods. *Ent. News* 74, 181—187.
- Hadley, N. F. 1970. Water relations in the desert scorpion, *Hadrurus arizonensis*. *J. exp. Biol.* 53, 547—558.
- Moore, S. & Stein, W. H. 1948. Photometric ninhydrin method for use in the chromatography of amino acids. *J. biol. Chem.* 176, 376—388.
- Riddle, W. A., Crawford, C. S. & Zeltone, A. M. 1976. Patterns of hemolymph osmoregulation in three desert arthropods. *J. comp. Physiol.* 112, 295—305.
- Riddle, W. A. 1981. Cuticle water activity and water content of beetles and scorpions from xeric and mesic habitats. *Comp. Biochem. Physiol.* 68A, 231—325.
- Robertson, H. G., Nicolson S. W. & Louw G. N. 1982. Osmoregulation and temperature effects on water loss and oxygen consumption in two species of african scorpion. *Comp. Biochem. Physiol.* 71A, 605—609.
- Röskaft, E., Zachariassen, K. E., Maloiy, G. M. O. & Kamau, J. M. Z. 1986. Temperature regulation and water balance of day-active *Zophosis congesta* beetles in East Africa. *J. trop. Ecol.* 2, 139—146.
- Warburg, M. R., Goldenberg, S. & Ben-Horin, A. 1980. Thermal effect on evaporative water loss and haemolymph osmolality in scorpions at low and high humidities. *Comp. Biochem. Physiol.* 67A, 47—57.
- Warburg, M. R. 1986. The distribution of water in the body compartments of four scorpion species. *Comp. Biochem. Physiol.* 84A, 637—641.
- Zachariassen, K. E., Baust, J. G. & Lee, R. E. Jr. 1982. A method for quantitative determination of ice nucleating agents in insect hemolymph. *Cryobiology* 19, 180—184.
- Zachariassen, K. E., Andersen, J., Maloiy, G. M. O. & Kamau, J. M. Z. 1987a. Transpiratory water loss and metabolism of beetles from arid areas in East Africa. *Comp. Biochem. Physiol.* 86A, 403—408.
- Zachariassen, K. E., Kamau, J. M. Z. & Maloiy, G. M. O. 1987b. Water balance and osmotic regulation in the East African tenebrionid beetle *Phrynoncolus petrosus*. *Comp. Biochem. Physiol.* 86A, 79—83.
- Zachariassen, K. E., Andersen, J., Kamau, J. M. Z. & Maloiy, G. M. O. 1988. Water loss in insects from arid and humid habitats in East Africa. *Acta entomol. Bohemoslov.* 85, 81—93.

Received 28 Oct. 1988

# Boreal insects in northernmost Greenland: palaeo-entomological evidence from the Kap København Formation (Plio-Pleistocene), Peary Land

JENS BÖCHER

Böcher, J. 1989. Boreal insects in northernmost Greenland: palaeo-entomological evidence from the Kap København Formation (Plio-Pleistocene), Peary Land. *Fauna norv. Ser B* 36, 37—43.

The Kap København Formation in northeastern Peary Land, Greenland, is assumed to be c. 2 Ma old, i.e., from the Plio-Pleistocene transition. Though deposited in coastal marine environments, the sediments contain abundant remains of terrestrial and limnic organisms. About 100 taxa of insects have so far been identified, most of them Coleoptera. At present only two beetle species are found in central Peary Land, and in entire Greenland only 33 indigenous Coleoptera. Especially remarkable is the presence of fossil ants (Formicoidea), which are totally absent from Greenland today. Nearly all the named fossil species are recent, generally of a present subarctic (boreal) and more or less circumpolar distribution. The plant fossils show that the area was covered with a varied forest-tundra with a number of different wetland biotopes. The insect remains strongly support this conclusion and add a number of details to a reconstruction of the palaeoecological conditions.

Jens Böcher, Zoologisk Museum, Universitetsparken 15, DK-2100 København, Danmark.

## INTRODUCTION

The Kap København Formation in Peary Land, Greenland, was discovered in 1979 (Funder & Hjort 1980), and detailed studies were carried out there in 1983 (Funder 1984; Funder et al. 1984, 1985a, 1985b). In July 1986 new field work was performed by O. Bennike and the author (Bennike 1987).

The Kap København sequence is a c. 300 km<sup>2</sup> deposit of coastal and shallow marine sand, silt and clay, more than 100 m thick, at the northern entrance to Independence Fjord in northeastern Peary Land (lat. 82°25'N; see Figs 1—2). The formation is dated at the Pliocene-Pleistocene transition by biostratigraphic, palaeomagnetic and amino acid studies (Funder et al. 1985; Bennike & Böcher, in press).

In spite of the deposition in marine environments, layers of organic detritus contain abundant well preserved limnic and terrestrial plant and animal remains (Fig. 3). The first analyses of these indicated warmer conditions than today at the time of sedimentation (Fredskild & Røen 1982).

A material of insects fragments, obtained

in 1983, represented such an astonishing diversity of species, that it was necessary to get much more material. In 1986 c. 200 kg sediment samples were collected and brought to the Zoological Museum, University of Copenhagen, where the work is being carried out. About 2/3 of the material has now been processed (sifting through a .6 mm mesh sieve, flotation with kerosene, washing through a .25 mm mesh sieve, sorting out under preparation microscope; see Coope 1986) and has yielded a wealth of insect fragments. The state of preservation is generally surprisingly good, with, e.g., scales, hairs and ommatidia of the compound eyes retained. However, only a few of the fragments are still articulated.

## RESULTS

The laborious procedure of identification is still in progress, and the following list (Table 1) is accordingly somewhat preliminary. Only a minor part of the fragments found are identifiable.

As usual regarding subfossil insect faunas,

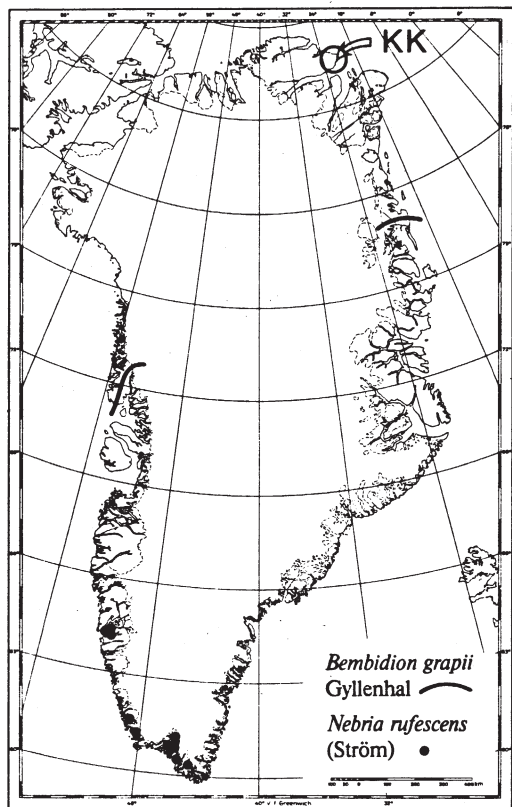


Fig. 1. Map of Greenland with position of Kap København (KK), probable northern limit of *Bembidion grapii* Gyllenhal and known distribution of *Nebria rufescens* (Ström) indicated.

beetles (Coleoptera) dominate the record due to their generally highly resistant exoskeleton. The ground beetles (Carabidae) are prevalent, but also rove beetles (Staphylinidae), predacious water beetles (Dytiscidae) and weevils (Curculionidae) are very well represented.

It has so far been possible to identify 39 species and 60 genera (25 families, 6 orders) of insects. All of the species are classed with extant species, but of course the unidentified material might comprise extinct taxa.

### DISCUSSION

The insect fauna found in northernmost Greenland at the Tertiary-Quaternary transition was indeed different from the present. Nowadays only 33 species of native beetles have been collected from entire Greenland, and only two are found in southern, central Peary Land (*Hydroporus morio* Aubé, *Gnypeta cavicollis* Sahlberg; Böcher 1988). No ants exist in Greenland today, but at least three species are found as fossils.



Fig. 2. View over the Kap København Formation in an easterly direction. JB phot., July 1986.



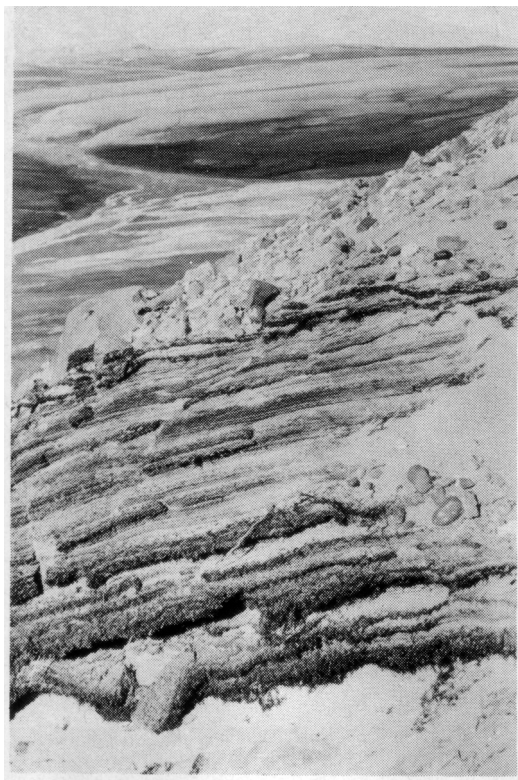


Fig. 3. About one metre thick lense of organic detritus, exposed close to the top of a large hill of sandy sediment belonging to the upper member of the Kap København Formation, Peary Land. JB phot., July 1986.

Whether the identified insect species are identical with their extant counterparts, or whether they represent very similar ancestors shall not be discussed here (but see Matthews 1974, 1977, 1979).

The palaeobotanical investigations of plant macro-fossils from the Kap København Formation suggest that this area, the northernmost land on earth, immediately prior to the Pleistocene glaciations was covered with a subarctic forest tundra rich in boreal plant species, but also including obligate arctic elements. Larch (*Larix cf. occidentalis*) was the dominant tree. The composition of species indicates a summer temperature of c. 10°C (now 3°C), a winter temperature above -15°C (now -31°C), and an annual precipitation of at least 600 mm (now c. 200 mm). The climate, which is now high arctic and fairly continental, was similar to the subarctic cli-

mate now found in southernmost Greenland, 2500 km south of Kap København. But there is one significant difference due to the difference in latitude: the more than four months without sunshine during winter in Peary Land and no months without sunshine in South Greenland (Bennike 1984; Funder et al. 1985a, 1985b, 1988; Bennike & Böcher, in press).

The fossil flora was mainly composed of species with a recent circumpolar distribution, but another prominent element, chiefly comprising trees and shrubs, is now confined to North America (*Thuja occidentalis*, *Picea mariana*, *Cornus stolonifera*). A few species are today mainly palaeartic (*Dryas octopetala*, *Betula nana*). Two plant species are extinct (Bennike 1984; Funder et al. 1988; Bennike & Böcher, in press).

The same recent biogeographic elements were represented among the insects inhabiting the ancient forest tundra of Kap København. The majority of the identified species today exhibit a circumpolar or holarctic distribution (55%). 30% are nearctic and 15% palaeartic. Some species are nowadays found far away from Greenland: *Elaphrus sibiricus* is distributed from central Siberia and Mongolia eastwards to China, Japan, and Kamchatka; *Asaphidion alaskanum* is restricted to Alaska, Northwest Territories and Yukon (Canada); *Bembidion planiusculum* is found in the northwestern coastland of North America (Alaska, British Columbia), and *Helophorus niger* in northwestern Siberia (Lindroth 1961—69, Angus 1970, Goulet 1983).

Only two species, *Nebria rufescens* and *Bembidion grapii*, are found in Greenland today. *N. rufescens* is confined to the subarctic and southern low arctic West Greenland, whereas *B. grapii* extends into the High Arctic (Fig. 1; Böcher 1988).

Assuming that the ecological demands of the species have not changed significantly since the Late Tertiary (see, e.g., Coope 1979), we shall consider the occurrence of the Kap København-insects in relation to the recent climatic zones. It is remarkable that none of them occur in the High Arctic, and only one species (*Pterostichus vermiculosus*) is confined to the (Low) Arctic. However, a number of species (14) extend into the Low Arctic, but are also found in subarctic environments. By far the majority of the named species (c. 90%) are mainly or partly found in

**Table 1. List of fossil insects from the Kap København Formation:**

COLEOPTERA

Carabidae:

- Cicindela sp.
- Carabus spp.
- Nebria cf. rufescens (Ström, 1768)
- Nebria spp.
- Notiophilus cf. aquaticus (Linnaeus, 1758)
- Notiophilus cf. biquittatus (Fabricius, 1770)
- Blethisa cf. catenaria Brown, 1944
- Diacheila polita (Faldermann, 1835)
- Elaphrus lapponicus Gyllenhal, 1810
- Elaphrus sibiricus Motschulsky, 1846
- Elaphrus tuberculatus Mäklin, 1877
- Miscodera arctica Paykull, 1798
- Patrobus cf. stygius Chaudoir, 1871
- Patrobus spp.
- Asaphidion alaskanum Wickham, 1919
- Bembidion (Chrysobracteon) cf. lapponicum Zetterstedt, 1828
- Bembidion (Chrysobracteon) sp.
- Bembidion (Plataphus) cf. planatum Leconte, 1848
- Bembidion (Plataphus) cf. planiusculum Mannerheim, 1843
- Bembidion (Plataphus) spp.
- Bembidion (Hirmoplataphus) sp.
- Bembidion (Peryphus) cf. mckinleyi Fall, 1926
- Bembidion (Peryphus) cf. gnapii Gyllenhal, 1827
- Bembidion (Peryphus) cf. sordidum Kirby, 1837
- Bembidion (Diplocampa) cf. transparens Gebler, 1829
- Pterostichus cf. adstrictus Eschscholtz, 1823
- Pterostichus (Cryobius) cf. brevicornis Kirby, 1837.
- Pterostichus (Cryobius) spp.
- Pterostichus cf. vermiculosus Menetries, 1851
- Pterostichus haematopus Dejean, 1831
- Agonum cf. exaratum Mannerheim, 1853
- Amara cf. glacialis Mannerheim, 1853
- Amara spp.
- Dromius sp. (palaeartic)

Dytiscidae:

- Hydrocorus spp.
- Oreodytes spp.
- Hydroporinae spp.
- Agabus bifarius (Kirby, 1837)
- Agabus spp.
- Ilybius spp.
- Colymbetinae spp.
- Dytiscidae spp.

Gyrinidae:

- Gyrinus spp.

Hydrophilidae:

- Melophorus (Meghelophorus) cf. niger J. Sahlberg, 1880
- Melophorus (Rhopalephorus) cf. frater Smetana, 1985
- Melophorus spp.
- Hydrophilidae sp.

Catopidae:

- cf. Catops sp.

Lioididae:

- cf. Anisotoma sp.

Silphidae:

- Heterosilpha ramosa (Say, 1823)

Staphylinidae:

- Philonthus sp.

- Quedius sp.
- Pycnoglypta sp.
- Olophrum cf. rotundicollis (C. R. Sahlberg, 1834)
- Olophrum cf. consimile (Gyllenhal, 1810)
- Eucnecosum cf. brachypterum (Gravenhorst, 1802)
- Eucnecosum spp.
- Omaliinae spp.
- Bledius spp.
- Mycetoporus sp.
- Tachyporus cf. nimbicola Campbell, 1979
- Tachyporus cf. rukomus Blackwelder, 1936
- Tachinus spp.
- Stenus spp.
- cf. Atheta sp.
- Aleocharinae spp.

Scarabaeidae:

- Aegialia cf. sabuleti (Panzer, 1797)
- Aegialia spp.

Elateridae:

- Hypnoidus spp.

Euprestidae:

- Galleries and exit holes in Larix wood.

Byrrhidae:

- Simplocaria spp.

Anobiidae:

- Hydrobregmus cf. perlinae (Linnaeus, 1758)

Lathridiidae:

- cf. Corticaria sp.
- Lathridiidae sp.

Cerambycidae:

- Cerambycidae sp.
- (Galleries in Larix wood)

Chrysomelidae:

- Hydrothassa sp.
- cf. Graphops sp.
- cf. Chrysomela sp.
- cf. Galeruca sp.
- Chrysomelidae spp.

Apionidae:

- Apion spp.

Curculionidae:

- cf. Otiophynchus spp.
- Pissodes sp.
- Grypus equiseti (Fabricius, 1775)
- Notaris sp.
- Rhynchaenus sp.
- Dorytomus sp.
- Rhyncolus sp.
- Curculionidae spp.

Scolytidae:

- Scolytus sp.
- Pityophthorus sp.
- Scolytidae spp. (galleries in Larix wood).

HYMENOPTERA

Siricidae:

- Urocerus cf. gigas (Linnaeus, 1758) (fly holes in Larix wood)

Tenthredinidae sp.

Ichneumonidae:  
 cf. Pimplinae sp.  
 Ichneumonidae spp.

Chalcididae spp.

Diapriidae sp.

Torymidae:  
Megastomus sp. (bore holes in Larix seeds).

Formicidae:  
Camponotus cf. herculeanus (Linnaeus, 1758)  
Camponotus sp.  
Formica sp.  
 Formicinae spp.

Hymenoptera spp.

DIPTERA  
 Chironomidae:  
 Tanypodinae sp.  
Orthocladius spp.  
Psectrocladius sp.  
 Orthoclaudiinae spp.  
 cf. Diamesa sp.  
Chironomus spp.  
Endochironomus sp.  
Microspectra sp.  
Corynocera ambigua Zetterstedt 1840  
 Chironomini spp.

Brachycera spp.  
 Cyclorrhapha: Schizophora spp.  
 LEPIDOPTERA sp.  
 TRICHOPTERA spp.  
 HEMIPTERA  
 cf. Cicadellidae sp.

the subarctic zone. Some species are temperate-boreal, extending into the subarctic zone (e.g., *Notiophilus biquttatus*, *Grypus equiseti*).

Most of the identified species are associated with fresh water localities. This is not surprising, since these species are the most likely to be carried along with streams and deposited. Many are hygrophilous species living in damp, luxuriant places close to the water (e.g., *Nebria rufescens*, *Patrobis stygicus*, *Bembidion transparens*, *Olophrum* spp., *Tachyporus* spp.; Lindroth 1961—69; Campbell 1979, 1983).

However, even more species are mainly found on open, sandy or gravelly shores and

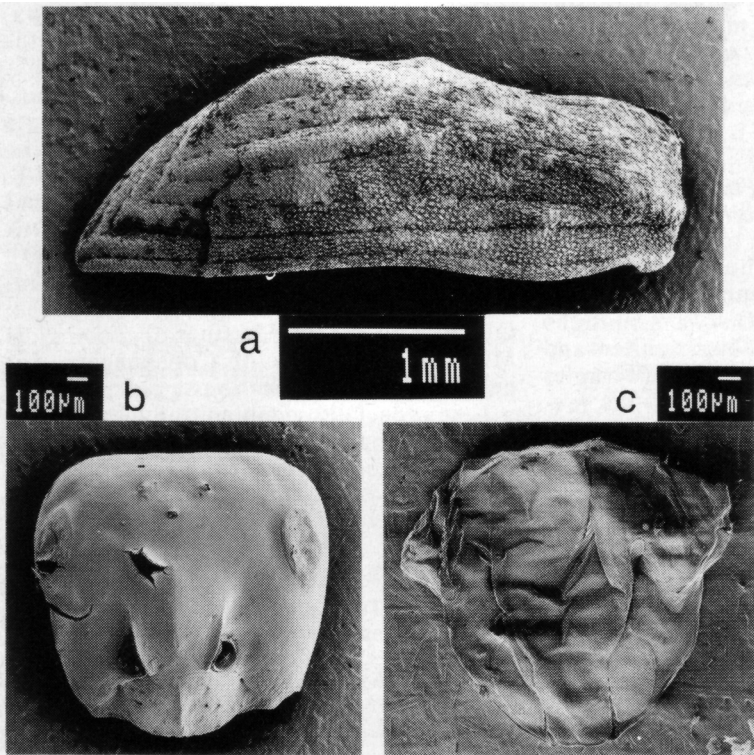


Fig. 4. SEM-photos of subfossil insect phragments from the Kap København Formation. a) elytron with retained covering of scales from the weevil *Grypus equiseti* (Fabricius); b) head of the carpenter ant, *Camponotus herculeanus* (L.); c) head of a leafhopper, probably Cicadellidae sp.

banks of lakes and streams. These species are generally thermophilous, diurnal and highly active predators hunting by means of vision and, accordingly, dependent on a high incidence of sunshine during the active season (species of *Cicindela*, *Elaphrus*, *Asaphidion*, *Bembidion*, *Notiophilus* and *Stenus*). Also *Aegialia* spp. exclusively occur in sandy areas, especially in seashore dunes.

Of the real freshwater inhabitants few are named, but the large number of unidentified Dytiscidae and some Gyrinidae and Hydrophilidae (altogether more than 20 species) and also many fragments of larval Trichoptera and Chironomidae indicate the presence of an abundance of different freshwater biotopes in the ancient landscape. *Helophorus niger* and *Tachyporus nimbicola* are found in and close to tundra ponds (Angus 1970, Campbell 1973), whereas *Corynocera ambigua* (Chironomidae) is indicative of lakes. Especially interesting is the concise description by Larson (1975: 367) of the typical habitat of *Agabus bifarius* as shaded, temporary ponds in rough fescue prairie.

One group of species is not dependent on the vicinity of water, preferring open tundra or fairly xeric heathland. This applies to *Notiophilus aquaticus*, *Blethisa catenaria*, *Diacheila polita*, *Miscodera arctica*, *Pterostichus brevicornis*, *P. vermiculosus*, *P. haematopus*, and *Agonum exaratum* (Lindroth 1961—69, 1985—86).

A number of species and genera (*Dromius*, *Hadrobregmus pertinax*, *Pissodes*, *Scolytus*, *Pityophthorus*, *Camponotus herculeanus*) are intimately connected with trees and thus represent another proof of the existence of forest when the Kap København Formation was formed. *C. herculeanus* always build the nest in living or dead trees, both conifers and hardwoods (Collingwood 1979). Fly holes and galleries in fossil wood reveal the presence of still more arboricolous forms (Buprestidae, Cerambycidae, *Urocerus*, *Megastigmus*). A few species prefer woodland but are not dependent on trees (*Notiophilus biguttatus*, *Bembidion grapii*; Lindroth 1985—86).

Altogether the insect fauna of the Kap København Formation presents a fairly detailed picture of the palaeo-ecological conditions, in harmony with the palaeo-botanical results: A varied environment, strongly characterized by different freshwater localities, in some places bordered by rich vegetation, in other

places with open, sunny and sandy shores. Also shrubs and trees were present, possibly forming small forests in sheltered places, separated by more xeric heath areas. Tundra-like vegetation presumably existed at higher altitude.

The general aspect and the generic composition of the insect fauna of the Kap København Formation greatly resembles that listed by Matthews (1977, 1979, 1986) from Late Tertiary sites (Beaufort Formation) in Meighen Island and Banks Island, Canadian Arctic Archipelago. A conspicuous common feature is the predominance of the two carabid genera, *Bembidion* and *Pterostichus*, and also a number of species are in common. It is possible that the similar fossil faunas and floras found at Kap København and in the extreme north of Canada in late Pliocene constituted parts of a coherent biota surrounding the Arctic Ocean.

#### ACKNOWLEDGEMENTS

The Carlsberg Foundation and the Commission for Scientific Research in Greenland are thanked for generous financial support.

Special thanks to John Matthews (Ottawa) for invaluable help and support regarding the identification of insect fragments. Thanks also to Matti Nuorteva (Helsinki) who identified insect galleries in the fossil wood, to Broder Bejer-Petersen (Copenhagen) who identified borings in larch seeds, and to B. Russell Coope (Birmingham), Scott Elias (Boulder, Colorado), Henri Goulet (Ottawa), Wolfgang Hofmann (Plön, BRD), Viggo Mahler (Århus, Denmark), Stig Andersen, Michael Hansen, Mogens Holmen, Ole Lomholt, Ole Martin (all Zoological Museum, University of Copenhagen), for help with the identifications.

I am especially indebted to Svend Funder and Ole Bennike, Geological Museum, University of Copenhagen, for an excellent collaboration.

#### REFERENCES

- Angus, R. B. 1970. A revision of the beetles of the genus *Helophorus* F. (Coleoptera: Hydrophilidae). Subgenera *Orphelophorus* d'Orchymont, *Gephelophorus* Sharp and *Meghelophorus* Kuwert. *Acta Zoologica Fennica* 129. 62 pp.
- Bennike, O. 1984. Skov-tundra i Nordgrønland i Plio-Pleistocen — plantegeografiske implika-

- tioner. *Dansk geologisk Forening. Årsskrift for 1984*: 111—112.
- Bennike, O. 1987. News from the Kap København Formation, Plio-Pleistocene, North Greenland. *Polar Research 5 n.s.*: 339—340.
- Bennike, O. & Böcher, J. (in press). Forest-tundra neighbouring the North Pole: Plant and insect remains from the Plio-Pleistocene Kap København Formation, North Greenland. *Arctic*.
- Böcher, J. 1988. The Coleoptera of Greenland. *Meddelelser om Grønland, Bioscience 26*. 100 pp.
- Campbell, J. M. 1979. A revision of the genus *Tachyporus* Gravenhorst (Coleoptera: Staphylinidae) of North and Central America. *Memoirs of the Entomological Society of Canada 109*. 95 pp.
- 1983. A revision of the North American Omaliinae (Coleoptera: Staphylinidae). The genus *Olophrum* Ericson. *Canadian Entomologist 115*: 577—622.
- Collingwood, C. A. 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica 8*. Scandinavian Science Press. Klampenborg, Denmark. 174 pp.
- Coope, G. R. 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. *Annual Review of Ecology and Systematics 10*: 247—267.
- Coope, G. R. 1986. Coleoptera Analysis, pp. 703—713 in: Berglund, B. E. (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley & Sons, Chichester-New York-Brisbane-Toronto-Singapore. 869 pp.
- Fredskild, B. & Røen, U. 1982. Macrofossils in an interglacial peat deposit at Kap København, North Greenland. *Boreas 11*: 181—185.
- Funder, S. 1984. Grønland før Istiden. *Forskning i Grønland/Tusaut 1/84*: 2—11.
- Funder, S. & Hjort, C. 1980. A reconnaissance of the Quaternary geology of Eastern North Greenland. *Grønlands geologiske Undersøgelser Rapport 99*: 99—105.
- Funder, S., Bennike, O., Mogensen, G. S., Noe-Nygaard, B., Pedersen, S. A. S., Petersen, K. S. 1984. The Kap København Formation, a late Cainozoic sedimentary sequence in North Greenland. *Grønlands geologiske Undersøgelser Rapport 120*: 9—18.
- Funder, S., Bennike, O., Mogensen, G. S., Pedersen, S. A. S., Petersen, K. S. 1985a. Mudder, mos og muslinger nær Nordpolen. *Naturens Verden 1985, 6-7*: 226—245.
- Funder, S., Abrahamsen, N., Bennike, O., Feyling-Hanssen, R. W. 1985b. Forested Arctic: Evidence from North Greenland. *Geology 13*: 542—546.
- Funder, S., Bennike, O. & Böcher, J. 1988. Kap København — et geologisk Pompeji. *Naturens Verden 1988, 7*: 241—256.
- Goulet, H. 1983. The genera of Holarctic Elaphrini and species of *Elaphrus* Fabricius (Coleoptera: Carabidae): Classification, phylogeny and zoogeography. *Quaestiones Entomologicae 19*: 219—482.
- Larson, D. J. 1975. The predacious water beetles (Coleoptera: Dytiscidae) of Alberta: Systematics, natural history and distribution. *Quaestiones Entomologicae 11*: 245—498.
- Lindroth, C. H. 1961—1969. The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. 1—6. *Opuscula Entomologica Supplementum 20, 24, 29, 33, 34, 35*. 1192 pp.
- Lindroth, C. H. 1985—1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica 15, 1-2*. E. J. Brill/Scandinavian Science Press Ltd., Leiden — Copenhagen. 497 pp.
- Matthews, J. V. 1974. Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): Evolution of a tundra ecosystem. *Geological Society of America Bulletin 85*: 1353—1384.
- Matthews, J. V. 1977. Tertiary Coleoptera fossils from the North American Arctic. *The Coleopterists Bulletin 31, 4*: 297—308.
- Matthews, J. V. 1979. Late Tertiary carabid fossils from Alaska and the Canadian Archipelago, pp. 425—445 in: Erwin, T. L., Ball, G. E. & Whitehead, D. R. (eds.) *Carabid Beetles, their Evolution, Natural History and Classification*. Junk, the Hague. 635 pp.
- Matthews, J. V. 1986. Preglacial and interglacial environments of Banks Island: Pollen and macrofossils from Duck Hawk Bluffs and related sites. *Géographie physique Quaternaire 40, 3*: 279—298.

Received 10 Aug. 1988



# Abundance and vertical distribution of watermites in the lakes of Finnish Lapland (Acari, Hydrachnellae)

PAULI BAGGE

Bagge, P. 1989. Abundance and vertical distribution of watermites in the lakes of Finnish Lapland. *Fauna norv. Ser. B* 36, 45—52.

The bathygraphic distribution and relative abundance of watermites in several silvatic lakes and tarns and in two subalpine lakes of Finnish Lapland are discussed. Most of the waters studied are situated in the Finnish biogeographical provinces of Li and Le, which belong to the area 21 in Limnofauna Europaea. Five of the lakes studied are situated outside this area in the commune of Muonio (Lkem). Totally about 47 species of watermites and 912 specimens were obtained in the waters studied. Of these, 18 species are new to the Limnofauna-area 21, and *Arrenurus coronator* which was caught in L. Särkijärvi (Muonio) is earlier known in Fennoscandia only in Norway. Considerable differences in the composition and abundance of mitefauna were obtained between the waters studied. Thus, in silvatic lakes (Muonio, Inari), the greatest densities of mites were usually observed at medium depths (5—10 m) and the mites were absent or very rare in the profundal area (probably due to the shortage of oxygen). In the subalpine L. Kilpisjärvi the abundance of watermites was highest in the littoral area and high densities were obtained also in the profundal. Pionids clearly dominated in the mitefauna of Muonio lakes, but were less common in more northern provinces, except in some shallow tarns of Le.

*Lebertia*- and *Hygrobates*-species dominated in the lakes of Inari and the mitefauna contained also several northern watermites such as *Hygrobates foreli*, *Pionacercus uncinatus* and *Neobrachypoda ekmani* (at deep waters of L. Inari). In the subalpine L. Kilpisjärvi, the total number of species was very low (only 6—7 species), but some northern species especially *Neobrachypoda ekmani* occurred abundantly at every depth.

Pauli Bagge, Dept. of biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100 Jyväskylä, Finland.

## INTRODUCTION

During the summers 1964—1987 the zoobenthos of several lakes of Finnish Lapland was studied by the staff of the University of Jyväskylä. Most of the lakes studied are situated in the Finnish biogeographical provinces Li and Le, which together with Finmark and N. part of Kola peninsula are included in the Limnofauna area 21 (Illies 1978). This area, which harbours numerous small waterbodies and some large lakes such as L. Inari, is hydrobiologically relatively poorly known, and in the list of K. O. Viets (1978) there are records of only 38 species of watermites in the whole area.

Thus one of the aims of the present work was to fill gaps in the older specieslists, to compare the diversity and structure of watermite communities in different lakes and especially to compare the abundance and ver-

tical distribution of watermites in high boreal and subalpine areas.

Reference material was collected in several lakes of Muonio (Lkem) which are situated in the northwestern part of Limnofauna area No 23 (Fig. 1).

## CHARACTERISTICS OF THE LAKES STUDIED

Most of the studied lakes are medium sized, only L. Inari (1085 km<sup>2</sup>) is characterized as a large lake. The water quality of hypolimnion (Table 1) shows that the humus contents (expressed as colour of the water) and concentrations of phosphorus are higher in the lakes of Muonio than anywhere else in the area sampled. In lakes loaded by humus-rich waters and or by wastes from fish farms (Jerisjärvi, Sarmijärvi, Sarmilompolo) also the sa-

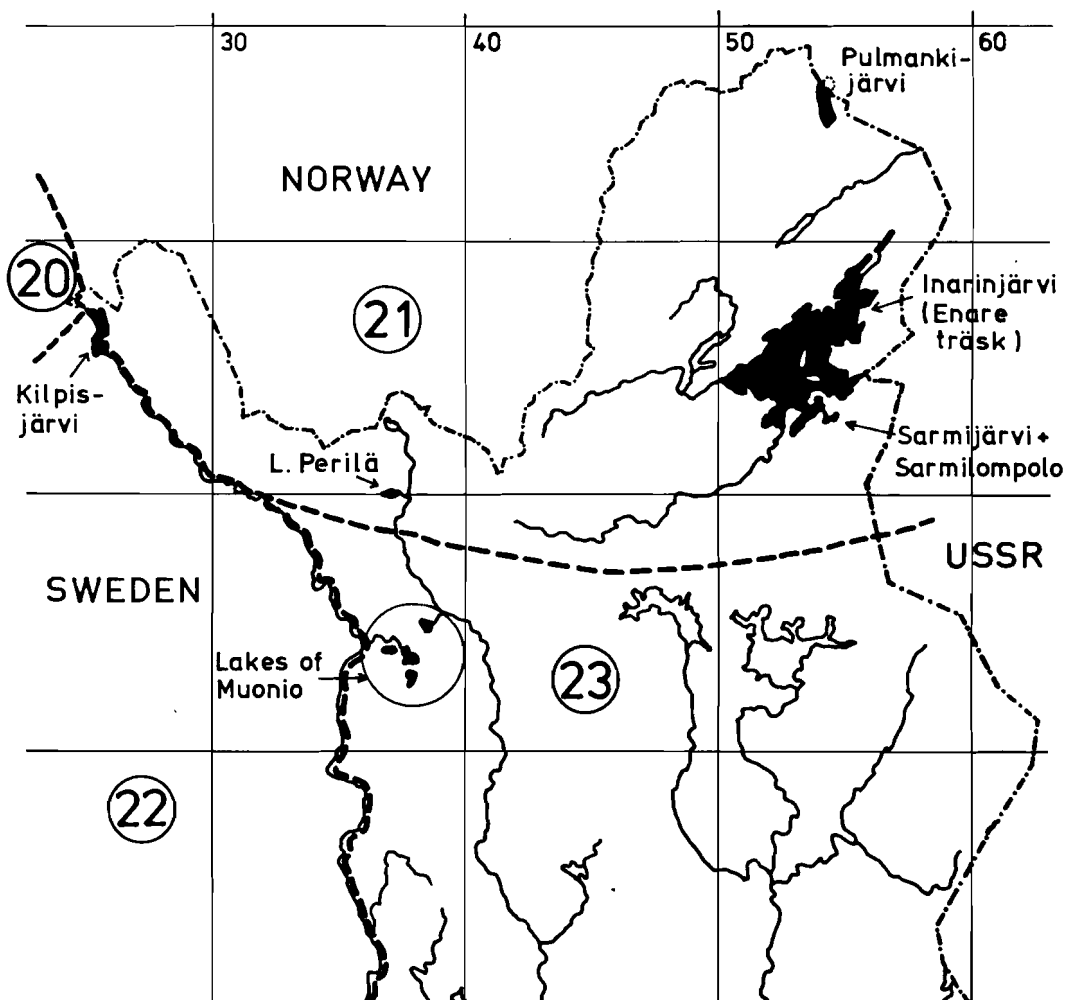


Fig. 1. The location of the waters sampled and the Limnofauna areas of northern Fennoscandia.

turation of oxygen in the hypolimnion may be very low during winter, which may limit the occurrence of some benthic animals.

Lake Kilpisjärvi which is situated c. 463 m a.S.l. in the subalpine zone deviates in many respects from other lakes studied having very clear water and low concentration of phosphorus. The lake has several ultraoligotrophic characters such as a low primary production of phytoplankton (c.  $1.5 \text{ g C/m}^2/\text{a}$ ) (Tolonen 1982) and a rich occurrence of Orthocladinae especially *Heterotrissocladius subpilosus* (Bagge 1968). The loss of ice in Lake Kilpisjärvi takes place in the middle of June, while the middle parts of L. Inari are ice free about June 5th and the lakes of Muonio about May 31st.

## MATERIAL AND METHODS

Benthos material from the lakes has been sampled mainly by means of grabs (types: Ekman & Birge or Petersen) or with plexiglass traps (model Bagge 1978) which were laid on the bottom overnight and then emptied. The sampling periods, type of gears and collectors (leg.) are presented in Table 2. In Lake Särkijärvi (Muonio) a considerable material of pelagic watermites (mainly males) was sampled using emergence traps (area  $0.5 \text{ m}^2$ ) which were placed over the deepest basins of the lake. The traps were emptied once a week. The mesh size of the net used in the gears was  $0.4 \text{ mm}$ .

In this connection I will thank all persons who have helped me in the sampling.



Table 1. Maximum depth (m) of the lakes studied and some water quality parameters of the hypolimnion in late winter (mainly according to measurements made by the Water District of Lapland).

<i>Lakes of Muonio</i>	<i>Max. depth</i>	<i>pH</i>	<i>Colour mgPt/l</i>	<i>Total P µg/l</i>	<i>O<sub>2</sub>-sat. %</i>	<i>Remarks</i>
Särkilompolo	8.3	6.4	150	48	19	sewage
Jerisjärvi	12.5	6.3	350	25	0	fish farm
Äkäsjärvi	13	6.4	180	24	11	
Särkijärvi	14	6.4	50	37	21	
Pallasjärvi	36	6.5	15	14	64	
<i>Lakes of Inari</i>						
Sarmilompolo	12	6.3	10	8	<6	fish farm
Sarmijärvi	26	6.6	15	8	6	fish farm
Pulmankijärvi	34	6.7	36	10	75	
Inari/Enare	96	6.8	12	8	87	regulated, max. amplitude 2.2 m
<i>Lakes of Enontekiö</i>						
Kilpisjärvi	>50	7.0	c.5	c.5	>90	
Perilä	<5	..	..	..	..	closely connected to L. Ounasjärvi

Table 2. The sampling scheme in the lakes (.. = no samples).

	Gear	Littor- ral	No. of samples		Leg.	Date
			Littor. prof.	Pro- fundal		
<i>Lakes of Muonio</i>						
5 lakes	E-B grab	24	15	21	Paasivirta	VI/82
L. Särkijärvi	emerg.traps	..	..	8	Metso	VII/82
<i>Lakes of Inari</i>						
Sarmilompolo	E-B grab	31	6	..	Palomäki	VIII/78
Sarmijärvi	E-B grab	30	6	9	Palomäki	VII/78
Pulmankijärvi	Plexiglass traps	3	..	3	Palomäki	X/84
Inari (Enare)	E-B grab	21	15	20	Palomäki	VI,VIII/77
	Plexi traps	9	6	9	Bagge	VII/87
<i>Lakes of Enontekiö</i>						
Tarns (2)	Plexi traps	12	..	..	Bagge	VII/82
L. Perilä	Plexi traps	16	..	..	Bagge	
L. Kilpisjärvi	Plexi traps	10	..	10	Bagge	VII/87
	Petersen grab	14	14	51	Bagge	VII/64

## RESULTS

Totally c. 47 species and 912 specimens of watermites (mainly adults) were sampled in the lakes studied. The exact number of species is somewhat unclear since all *Lebertia* specimens and some nymphs of pioniids and arrenurids were not determined to the species level.

In the lakes of Muonio (Table 3), which are the warmest and most humic lakes, we have found c. 20 species and 323 specimens. In the

benthic material caught in June, the mean density of watermites was highest at medium depths (5—10 m) and clearly lower in other depth zones. *Lebertia* species and *Oxus setosus* dominated in the littoral samples, and pioniids at deeper bottoms. A surprisingly rich occurrence of watermites (especially males of *Piona* species) was sampled in July in the pelagic traps of L. Särkijärvi.

The material caught in the lakes of Inari

Lapland (Table 4) contained c. 34 species and 218 specimens. The highest diversity of watermites (22 species) was found in the littoral area of the large L. Inari, while the diversity was extremely low in the subalpine L. Pulmankijärvi, which was sampled in October, and in the deeper parts of L. Sarmijärvi, which are loaded by wastes from a fish farm.

The abundance of mites was usually highest at medium depths in June and in the littoral in July (highest values of trappability). The most abundant species in the littoral of the small lakes were *Oxus ovalis* and *Frontipoda musculus*, while deeper waters were dominated by *Lebertia* species and *Acalyptonotus violaceus*. In the large lake Inari, *Lebertia* species dominated at most depths together with *Hygrobates nicromaculatus* at medium depths and with *Neobrachypoda ekmani* at greater depths.

Totally c. 27 species and 371 specimens of mites were identified in the material caught in the lakes of Enontekiö (Table 5). The diversity of species was highest in the shallow lake Perilä (19 species) and clearly lower in small tarns as well as in the deep subalpine lake Kilpisjärvi (6–7 species). The vertical

distribution of mites was studied in more detail only in L. Kilpisjärvi. There the maximum density (>100 ind./m<sup>2</sup>) occurred in the littoral areas in July, but owing to rich occurrence of *Neobrachypoda ekmani* the densities of mites were relatively high also at deep water. The trappability of watermites was very low at all depths in July 1987 when the temperature of water was exceptionally low (5–6°C).

## DISCUSSION

Totally c. 47 species of watermites were identified in the waters sampled. Many of them are earlier not known from the Limnofauna area No. 21, and *Arrenurus coronator* which was found in L. Särkijärvi (Muonio) is a new species to Finland's fauna. The lentic watermites of Finnish Lapland may be divided into several groups on the basis of their general distribution and habitats. Species new to Limnofauna area 21 are marked with an asterisk:

1. Species which are relatively common in the whole area:

*Lebertia porosa*, *Lebertia* spp., *Oxus setosus*, *Piona pusilla*

Table 3. Bathygraphic distribution and mean density (ind./m<sup>2</sup>) of watermites in five lakes of Muonio (Lkem).

	Littoral	Littori- profundal	Profundal	Pelagial of Lake Särkijärvi
No. of species (20)	9	12	8	(9)
No. of specimens (323)	23	36	34	(230)
X ind./m <sup>2</sup>	33	83	56	..
		X ind./m <sup>2</sup>		(total N)
<i>Lebertia</i> spp.	1	-	2	-
<i>Lebertia porosa</i> Thor	6	5	-	-
<i>Oxus setosus</i> (Koen.)	7	2	2	-
<i>Limnesia maculata</i> (Müll.)	-	2	3	(2)
<i>L. undulata</i> (Müll.)	-	5	-	-
<i>Neumania callosa</i> (Koen.)	-	9	2	-
<i>Huitfeldtia rectipes</i> Thor	-	-	-	(1)
<i>Piona coccinea</i> (Koch)	4	18	2	(15)
<i>P. disparilis</i> (Koen.)	-	12	21	-
<i>P. paucipora</i> (Thor)	4	2	7	(57)
<i>P. pusilla</i> (Neum.)	4	21	18	(68)
<i>P. stjördalensis</i> (Thor)	-	-	-	(40)
<i>P. variabilis</i> (Koch)	1	-	-	-
<i>Hydrochoreutes krameri</i> Piers.	-	-	-	(32)
<i>Forelia liliacea</i> (Müll.)	-	2	-	(14)
<i>Brachypoda versicolor</i> (Müll.)	1	-	-	-
<i>Arrenurus coronator</i> Thor	-	2	-	-
<i>A. nobilis</i> Neum.	1	2	-	(1)
<i>A. securiformis</i> Piers.	1	-	-	-

Table 4. Bathographic distribution and mean abundance (ind./m<sup>2</sup> or ind./trap/day) of watermites in the lakes of Inari Lapland. L = littoral, LP = littori-profundal and P = profundal.

Depth zone	SARMI-LOMPOLO		SARMI-JÄRVI		INARI ind./m <sup>2</sup>			INARI ind./trap/d		
	L	LP	L	LP	L	LP	P	L	LP	P
<i>Limnochares aquatica</i> (L.)	1	-	-	-	-	-	-	-	-	-
<i>Lebertia</i> spp.	3	45	8	-	6	33	4	0.2	1.2	0.4
<i>Frontipoda musculus</i> (Müll.)	7	-	4	-	-	-	-	-	-	-
<i>Oxus ovalis</i> (Müll.)	18	-	-	-	-	-	-	-	-	-
<i>O. setosus</i>	2	-	-	-	1	2	-	0.2	-	-
<i>Limnesia maculata</i>	2	-	-	-	-	-	-	-	-	-
<i>L. undulata</i>	-	-	1	6	-	-	-	-	-	-
<i>Hygrobates foreli</i> (Leb.)	1	-	-	-	-	-	-	-	-	-
<i>H. nigromaculatus</i> Leb.	-	-	1	-	2	5	-	1.3	0.8	0.1
<i>Unionicola crassipes</i> (Müll.)	-	-	-	-	-	-	-	0.1	-	-
<i>Piona ambigua</i> (Piers.)	-	-	-	-	-	-	-	0.8	0.3	-
<i>P. brehmi</i> Walt.	-	-	1	-	-	-	-	0.1	0.8	-
<i>P. coccinea</i>	-	6	-	-	1	-	-	0.1	-	-
<i>P. conglobata</i> (Koch)	1	-	-	-	-	-	-	-	-	-
<i>P. pusilla</i>	-	-	1	-	-	-	2	0.2	0.2	0.1
<i>P. rotundoides</i> (Thor)	1	-	1	-	-	-	-	0.1	-	-
<i>P. stjärdalensis</i>	-	-	-	-	-	-	-	0.1	-	-
<i>Hydrochoreutes unguatus</i> (Koch)	-	-	-	-	-	-	-	0.1	-	-
<i>Tiphys lapponicus</i> (Neum.)	-	-	-	-	-	-	2	0.2	-	-
<i>Pionopsis lutescens</i> (Herm.)	-	-	-	-	-	-	-	0.1	-	-
<i>Pionacercus leuckarti</i> Piers.	1	-	-	-	-	-	-	0.2	-	-
<i>P. uncinatus</i> (Koen.)	-	-	1	-	-	-	-	-	-	-
<i>Forelia liliacea</i>	6	-	1	6	1	-	-	0.3	0.2	-
<i>F. longipalpis</i> Maglio	1	-	-	-	-	-	-	-	-	-
<i>Brachypoda versicolor</i>	-	-	-	-	-	-	-	0.8	0.2	-
<i>Neobrachypoda ekmani</i> (Walt.)	-	-	-	-	-	-	-	-	-	0.2
<i>Mideopsis orbicularis</i> (Müll.)	2	-	-	-	-	-	-	-	-	-
<i>Acalyptonotus violaceus</i> Walt.	-	11	-	6	-	-	-	-	-	-
<i>Arrenurus adnatus</i> Koen.	-	-	-	-	-	-	-	0.9	0.3	-
<i>A. albator</i> (Müll.)	-	-	1	-	-	-	-	-	-	-
<i>A. nobilis</i>	1	-	-	-	2	-	-	0.4	-	-
<i>A. securiformis</i>	-	-	-	-	-	-	-	0.1	-	-
<i>Arrenurus</i> (indet.)	-	-	-	-	-	-	-	-	0.2	-
Total mean	47	63	21	17	12	39	7	7	5	1

2. Southern species which are relatively common in the lakes of Muonio, but are absent in more northern provinces:

Mainly pelagial: *Hydrochoreutes krameri*, *Huitfeldtia restipes*.

Sublittoral: *Arrenurus coronator*, *Neumania callosa*

Profundal: *Piona disparilis*

3. Species of small waterbodies: *Eylais infundibulifera*\*, *E. setosa*\*, *Piona carnea*

4. Southern littoral species which have their northernmost limit in the coniferous zone either in the basin of Inari (Li) or in southern Enontekiö (Le):

*Limnochares aquatica*\* (Li) *Hydrochoreu-*

*tes unguatus* (Li, Le), *Frontipoda musculus*\* (Li), *Pionopsis lutescens*\* (Li), *Oxus ovalis*\* (Li, Le), *Limnesia maculata* (Li), *Unionicola crassipes* (Li, Le), *U. minor*\* (Le), *Piona ambigua* (Li), *P. conglobata* (Li), *P. paucipora*\* (Li), *P. rotundoides* (Li, Le), *P. stjärdalensis* (Li), *Pionacercus leukarti* (Li), *P. vatrax*\* (Le), *Forelia longipalpis*\* (Li), *Brachypoda versicolor*\* (Li, Le), *Mideopsis orbicularis*\* (Li, Le), *Arrenurus albator*\* (Li), *A. securiformis*\* (Li).

5. Southern sublittoral species which occur in the silvatic lakes: *Limnesia undulata* (Li), *Piona brehmi*\* (Li), *P. coccinea* (Li),

Table 5. Bathygraphic distribution and mean abundance (ind./trap/d. or ind./m<sup>2</sup>) of watermites at different depths (L = littoral, LP = littoriprofundal, P = procundal) in the waters of Enontekiö Lapland.

Veget. zone: Depth Abundance	CONIFEROUS TARNS L. PERILÄ			SUBALPINE (BIRCH) L. KILPISJÄRVI				
	L	L	L	LP	P	L	LP	P
	ind./	trap/d		ind./	trap/d	ind./m <sup>2</sup>		
<i>Eylais infundibulifera</i> Koen.	0.2	-	-	-	-	-	-	-
<i>E. setosa</i> Koen.	0.1	-	-	-	-	-	-	-
<i>Lebertia</i> spp.	0.2	1.2	1.0	-	2.0	42	9	3
<i>Oxus ovalis</i>	-	0.1	-	-	-	-	-	-
<i>O. setosus</i>	-	1.2	0.1	-	0.1	18	11	-
<i>Limnesia maculata</i>	0.1	0.1	-	-	-	-	-	-
<i>Hygrobatas foreli</i>	-	-	-	-	0.1	-	2	1
<i>H. longipalpis</i>	1	0.6	-	-	-	-	-	1
<i>Unionicola crassipes</i>	-	0.3	-	-	-	-	-	-
<i>U. minor</i> (Soar)	-	1.9	-	-	-	-	-	-
<i>Piona carnea</i> (Koch)	0.1	-	-	-	-	-	-	-
<i>P. coccinea</i>	-	0.2	-	-	-	-	-	-
<i>P. pusilla</i>	-	-	0.1	-	-	-	-	-
<i>P. rotundoides</i>	0.1	1.0	-	-	-	-	-	-
<i>P. variabilis</i>	1.1	-	-	-	-	-	-	-
<i>Piona</i> (indet.)	-	0.1	-	-	-	-	-	-
<i>Hydrochoreuters ungulatus</i>	0.1	2.1	-	-	-	-	-	-
<i>Tiphys lapponicus</i>	0.1	0.3	-	-	-	-	-	-
<i>Pionacercus vatrax</i> (Koch)	-	0.1	-	-	-	-	-	-
<i>Forelia liliacea</i>	0.6	2.1	-	-	-	-	-	-
<i>F. variegator</i> (Koch)	-	0.1	-	-	-	-	-	-
<i>Brachypoda versicolor</i>	-	0.3	-	-	-	-	-	-
<i>Neobrachypoda ekmani</i>	-	-	0.1	-	-	42	13	12
<i>Acalyptonotus violaceus</i>	-	-	-	-	0.1	-	-	1
<i>Arrenurus adnatus</i>	-	0.1	-	-	-	-	-	-
<i>A. nobilis</i>	-	0.7	-	-	-	-	-	-
<i>Arrenurus</i> (indet.)	-	0.1	-	-	-	-	-	-
Total mean	2.5	13.3	1.3	0	2.3	101	35	18

*Forelia liliacea* (Li, Le), *Arrenurus adnatus* (Li, Le), *A. nobilis*\* (Li, Le).

6. Northern species:

Littoral: *Pionacercus uncinatus* (Li)

Sublittoral or profundal: *Hygrobatas foreli*, *Tiphys lapponicus*, *Neobrachypoda ekmani*, *Acalyptonotus violaceus*.

The diversity of watermites (Table 6) was highest in the lakes of Inari and in L. Perilä which is closely connected with the larger L. Ounasjärvi. Generally the diversity of mites was higher in lakes situated in the silvatic zone than in lakes in the subalpine zone. The low diversity of mites in the subalpine L. Kilpisjärvi may depend on the isolated position of the lake and harsh climatic conditions which have effect on the distribution of the hosts suitable for mite larvae. A positive ef-

fect of the size of the lake to the diversity of watermite fauna is seen only in the lakes of Inari basin; in other areas the sampling has been insufficient or the conditions between the lakes differ too much to make conclusions. However, even in L. Inari the diversity of species is only 1/3 of that found in the large lakes of southern Finland (Bagge 1983, 1986), which indicates that the diversity of watermites clearly decreases when moving to the North. The vertical distribution of watermites in the lakes (Tables 6 and 7) depends a.o. on the oxygen conditions of hypolimnion and on the season. In lakes, where the oxygen conditions during late winter are depleted (Sarmijärvi and some lakes of Muonio) the number of species of watermites was very low, or the mites were totally absent from the deepest waters. In the lakes of Inari and

Enontekiö, where the sampling were made in July-August the maximum occurrence of species was recorded in the littoral area, as is usual during this season in Finnish lakes. In the lakes of Muonio maximum occurrence of species was recorded in June at medium depths (5–10 m), and in July (Lake Särkijärvi); totally nine species and more than 200 specimens were sampled in the pelagic emergence traps.

The abundance of watermites at different depth zones of the lakes has been presented by two ways (Table 7). The left part of the table shows the results obtained by means of grabs and the right part, the trappability (ind./trap/day) of mites caught by means of plexiglass traps. The data show that in general the maximum density of mites was recorded at medium depths, except in L. Jerisjärvi and L. Kilpisjärvi.

The densities of mites were rather even in the littoral area but fluctuated greatly in the profundal samples. The trappability which depends a.o. on the abundance, activity and habitat of the watermites was usually highest in the littoral area and lowest in the profundal where also temperature is low. Very high trappability (13 ind./trap/day) was found in the shallow lake Perilä during a warm period in July 1982, while the trappabilities in L.

Inari and L. Kilpisjärvi were low during the cool summer 1987. The traps catch especially species actively swimming near the bottom but may be less suitable in catching species living in the sediment. The results from L. Kilpisjärvi indicate that the most abundant species of the lake, *Neobrachypoda ekmani*, is a sediment living species with a low trappability.

There were great differences in the structure of watermite communities between the lakes and even between different depth zones within the same lake.

Thus in the lakes of Muonio, the pionids clearly dominated at deeper bottoms and in the pelagic samples. In more northern waters pionids were less common, except in the shallow tarns of Enontekiö where *Piona variabilis* occurred abundantly. In the smaller lakes of Inari basin (Sarmijärvi and Sarmilompolo) Oxinae and *Lebertia* species dominated and the «deep water species» *Acalyptonotus violaceus* was common at medium depths.

In the regulated large L. Inari *Lebertia* spp. and *Arrenurus adnatus* dominated at most depth zones while *Neobrachypoda ekmani* occurred only at deep water.

Watermite fauna in the subalpine L. Kilpisjärvi which is very poor of species is characterized especially by a rich occurrence of

Table 6. Number of species at different depth zones in the lakes studied (.. = no samples)

Lake:	Littoral	Littori- profundal	Habitat Profun- dal	Pelag.	Total
Lakes of Muonio Σ	10	12	8	9	23
Särkilompolo	2	4	..	..	5
* Jerisjärvi	4	..	3	..	7
Äkäsjärvi	2	8	1	..	8
Särkijärvi	3	7	4	9	13
* Pallasjärvi	3	2	2	..	4
Lakes of Inari Σ	31	14	6	1	34
Sarmilompolo	14	3	..	..	16
Sarmijärvi	11	3	0	..	12
Inari (Enare)	22	10	6	1	23
* Pulmankijärvi	2	..	0	..	2
Lakes of Enontekiö Σ	23	4	5	..	26
Tarns (2)	10	..	..	..	10
Perilä	19	..	..	..	19
Kilpisjärvi	5	4	5	..	7-8

\* inadequately sampled

Table 7. Mean abundance of watermites at different depth zones in the lakes studied (.. = no samples)

	Littoral	Density ind./m <sup>2</sup> Littori- profundal	Profund.	Littoral	Trappability ind./trap/day Littori- profundal	Profundal
<b>Lakes of Muonio</b>						
Särkilompolo	46	93	..	..	..	..
Jerisjärvi	23	..	242	..	..	..
Äkäsjärvi	23	104	35	..	..	..
Särkijärvi	23	38	31	..	..	..
Pallasjärvi	35	..	12	..	..	..
<b>Lakes of Inari</b>						
Sarmilompolo	47	63	..	..	..	..
Sarmijärvi	21	17	0	..	..	..
Inari (Enare)	12	39	7	7	5	1
Pulmankijärvi	..	..	..	4	..	0
<b>Lakes of Enontekiö</b>						
Tarns (2)	..	..	..	2.5	..	..
Perilä	..	..	..	13	..	..
Kilpisjärvi	101	35	18	1	..	2

*Neobrachypoda ekmani* and *Lebertia* spp. Pionids were found only occasionally and *Unionicola* species were totally absent.

## REFERENCES

- Bagge, P. 1968. Ecological studies on the fauna of subarctic waters in Finnish Lapland. *Ann. Univ. Turku, A, II:40 (Rep. Kevo Subarctic Sta 4)*, 28—79.
- Bagge, P. 1978. Vattenkvalster (Acari: Hydrachnellae) i skogssjön Rautiaislampi (Östra Finland). *Jyväskylän Yliopiston biologian laitoksen Tiedonantoja* 19, 42—50.
- Bagge, P. 1983. The seasonal and bathygraphic occurrence of watermites (Acari: Hydrachnellae) in Lake Konnevesi and Lake Keitele (Central Finland). *Jyväskylän Yliopiston biologian laitoksen Tiedonantoja* 34, 5—23. (In Finnish with an English abstract).
- Bagge, P. 1986. Phenology and bathygraphic occurrence of watermites (Acari, Hydrachnellae) in some brown and clear water lakes of south-eastern Finland. *Memoranda Soc. Fauna Flora Fennica* 62, 17—25.
- Illies, J. 1978. *Limnofauna Europaea*. 2nd edition. Fischer Verlag, Stuttgart, New York; Swets & Zeilinger B.V., Amsterdam.
- Tolonen, A. 1980. Phytoplankton primary production in Lake Kilpisjärvi. *Luonnon Tutkija* 84, 49—51. (In Finnish).
- Viets, K. O. 1978. *Hydracarina*. In: *Limnofauna Europaea* 2nd edition. (J. Illies ed.), p. 154—181. Fischer Verlag, Stuttgart, New York; Swets & Zeilinger B. V. Amsterdam.

Received 20 Aug. 1988

# The problem of arctic Chrysomelidae (Coleoptera)

HANS SILFVERBERG

Silfverberg, H. 1989. The problem of arctic Chrysomelidae (Coleoptera). *Fauna norv. Ser. B* 36, 53—55.

In Eurasia and North America, 11 species are distributed only, or have their main distribution, in the arctic zone; none of these are recorded in Fennoscandia. However, 18 palaeartic and 6 nearctic species penetrate into the arctic zone, but their main distribution area is the boreal zone. Some of these species are recorded south to the Mediterranean area or to North India. Of the 18 palaeartic species, 6 occur in alpine areas of Fennoscandia.

Some Coleoptera families, e.g. Byrrhidae, have a strong arctic element, and Carabidae and Staphylinidae have a great number of arctic species. Curculionidae also have many arctic species, but compared with the total number of species in this family, the number of arctic species is low.

A low number of arctic species in Chrysomelidae may be explained by a low number of suitable habitats, and it is of interest to notice that the number of species in alpine areas is definitely much higher. May this difference be explained by the isolation that easily occur in alpine areas, and which are followed by a more rapid speciation? The mechanisms for adaptation to arctic biota need much research. Obviously, predators have a greater potential for exploring the resources in the arctic than the herbivores. Do the herbivores and predators show differences in their adaptation to the arctic?

Hans Silfverberg, Zoologiska Museet, Helsingfors Universitet, N. Järnvägsg. 13, SF-00100 Helsingfors, Finland.

In the alpine zone of the Scandinavian mountain chain live numerous species of Coleoptera, particularly from the families Carabidae and Staphylinidae. Many of these species are arctic, with a wide distribution in northernmost Eurasia. Contrastingly, the family Chrysomelidae is represented in the alpine zone by only six species, namely *Chrysomela lapponica*, *Chrysomela collaris*, *Phratora vitellinae*, *Phratora polaris*, *Gonioctena decaspilota* (= *G. affinis* auct.) and *Gonioctena pallida*. A few additional species approach the zone. For details, see e.g. Brundin (1934), Brinck & Wingstrand (1951) and Holmström (1972).

No one of these species is truly arctic. *C. lapponica*, *C. collaris*, *P. vitellinae* and *G. pallida* are found over all or most of Fennoscandia, and widely in Central Europe, even approaching the Mediterranean. *P. polaris* and *G. decaspilota* have a more restricted distribution range, but even they must be classed as high boreal rather than arctic. *P. polaris* is found e.g. over most of Finland

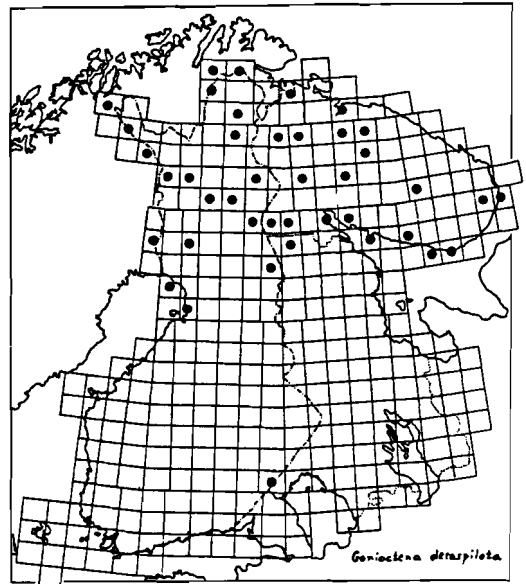


Fig. 1. Records of *Gonioctena decaspilota* from Eastern Fennoscandia shown in the UTM-squares.

Table 1. Chrysomelidae recorded from the Arctic zone of the Palaearctic (PA) and Nearctic (NA). Entirely or mainly arctic species are listed with A, species that merely reach the arctic with a.

	PA	NA	general distr.
<i>Cryptocephalus krutovskyi</i> Jacobs.	a		E Siberia
<i>Pachybrachis amurensis</i> Medv.	a		E Siberia
<i>Chrysolina graminis</i> (L.)	a		Transpalaearctic
<i>exanthematica</i> (Wied.)	a		E Palaearctic (to Himal.)
<i>subsulcata</i> (Mannh.)	A	A	Transberingian
<i>septentrionalis</i> (Mén.)	A		Arctic Siberia
<i>caurina</i> Brown		A	N Alaska
<i>bunnei</i> (Jacobs.)	A		Arctic Siberia
<i>cavigera</i> (J. Sahlb.)	A	A	Transberingian
<i>arctica</i> Medv.	A		Wrangel I.
<i>brunnicornis</i> (Wse.)	a		E Siberia
<i>instabilis</i> Mäkl.	a		N Siberia
<i>marginata</i> (L.)	a		Transpalaearctic (to N Afr.)
<i>basilaris</i> (Say)		a	W Nearctic
<i>hudsonica</i> Brown		A	Arctic Canada
<i>finitima</i> Brown		A	Alaska
<i>Hydrothassa hannoveriana</i> (F.)	a		Transpalaearctic
<i>Phaedon concinnus</i> (Steph.)	a		Transpalaearctic
<i>Chrysomela lapponica</i> L.	a		Transpalaearctic
<i>falsa</i> Brown		a	Canada, Alaska
<i>collaris</i> L.	a		Transpalaearctic
<i>taimyrensis</i> Medv.	A		Arctic Siberia
<i>wrangelina</i> Medv.	A		Wrangel I.
<i>blaisdelli</i> (VanDyke)		a	N Nearctic
<i>Phratora vitellinae</i> (L.)	a		Transpalaearctic
<i>polaris</i> (Sp.Schn.)	a		Transpalaearctic
<i>hudsonia</i> Brown		a	N Nearctic
<i>interstitialis</i> Mannh.		a	NW Nearctic
<i>laticollis</i> (Suffr.)	a		Eurosiberian
<i>Cercyonops caraganae</i> (Gebl.)	a		W Siberian
<i>Gonioctena linnaeana</i> (Schr.)	a		Transpalaearctic
<i>decaspilota</i> (Ach.)	a		Transpalaearctic
<i>nivosa</i> (Suffr.)			Alps, Pyreneans
<i>arctica</i> Mannh.		a	NW Nearctic
<i>pallida</i> (L.)	a		Eurosiberian
<i>Galerucella stephansoni</i> Brown		A	N Nearctic

(Palmén 1945), and in Asia south to Mongolia (Medvedev 1982). *G. decaspilota*, which seems to have the most restricted distribution, at least in Europe, is still found over large areas in the taiga zone (Fig. 1.), and in Asia it also goes south to Mongolia (Medvedev 1982). In the Alps and Pyreneans there is a closely related species, *G. nivosa*, which occasionally has been considered conspecific with the northern one. Also the relations between the North Palaearctic species and the North American *G. arctica* still need illumination.

Truly arctic species are known from Siberia (cf. Medvedev & Korotyaev 1980) and North America (Danks 1981). They are lis-

ted in table 1. It can be seen that there are just 11 truly arctic species, with additionally 18 Palaearctic and 6 Nearctic boreal species that reach the arctic zone, at least somewhere. Certain species, such as *Hydrothassa hannoveriana* and *Phaedon concinnus* reach the arctic in Siberia although in Europe they do not even approach the area.

In comparison some other Coleopteran families show clearly higher relative numbers of arctic species. In Byrrhidae this is quite conspicuous; among the larger families particularly Carabidae and Staphylinidae are well represented in the arctic (cf. Danks 1981). Curculionidae also includes a considerable number of arctic representatives, although



compared with the total number of species in the family they are rather few; Curculionidae also reaches further to the north than does Chrysomelidae, and is for instance represented in Greenland (Henriksen 1939).

A low number of species does not necessarily mean a low number of individuals — in fact herbivorous beetles are known occasionally to have occurred in very high numbers. The low species number can to a large degree be explained by decreasing numbers of available biota. Yet in alpine areas further south the species number is much higher. In the Austrian Alps at least 19 species are recorded from the alpine zone (Jakob 1979); of these only 3 are mentioned as going below the sub-alpine zone. In the Alps the genus *Oreina* has particularly many representatives in the alpine zone; in other mountain areas, genera such as *Oreomela* and *Mahutia* have a similar role. Can the differences to the arctic fauna be explained by differences in speciation rate due to local isolation? The postglacial faunal history is naturally another factor to keep in mind.

The mechanism of insect adaptation to arctic environments needs much study. Apparently predators have a greater potential for resource partition in these areas. Are there important differences in life-form strategies between Chrysomelidae and Curculionidae? The arctic faunas are being studied in many countries, both as a simplified ecosystem, due to decreased species numbers, and as an example of adaptation to inhospitable environments.

## REFERENCES

- Brinck, P. & Wingstrand, K. G. 1951: The mountain fauna of the Virihaure area in Swedish Lapland. II. Special account. — *Lunds Univ. Årsskr., N.F. (2)* 46(2): 1—173.
- Brundin, L. 1934: *Die Coleopteren des Torne-träskgebietes*. — Lund, 1—436.
- Danks, H. V. 1981: *Arctic Arthropods. A review of systematics and ecology with particular reference to the North American fauna*. — Entomol. Soc. Canada, Ottawa, 1—608.
- Henriksen, K. 1939: A revised index of the insects of Grönland. — *Medd. Grönland* 119(10): 1—112.
- Holmström, Å. 1972: The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland. 12. List of Coleoptera species. — *Acta Soc. Fauna Flora Fenn.* 80: 165—180.
- Jakob, H. 1979: Coleoptera, Fam. Chrysomelidae. — *Catal. Faunae Austriae XVp*: 1—36.
- Medvedev, L. N. 1982: *Listoedy MNR. Opredelitel'*. — Moskva, 1—303.
- Medvedev, L. N. & Korotyayev, B. A. 1980: Očerki po fauna listoedov (Coleoptera, Chrysomelidae) Arktičeskoj Azii i Kamcatki. — *Issledovanija po entomofaune Severo-Vostoka SSSR*, Vladivostok, pp. 77—95.
- Palmén, E. 1945. Zur Systematik finnischer Chrysomeliden. 2. Taxonomisches und Zoogeographisches über *Phyllodecta polaris* Sp.-Schn. — *Ann. Entomol. Fenn.* 11: 196—203.

Received 10 Aug. 1988



# Metabolic rates of alpine and high arctic *Amara quenseli* (Col. Carabidae) beetles

JOHN ALEXANDER STRØMME

Strømme, J. A. 1989. Metabolic rates of alpine and high arctic *Amara quenseli* (Col. Carabidae) beetles. *Fauna norv. Ser. B* 36: 57—58.

Metabolic rates of alpine *Amara quenseli* beetles from South Norway were measured, and compared with rates of arctic *A. quenseli* specimens from Spitsbergen. The study reveals that alpine specimens have metabolic rates lower than arctic specimens. This indicates that *A. quenseli* has developed different adaptation as a response to different climatic conditions.

John Alexander Strømme. Department of Zoology, The University of Trondheim, N-7055 Dragvoll, Norway.

## INTRODUCTION

The Spitsbergen area and alpine regions in Norway have in several respects similarities in fauna, flora and climate. Quite a few species of animals and plants living on Spitsbergen are also living in Norwegian mountains. Both areas have long winters, short summers and low temperatures throughout the year. The mean air-temperature in July is below 10°C (Klima, 1982).

Some studies have been carried out in order to study physiological adaptations in arthropods to arctic climate (Aunaas *et al.*, 1983 and Strømme *et al.*, 1986). These studies reveal that arthropods on Spitsbergen have both elevated metabolic rates and  $Q_{10}$  values compared to related arthropods from alpine regions in Norway. However, little attention has been paid to compare physiological adaptations of populations of one species, inhabiting alpine and high arctic regions.

The purpose of the present study was to investigate possible differences in metabolic adaptations in the carabid beetle *Amara quenseli* from a Norwegian alpine habitat and Spitsbergen arctic habitat (Strømme *et al.*, 1986).

## MATERIALS AND METHODS

The investigations were carried out on 6 specimens of *Amara quenseli* beetles collected in Grøvdalen, at the base of the Dovre Mountain plateau, in early June 1988. The animals were found under, or close to, dry cowpats

and transported to the laboratory where they were kept at 4 to 6°C. The experiments were carried out within 48 hours after the collection.

The oxygen consumption of the beetles was measured with Engelmann constant pressure respirometers as described by Aunaas (1983), and calculated as described by Strømme *et al.* (1986). The mean weight of the beetles was  $0,0239 \pm 0,00207$  g.

## RESULTS

The values of the oxygen consumption are plotted against the temperature in Fig. 1. The data from the Spitsbergen populations taken from Strømme *et al.* (1986), are also plotted in the figure. At low temperatures the alpine beetles have considerable lower rates of oxygen consumption than the beetles from Spitsbergen. The rates converge with increasing temperatures, and display only moderate differences at temperatures above 10°C.

## DISCUSSION

The data from both studies reveal that *Amara quenseli* have relatively high metabolic rates compared to carabids from warmer regions (Conradi-Larsen and Sømme, 1973; Hågvær and Østbye, 1974). This is likely to reflect an adaptation to low temperatures and short activity periods in alpine and arctic regions.

The present data indicate that *A. quenseli* beetles from the alpine population have lo-

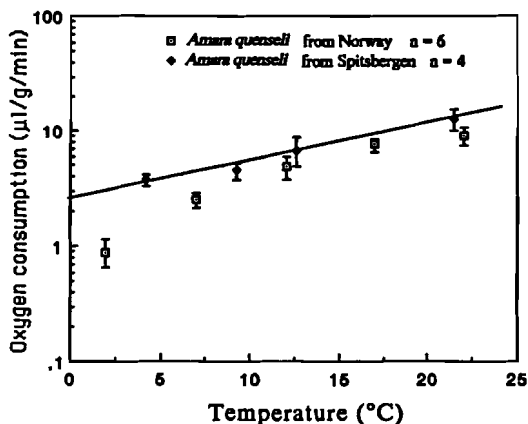


Fig. 1. Rates of oxygen consumption of *Amara quenseli* beetles from a Norwegian alpine region and from Spitsbergen, plotted as a function of temperature. Ordinate scale is logarithmic. Vertical bars represent standard deviation. Data for the Spitsbergen beetles are from Strømme *et al.* (1986).

wer rates of oxygen consumption than beetles from the Spitsbergen population. The heavier the beetles, the lower is their oxygen consumption per unit weight (Schmidt-Nielsen, 1975). The alpine beetles are heavier than the arctic beetles. At higher temperatures (above 10°C) the discrepancy in oxygen consumption can partly be ascribed to the differences in weight. However, at lower temperatures, the discrepancy is so marked that it is likely to reflect differences in physiological adaptations.

Although the climate in arctic and alpine regions display similarities, the microclimate conditions in the two regions may differ considerably. Beetles living on the ground may experience temperatures substantially above air temperature due to insolation. Because of the lower latitude and the higher altitude, the most intense radiation will be in the Norwegian mountains and cause a warmer microclimate when sun-exposed. In the arctic regions there are small variations in light conditions and air temperature throughout the day.

Such variations may be substantial in Norwegian alpine regions.

The Spitsbergen population experiences a relatively short time when activity can be performed and are also exposed to relatively low air temperatures (Klima, 1982; Temperaturnormaler 1931—1960, 1985).

One should expect, according to the climatic factors mentioned above, that arthropods living in the arctic would benefit more from having higher metabolic rates, especially at lower temperatures, than their relatives living in Norwegian alpine regions. The present study indicates that at least *A. quenseli* beetles show such physiological adaptations as a response to the different climatic conditions at the two sites.

#### ACKNOWLEDGEMENTS

I would like to thank Dr. Karl Erik Zachariassen for his ideas and inspiration, and Oddvar Hanssen for his help to collect the beetles.

#### REFERENCES

- Aunaas, T., Baust, J. G. & Zachariassen, K. E. 1983. Ecophysiological studies on arthropods from Spitsbergen. *Polar Research* 1: 235—240.
- Conradi-Larsen, E. M. & Sømme, L., 1973. The overwintering of *Pelophila borealis* Payk. II. Aerobic and anaerobic metabolism. *Nor. Ent. Tidsskr.* 73A, 545—555.
- Hågvar, S. & Østbye, E. 1974. Oxygen consumption, caloric values of water and ash content of some dominant terrestrial arthropods from alpine habitats at Finse, South Norway. *Nor. J. Zool.* 24, 407—417.
- Klima-The Climate at Norwegian Arctic Stations, 1982. Det norske meteorologiske institutt, 5.
- Schmidt-Nielsen, K. 1975. *Animal Physiology*. Cambridge University Press.
- Strømme, J. A., Ngari, T. W., Zachariassen, K. E. 1986. Physiological adaptations in Coleoptera on Spitsbergen. *Polar Research* 4, 199—204.
- Temperaturnormaler, 1931—1960. 1985. Det norske meteorologiske institutt.

Received 11 Oct. 1988

# The egg-laying behaviour of *Glyptotaelius pellucidus* (Retzius) (Trichoptera: Limnephilidae)

BO GULLEFORS

Gullefors, B. 1989. The egg-laying behaviour of *Glyptotaelius pellucidus* (Retzius) (Trichoptera: Limnephilidae). *Fauna norv. Ser. B* 36, 59—63.

Females of the caddis fly *Glyptotaelius pellucidus* laid egg masses on leaves hanging over the stream Forsån in central Sweden. The egg-laying period was from 23 July to 3 September 1987 and eggs were deposited during the night. Egg-laying females stood with their heads downwards, often on an old egg mass, bending their abdomens towards the leaf surface. The egg masses were deposited at various heights on the upper side of leaves of several plant species, but preferably on willows, bird cherries and alders. Sixty per cent of deposited egg masses were in contact with another mass on the same leaf. The deposited egg mass had swollen to double the size the following morning. On an average, egg masses contained 169 eggs and this value is lower than those found in more southerly areas.

Bo Gullefors, Department of Zoology, Section of Entomology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden.

## INTRODUCTION

Species of the Trichoptera family Limnephilidae deposit their egg masses on objects below as well as above the water surface (Silfvenius 1906, Wiggins 1973). At least two European species, *Glyptotaelius pellucidus* (Retzius, 1783) and *Nemotaulius punctatolineatus* (Retzius, 1783), oviposit on leaves hanging over the water surface or sometimes above the ground (Silfvenius 1906, Wesenberg-Lund 1908, 1910, Middleton 1977, Crichton 1987, Otto 1987). The purpose of this paper is to give additional information on the egg-laying behaviour of *G. pellucidus*, especially the act of egg-laying, which has not earlier been described.

## MATERIAL AND METHODS

The study was performed along 80 m of the north side of the upper part of the small stream Forsån (63°00'N, 17°32'E) in central Sweden.

Additional observations were made along the shore of the lake Valasjön (approx. 63°00'N, 17°30'E). Leaves of the riparian plants as well as other objects on the bank, such as stones, roots, logs etc, were examined nearly every day from mid-July to mid-September in 1987. Leaves which carried egg

masses were marked with numbered paper labels. The dates when the masses were laid, the height above the ground or water surface and the plant species were recorded. Egg masses collected in the field were taken to the laboratory and examined. Larvae were reared to adults in laboratory aquaria with aeration. The water temperature was about 15°C. The number of eggs in each of 28 masses was counted. The method used for counting the eggs is described by Crichton (1987). The egg masses were soaked in 5% KOH for about an hour. This dissolved the jelly and the eggs were counted easily.

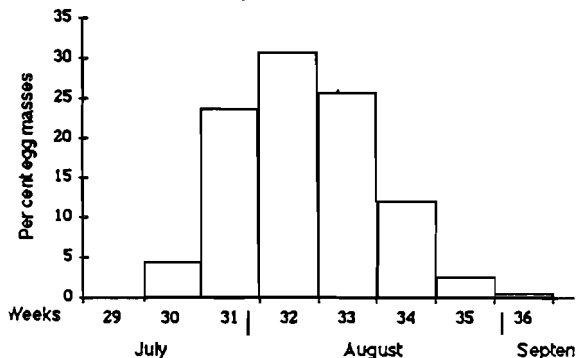


Fig. 1. The egg-laying period of *Glyptotaelius pellucidus* in 1987. The bars show the frequencies of egg masses found per week. N = 564.

Table 1. The distribution of egg masses of *Glyptotaelius pellucidus* on leaves of plant species found along the bank of the stream Forsån in central Sweden in 1987.

Plant species	Number of egg masses per leaf						No of masses
	1	2	3	4	5	6	
<i>Salix</i> spp.	136	43	15	5	1	3	310
<i>Prunus padus</i>	26	19	7	-	2	-	95
<i>Alnus incana</i>	30	16	4	1	-	-	78
<i>Lysimachia thyrsiflora</i>	20	4	2	-	-	-	34
<i>Filipendula ulmaria</i>	5	6	1	-	-	-	20
<i>Betula pubescens</i>	6	-	1	-	1	-	14
<i>Menyanthes trifoliata</i>	2	1	-	-	-	-	4
<i>Populus tremula</i>	2	1	-	-	-	-	4
<i>Valeriana sambucifolia</i>	1	-	-	-	-	-	1
<i>Alisma plantago-aquatica</i>	1	-	-	-	-	-	1
<i>Carex vesicaria</i>	1	-	-	-	-	-	1
<i>Calamagrostis pupurea</i>	1	-	-	-	-	-	1
<i>Comarum palustre</i>	1	-	-	-	-	-	1
Number of leaves	232	90	30	6	4	3	564

Observations of egg-laying females were made four nights in July and August. Photographs were taken. Some specimens captured in the summer 1987 were dissected.

The nomenclature for the plant species follows Lid (1963).

## RESULTS

The egg laying period was from 24 July to 3 September. The peak period was from late July to mid August (Fig. 1). The eggs were deposited on the upper side of leaves of mainly willows (*Salix spp.*), bird cherries (*Prunus padus*) and alders (*Alnus incana*) but also on ten other plant species (Table 1). No eggmasses were seen on other objects than plants. The average height was 1.0 m above the water (N = 365, range: 0.1—2.6, S.D. = 0.4). Most eggs were found on leaves hanging over the course of the stream. Along the shore of the lake Valasjön only few egg masses were found directly over the water. Most of these were deposited on plants mainly 2—4 meters from the water line, especially in shallow areas. At low water levels, distances of more than ten meters were recorded.

Sixty per cent of the 564 egg masses found were in contact with other masses on the same leaf (Table 1). Eggs were laid at night. Many times several egg masses were deposited on the same leaf, the same night. Sometimes depositions were repeated after a long

time. Thus, on one leaf, for example, a second egg mass was laid 31 days after the first one.

Four females were observed when laying at midnight on 28 July, 11, 21, and 27 August. The first female was seen when she carefully examined leaves of an alder. She sucked dew from all the area of the leaves. After having gone over seven nearly horizontal leaves for seven minutes she returned back to the last one but two and stood near the tip with her head and antennae outside the leaf. The act of egg-laying lasted for 15 minutes. Afterwards she stood «exhausted» for another 15 minutes a few millimeters from the egg-mass. The other three females were observed standing on old egg masses, bending their abdomens towards the leaf surface (Fig. 2). Oviposition then took about half an hour. The deposited egg masses were white and near-rectangular with round corners. Later when moistened they became translucent (cf Crichton 1987). The length of the newly laid eggmasses was 4—7 mm, the breadth 3—5 mm and the height 2—3 mm. The size of the egg-mass jelly had often swollen to more than double the following morning and the shape was then more rounded (Fig. 3). The eggs were of a yellowish colour. In a sample of 28 egg masses the average number of eggs was 169 (range: 117—257, S.D. = 32.5).

In the jelly eggs were seen with eye spots on developing embryos after four or five days. Larvae hatched within the gelatinous matrix

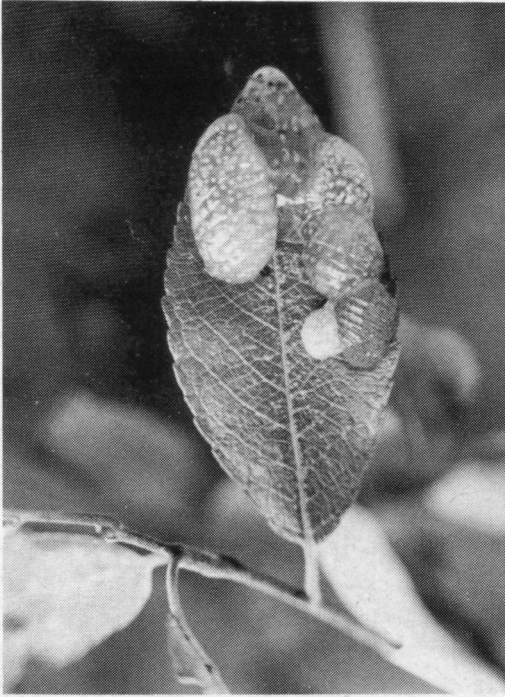


Fig. 2. An egg-laying female of *Glyphotaelius pellucidus* standing on an old egg mass with her head downwards.

after about two weeks. In a very favoured position and suitable weather conditions the first larvae were seen after only ten days, but very often it was not until after about three weeks that larvae could be detected. However, the development rate of the eggs in the same mass varied. Eggs and embryos of different stages were found together with first instar larvae. In dry and windy weather some of the swollen egg masses would dwindle, even into the same size as newly laid ones. This was found especially for egg masses in exposed positions. After being soaked with water the jelly recovered its normal swollen size. However, the embryonic development was then inhibited and prolonged. This could also reduce the number of hatched larvae. For example, from an egg mass severely dried for four days and then moistened daily until hatching, only 44 larvae hatched. The gelatinous material became gradually more fluid and appeared more often after rainy days. The larvae were seen crawling around within the fluid jelly. Wiggins (1977) reported that

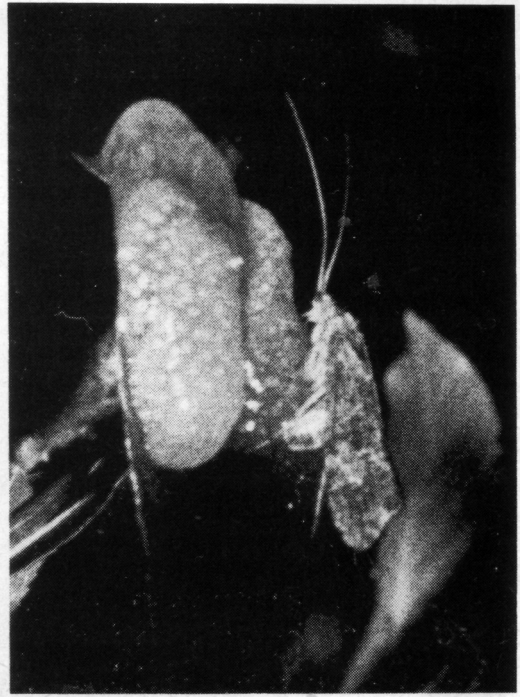


Fig. 3. A leaf of Great Sallow (*Salix caprea*) on 28.viii.87 with egg masses of *Glyphotaelius pellucidus* laid on 3.viii, 1.viii, 3.viii, 7.viii, 11.viii and 27.viii (from bottom right to top left respectively). The bottom egg mass contains larvae.

the activity within the matrix of the larvae of a North American limnephilid species (probably *Nemotaulius hostilis*) caused the liquefaction, since the jelly became fluid even in the absence of rain or other water. After three weeks or more the larvae dropped to the ground or water surface (Fig. 4). On a desk in the laboratory, larvae were seen crawling with their bodies raised from the surface after leaving a dried three-week-old egg mass. They bent their abdomens upward and ran until they met a damp paper towel connected to a petri dish with water and pieces of plant material. They crawled along the paper towel into the petri dish. There they constructed cases from tiny pieces of paper and plant debris.

From the larvae reared in aquaria adults emerged in January 1988.

A dissected female, which oviposited in the beginning of the general egg-laying period, had about 100 more eggs of different stages of development and would thus apparently have been able to oviposit again.



Fig. 4. Gradually the jelly containing the larvae became more fluid and spread downward towards the ground or water surface. The photograph was taken on 15.viii 87. The jelly string with larvae laid as an egg mass on 27.vii and the egg mass above on 13.viii.

## DISCUSSION

The females choice of plant species when laying eggs varied but willows, bird-cherries and alders were preferred. Leaves of the dominant plant species were also given as food to the reared larvae. The leaves were consumed voraciously by the larvae. The heights over the water/ground correspond very well to those measured by Crichton (1987) in South England while Otto (1987) in southern Sweden found deposited eggmasses at an average height of two meters. The height of the oviposition site reflects the riparian vegetation; for example on the shore of the lake Valasjön with low bushes the average height of the deposited egg masses was only 0.5 m.

The egg-laying period in central Sweden is considerably earlier than the one found at Millbarn Pond in Berkshire, England

(51°23'N, 1°02'W). There the first egg masses were laid in the night between 3/4 September and the last ones on 18 October 1984 (Crichton 1987). According to Crichton (1987) there was a dry spell in July and August and no outflow of water from the pond until 18 September. Dry weather would be rather risky for eggmasses. Although the jelly would give the eggs and larvae protection against desiccation to some extent, especially if several eggmasses were laid together (Otto 1987), the development of larvae could be retarded and their survival might even be endangered. In the stream Forsån there is always flowing water and, with the exception of the period 11–22 July, there were many rainy days and nights during the summer of 1987. In Sweden an early oviposition in July and August would be more favoured than later on, when risks for nights with low temperature rapidly increase. Four nights in both September and October had temperatures below the freezing point; the first one as early as 16 September with  $-4^{\circ}\text{C}$ . It has been suggested that one of the purposes of the gelatinous matrix is to protect eggs and larvae against sudden changes of temperature and freezing (Silfvenius, 1906 and Wiggins, 1973). Probably the eggs and larvae can withstand a few chilly nights but they would certainly not sustain longer periods of constantly low temperature.

Night activity appears as an adaptation of both the female and the eggs. Thus, laying in darkness may be seen as an advantage to the female in order to avoid predators and night humidity is no doubt favourable to the eggs.

Crichton (1987) suggested that rain might act as a releasing stimulus for egg-laying. This is supported by the fact that the first eggmasses appeared on the first rainy night for nearly a fortnight. The last week in July and the first in August, when many eggmasses were recorded, were also very rainy. However, during the second week in August it only rained 0.9 mm although 25% of the eggmasses were then laid. High relative humidity and dew seem to be other important factors for the egg-laying on leaves.

The average number of eggs per mass (169) is lower (t-test,  $p < 0.001$ ) than Crichton (1987) found in South England (245) and somewhat lower than that found in southern Sweden (Otto 1987). Does this mean that the fecundity of *G. pellucidus* decreases towards the north? To answer this, careful informa-



tion on clutch size and number of egg masses laid per female over a wider geographical range are needed.

#### ACKNOWLEDGEMENTS

I thank Dr Bo W. Svensson who critically read the manuscript and suggested several improvements. I also thank Dr M. I. Crichton who kindly provided me with data on egg masses from Millbarn Pond. Mr PG Sjölund improved the English and my wife Agneta Gullefors assisted in the field work. I also acknowledge a grant from Stiftelsen för Zoologisk Forskning, Uppsala University towards the cost of attending XXI. Nordiska Entomologmötet, Trondheim, Norway.

#### REFERENCES

Crichton, M. I. 1987. A study of egg masses of *Glyptotaelius pellucidus* (Retzius), (Trichoptera: Limnephilidae), pp. 165—169 in: Bournaud, M. & Tachet, H. (eds.) *Proc. of the 5th Int. Symp. on Trichoptera*. Junk Publishers, Dordrecht.

Lid, J. 1963. *Norsk og svensk flora*. Det norske samlaget. Oslo.

Middleton, M. I. 1977. The possible discovery of the egg masses of *Nemotaulius punctatolineatus* (Retzius) in Britain (Trichoptera: Limnephilidae). *Entomologist's Gaz.*, 28: 45—50.

Otto, C. 1987. Adaptive egg laying behaviour in two species of caddisflies, pp. 171—174 in: Bournaud, M. & Tachet, H. (eds.) *Proc. of the 5th Int. Symp. on Trichoptera*. Junk Publishers, Dordrecht.

Silfvenius, A. J. 1906. Trichopterologische Untersuchungen 1. Über den Laich der Trichopteren. *Acta Soc. Fauna Flora Fenn.*, 28(4): 1—128.

Wesenberg-Lund, C. 1908. Über tropfende Laichmassen. *Int. Rev. ges. Hydrobiol.*, 1: 869—871.

Wesenberg-Lund, C. 1910. Über die Biologie von *Glyptotaelius punctatolineatus* Retz. nebst Bemerkungen über das freilebende Puppenstadium der Wasserinsekten. *Int. Rev. ges. Hydrobiol.*, 3: 93—114.

Wiggins, G. B. 1973. A contribution to the biology of caddis flies (Trichoptera) in temporary pools. *Life Sci. Contr., R. Ont. Mus.*, 88: 1—28.

Received 22 Sept. 1988



# Group Effect during Postembryonic Development in *Eurycantha calcarata* Lucas (Insecta: Phasmida)\*

ULF CARLBERG

Carlberg, U. 1989. Group effect during postembryonic development in *Eurycantha calcarata* Lucas (Insecta: Phasmida). *Fauna norv. Ser. B* 36, 65—66

The New-Guinean stick-insect *Eurycantha calcarata* Lucas normally lives collectively in hollow logs. While rearing individuals solitarily some differences compared with group reared individuals were observed, viz. an extra nymphal instar, a longer development time for the nymphal instars, a total longer nymphal life, and a smaller size of hind femur in males. This indicates a group effect in the individuals normally living collectively.

Ulf Carlberg, Atlasvägen 53, S-131 34 Nacka, Sweden.

## INTRODUCTION

*Eurycantha calcarata* Lucas is an apterous ground-living stick-insect occurring in Papua-New Guinea. During day time the individuals collectively inhabit hollow logs, which they leave for feeding during night. Both sexes have equal number of nymphal instars, and the adults are of similar size, viz. ca. 90—130 mm in length and 8—18 g in mass of body. The postembryonic development was studied with respect to growth in length and mass, and development time for individuals reared solitarily and collectively in order to see if any group effect could be present in this species.

## RESULTS AND DISCUSSION

Insects reared collectively (normal conditions) underwent 6 nymphal instars with a mean duration of 23 days, giving a total development time of 138 days. Insects reared solitarily underwent 7 nymphal instars with a mean duration of 26 days, giving a total development time of 182 days. No difference in adult size could be observed between the two categories of insects, i.e. the species' adult size is restricted by some physiological limit. A decreased growth in mass and length occurred in individuals reared solitarily. No difference in food consumption occurred between the two categories of insects. Hence indivi-

duals reared solitarily with an extra nymphal instar and a longer duration of each instar had a considerable higher total food consumption during the nymphal development when compared with individuals reared collectively, viz. 25 g compared with 15 g, respectively. The result is summarized in Table 1.

The present result is new to the Phasmida and highly interesting. Previous studies have shown that temperature and light were responsible factors for causing postembryonic variations (Carlberg 1983). Furthermore, when extra stages have been produced, the duration of each nymphal instar was shortened in order to produce an adult within the same time as in normal development. The results on *E. calcarata* shows the reverse pattern. However, the fact that adults with different number of nymphal instars were of similar size (i.e. no difference in adult size) is in

Table 1. Differences and similarities in solitarily reared individuals of *E. calcarata* compared with normal group reared ones.

---

Differences:	— one extra nymphal instar
	— a longer development time for each nymphal instar
	— a longer total development time
	— a slower growth (mg/day)
	— a higher total food consumption
Similarities:	— a smaller mass of hind-leg in males
	— similar size of adults (length and mass)
	— similar food consumption (mg/day)

---

\* A complete manuscript of this paper is accepted for publication with *Zool. Jb. Anat.*

agreement with previous results (Carlberg 1985).

Future studies will show if this group effect can be an easy method for artificially producing extra stages at specific times, and thus be able to study morphological changes without having to administring hormones.

#### ACKNOWLEDGEMENTS

I am most grateful to the Längmanska kulturfonden (Stockholm) for economic support to participate to the 21. Nordiska Entomologmötet in Trondheim 1988.

#### REFERENCES

- Carlberg, U. 1983. An analysis of variations in postembryonic development of Phasmida (Insecta). *Biol. Zbl.* 102: 445—450.
- Carlberg, U. 1985. Postembryonic variations in *Extatosome tiaratum* (MacLeay) (Insecta: Phasmida). *Zool. J.b. Anat.* 113: 165—169.

Received 26 Aug. 1988

# Aspects of Evolution and Ecology in Relation to Defecation and Oviposition Behaviour of *Extatosoma tiaratum* (MacLeay) (Insecta: Phasmida)\*

ULF CARLBERG

Carlberg, U. 1989. Aspects of evolution and ecology in relation to defecation and oviposition behaviour of *Extatosoma tiaratum* (MacLeay) (Insecta: Phasmida). *Fauna norv. Ser. B* 36, 67—68

The Australian stick-insect *Extatosoma tiaratum* (MacLeay) passively drops the fecal pellets while the eggs are actively flicked away some 2—3 metres. A model is presented and discussed, which explains the evolutionary and ecological background for these two behaviours.

Ulf Carlberg, Atlasvägen 53, S-131 34 Nacka, Sweden.

## INTRODUCTION

The Australian stick-insect *Extatosoma tiaratum* (MacLeay) inhabits Eucalyptus forests and oviposits by throwing away its eggs some metres (Carlberg 1984). Defecation studies showed that defecation occurred randomly over a 24 hour period without any circadian rhythm. With respect to recent results by Silander *et al.* (1983, 1985) on insect frass mediated allelopathy in *Eucalyptus* spp. (Fig. 1), three different models for habitat selection, defecation and oviposition behaviour are discussed. From these models, one theory finally was adopted.

## RESULTS AND DISCUSSION

The ancestral *E. tiaratum* was probably a polyphagous shrub living insect which dropped its eggs onto the ground. Recent evolutionary and ecological studies has shown that primitive forms are ground living and deposits the elongated eggs in substrate, while advanced forms inhabits trees and actively disperses the round eggs (Carlberg 1983, 1986, 1987). Then over evolutionary time it changed habitat and ascended the crown of the

*Eucalyptus* tree where it became an ecological monophagous species, although still retaining a genotypic polyphagocity. As insect-frass mediated allelopathy occurs in some species of *Eucalyptus* resulting in the creation of bare zones below the trees, the eggs became vulnerable to natural enemies and hostile climatic factors. Furthermore, olfactory attraction by frass and food plant residues may have directed predators and parasitoids towards the eggs. Thus *E. tiaratum* had to change oviposition behaviour. It did so by actively throwing its eggs outside the bare zone into the protective vegetation to reduce predation pressure. It is also proposed that the daily active newly hatched nymph (Carlberg 1985) is directed into the bare zone of the host tree by olfactory attractants from frass and food plant residues. After climbing the tree trunk nymphs congregate within the periphery of the host tree crown where they mature. This choice of habitats is of greatest importance for survival of the species, because it will ensure that most eggs will fall outside the bare zone into the protective vegetation.

## ACKNOWLEDGEMENTS

I am most grateful to the Långmanska kulturfonden (Stockholm) for economic support to participate to the 21. Nordiske Entomolog-nøtet in Trondheim 1988.

\*A complete manuscript of this paper (including full references) has been published in *Biol. Zbl.*, 107 (1988): 541—551.

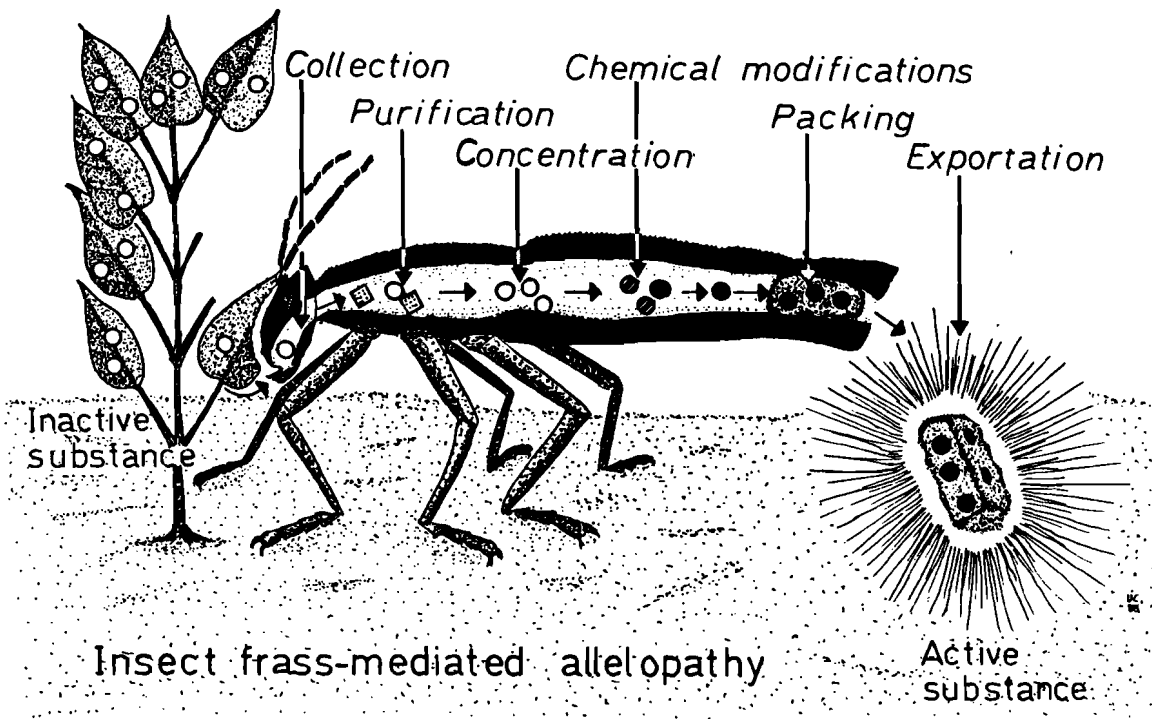


Fig. 1. Schematic illustration of insect frass mediated allelopathy regarding the insect as a vessel for an organic chemical synthesis reaction. The insect consumes the plants secondary compounds which is inactive at this stage. After collection of this inactive precursor, the substance is purified, concentrated and finally chemically modified into the active compound. Now it is ready to be packed in the fecal pellets and exported to the ground where it can be used in allelopathy.

## REFERENCES

- Carlberg, U. 1983. A review of the different types of egg-laying in the Phasmida in relation to the shape of eggs and with a discussion on their taxonomic importance (Insecta). *Biol. Zbl.* 102: 587—602.
- Carlberg, U. 1984. Oviposition behaviour in the Australian stick insect *Extatosoma tiaratum*. *Experientia* 40: 888—889.
- Carlberg, U. 1985. Evolutionary and ecological aspects on hatching time and defensive behaviour of Phasmida (Insecta). *Biol. Zbl.* 104: 529—537.
- Carlberg, U. 1986. Evolutionary and ecological on reproduction adaptations in Phasmida (Insecta). *Biol. Zbl.* 105: 651—661.
- Carlberg, U. 1987. Evolutionary and ecological aspects on ovarian diversity in Phasmida (Insecta). *Zool. Jb. Syst.* 114: 45—63.
- Silander, J. A. Jr., Fox, L. R. & B. R. Trenbath. 1985. The ecological importance of insect frass: allelopathy in eucalyptus. *Oecologia* 67: 118—120.
- Silander, J. A. Jr., Trenbath, B. R. & L. R. Fox. 1983. Chemical interference among plant mediated by grazing insects. *Oecologia* 58: 415—417.

Received 26 Aug. 1988

# Worker — queen conflict and fitness consequences in a colony of *Bombus hypnorum* L. (Hymenoptera)

TOR BOLLINGMO

Bollingmo, T. 1989. Worker-queen conflict and fitness consequences in a colony of *Bombus hypnorum* L. (Hymenoptera). *Fauna norv. Ser. B* 36, 69—73

Socio-ethological theory predicts a conflict of interest between the queen and the workers in eusocial hymenopteran colonies. Bumblebee workers develop ovaries and lay unfertilized, male-producing eggs. This study quantifies the reproductive output of worker egg-laying. Conflict is recorded in the form of aggression and dominance fights, and egg-eating. This antagonism seems to maximize the classical fitness of the queen, and leaves some true sons for the dominant (alpha) worker. To maximize inclusive fitness, workers should not sacrifice potentially reproductive sisters to produce their own sons, as they apparently do.

Tor Bollingmo, Dept. of Zoology, AVH, University of Trondheim, N-7055 Dragvoll.

## INTRODUCTION

Eusocial reproductive systems are defined as groups of individuals with overlapping generations, cooperative brood care, and sterile castes (Wilson 1971). The complex aspects of structure, physiology, genetics, taxonomy, ecology, and behaviour, have been described in detail for a number of eusocial species within the order Hymenoptera, and a huge body of theoretical literature analyzes the different aspects of evolution of eusociality (Andersson 1984). Eusocial characteristics are thought to have resulted from natural selection acting on selfish individuals as genetic units (classical individual selection) or from selection at the level of individual genes (kin selection maximizing inclusive fitness). In the first case, a queen is thought to be selected to manipulate her daughters to become workers (Alexander 1974). In the second case, workers are thought to take advantage of the fact that hymenopteran males are produced from unfertilized, haploid eggs. To gain genetic profit, workers should thus prefer to stay at the maternal nest to raise sibling sisters that they have an exceptionally high probability of sharing genes with (Hamilton 1964; Trivers and Hare 1976).

In support of kin selection, Trivers and Hare (1976) predicted a conflict of interest between the colony-founding female (the queen) and the first batches of female off-

spring (the workers). For more details on this, see Krebs and Davies (1987).

Bumblebees (genus *Bombus* Latreille) have been regarded as primitively eusocial. One such feature is the ability of workers to develop ovaries and lay eggs. These unfertilized eggs produces males. The author observed a number of colonies of *Bombus hypnorum* to try to answer the following questions:

1. Is there a visible queen-worker conflict in *B. hypnorum* colonies?
2. What effect does such a conflict have on the classical fitness of the queen?
3. What effect does a conflict have on the fitness of the workers?

## METHODS AND MATERIAL

Post-hibernating bumblebee queens were confined in laboratory units, each unit consisting of a cage for feeding and flight exercises, and a nesting box. The queens soon started breeding, and produced a number of workers. All individuals were marked with numbered tags. The nest structures were mapped daily, so that the development of each larva could be followed in detail, until the imago insect hatched. Cases of egg-laying could be recorded by observing the early construction of small wax-cells (egg-cells), and surveying these cells using a video-connected fiberoptic. The identity of the egg-laying indivi-

dual, the number of eggs laid, and behavioural interactions during and some time after the egg-laying, could then be screened.

A dominance hierarchy was established among the workers as the colony production culminated or when the influence of the queen declined. One particular worker took the alpha position, and performed dominant (alpha) behaviour for a shorter or longer period. Alpha behaviour included harassing other workers by bumping and biting (even stinging), and eating some or all of their eggs. An alpha individual was never seen to challenge the queen.

The preliminary results in this paper is mainly based on the continuous observation of one particular nest (colony No. 60) for a period of 14 days in the autumn of 1987. One worker, G-98 (yellow-98), held the alpha position during the whole period.

## RESULTS

A total of 40 out of 75 cases of worker egg-laying, was video-recorded. Mean number of eggs per cell was significantly higher in the

alpha worker than in the other 11 egg-laying workers (Tab. 1). The alpha worker laid more than 30% of the batches and more than 40% of the total number of eggs that the workers produced (Tab. 1). Imago males were only produced from the egg-batches of the alpha worker, with the exception of a single case (Tab. 2). As long as the queen stayed alive, she seemed to be able to detect all cases of worker egg-laying, and to eat the eggs (Fig. 1). As the influence of the queen declined (the queen died in the middle of the observation period), aggression and egg-eating was taken over by the alpha worker. This was also a period of slightly increased egg-laying activity, and the alpha worker managed to cover and defend some batches of eggs that eventually produced imagos (Fig. 1; Tab. 2).

## DISCUSSION

The present data, which is part of a more extensive study, produced 3 preliminary main conclusions:

Table 1. Frequency of different numbers of eggs (clutch-sizes) laid by the dominant worker (G-98) and the other 11 egg-laying workers. A total of 40 out of 75 cases of worker egg-laying was video-recorded in Colony No. 60 during the observation period 29 Sept.—13 Oct. 1987. The total number of eggs is given in brackets. Cases have been treated separately when the recordings were good enough to permit counting of all the eggs.

Clutch size	Number of observed cases			
	Minimum numbers (1		All eggs seen	
	G-98	Others	G-98	Others
1	0 ( 0)	6 ( 6)	0 ( 0)	6 ( 6)
2	1 ( 2)	4 ( 8)	0 ( 0)	2 ( 4)
3	6 (18)	10 (30)	4 (12)	5 (15)
4	2 ( 8)	1 ( 4)	2 ( 8)	1 ( 4)
5	2 (10)	0 ( 0)	1 ( 5)	0 ( 0)
6	1 ( 6)	1 ( 6)	1 ( 6)	1 ( 6)
Unknown	1 —	5 —	— —	— —
Total	13 (44+)	27 (54+)	8 (31)	15 (35)
Mean(2	3.7*	2.5	3.9**	2.3
Estim.tot.(3	13 (48)	27 (66)	— —	— —
%	32.5 (42.1)	67.5 (57.9)	34.8 (47.0)	65.2 (53.0)

(1 Includes the cases when all eggs were seen.

(2 Mean clutch size when unknown cases are not included.

(3 When "unknown" cases is given same mean as the observed mean in the same category.

\*  $p < 0.05$  (Median test using one-tailed Fisher's exact test).

\*\*  $p < 0.01$  (Mann Whitney U-test, one-tailed).



Table 2. Number of observed cases of egg-laying by each of the 12 egg-laying workers in colony 60, and the resulting number of imago males (worker fitness). Same data as in Tab. 1.

Worker (n=12)	Observed cases	Number of eggs (Cases)		Minimum clutch-size		Resulting no. of imago males
				Mean	Range	
G-98	13	44	(12)	3.7	2 - 6	12
G-73	7	21	(6)	3.5	2 - 6	0
G-75	5	9	(4)	2.3	1 - 3	0
R-82	4	6	(3)	2.0	1 - 3	0
G-74	2	4	(2)	2.0	1 - 3	0
B-15	2	4	(2)	2.0	1 - 3	0
B-06	2	-	-	-	-	0
B-02	1	3	(1)	-	-	1
B-54	1	3	(1)	-	-	0
B-09	1	2	(1)	-	-	0
G-13	1	1	(1)	-	-	0
G-77	1	1	(1)	-	-	0
<b>Total</b>	<b>40</b>	<b>98</b>	<b>(34)</b>	-	-	<b>13</b>

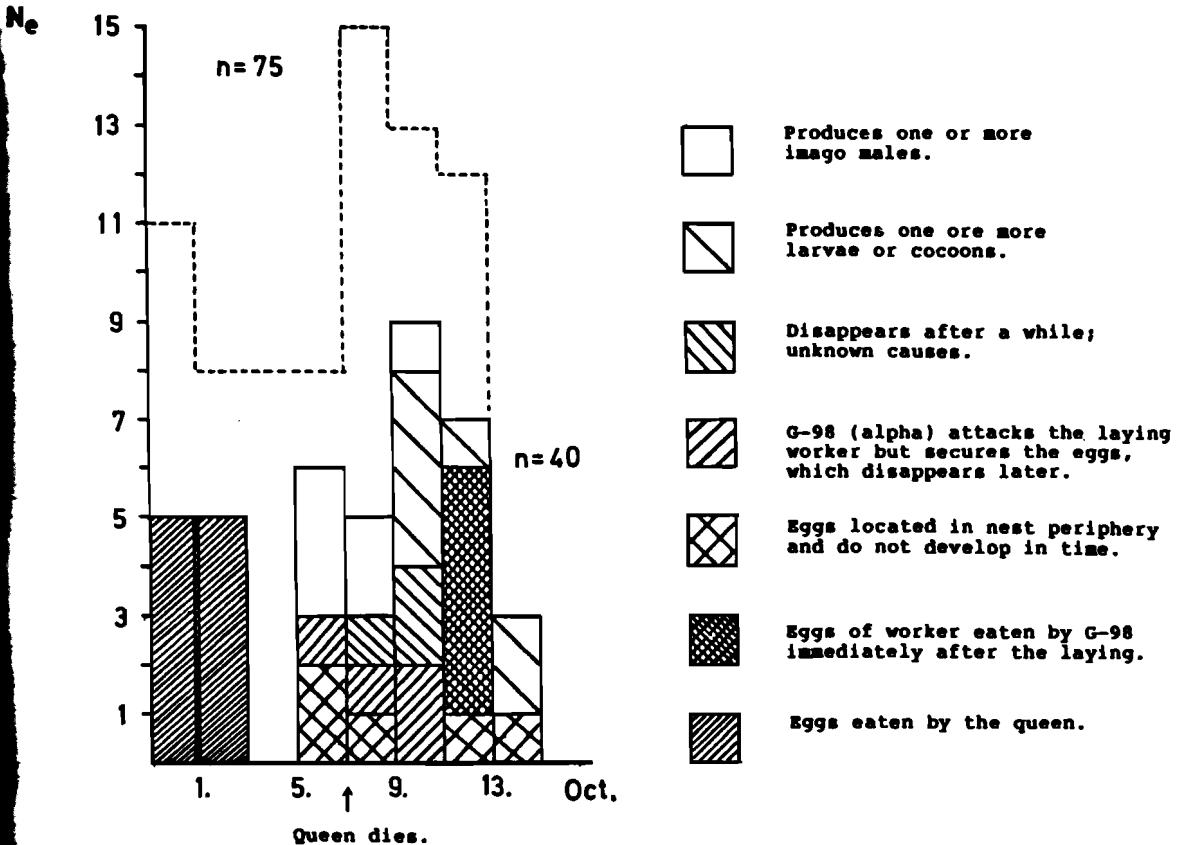


Fig. 1. Number of cases of worker egg-laying ( $N_e$ ) per two days during the observation period 29 Sept.—13 Oct. 1987 (same data as in Table 1 and 2). Total number of layings is indicated with a stippled line. Cases recorded using a video-connected fiberscope and later followed throughout the egg- and larvae development periods, are given in various hatching.

1. A worker — queen conflict was observed in the *Bombus hypnorum* colony. Two main categories of conflict were recorded:
  - a. Egg-eating:
    - The queen ate or destroyed eggs laid by workers, as long as she stayed healthy.
    - The alpha worker ate the eggs laid by other workers.
  - b. Aggressive interactions:
    - Some times (but rarely) the queen bumped the workers, — and then not only the alpha worker.
    - The alpha worker showed strong aggression towards other workers, often initiating prolonged fights. The alpha worker was never seen to challenge the queen.
2. Queen fitness: Egg-eating did not seem to reduce the classical fitness of the queen. Workers always raise the offspring of a queen, even if she dies at an early stage of colony development (Bollingmo unpubl.). Workers eating the eggs of the queen have been reported by others (Röseler 1977), and there is some evidence for this kind of behaviour in colonies that have been watched in 1988 (Bollingmo unpubl.).
3. Worker fitness: Aggression and egg-eating seemed to affect the fitness of the workers significantly:
  - a. Subordinate workers produced few or no offspring, as their eggs were eaten by the queen or by the alpha worker.
  - b. The dominant worker (the alpha) produced some sons towards the end of the season, but at least some of these emerged too late to take part in the late-summer courtship flights.

Trivers and Hare (1976) predicted the observed worker — queen conflict. It is, however, easy to think of alternatives to the inclusive fitness interpretation. The behaviour of the queen and the workers could be seen as purely selfish, each individual then attempting to maximize its genetic contribution to the next generation. Workers could be behaviourally and genetically manipulated by the queen to maximize queen fitness. Queen mortality in the period of colony growth is high, at least in the laboratory (Bollingmo unpubl.), but may be even higher in nature when the animals are exposed to predation,

parasitism and natural hazards. If a queen dies at an early stage of colony development, she is leaving female (and male) offspring in the form of eggs, larvae and pupae in a vulnerable situation. A high number of worker-laid eggs would quickly outnumber the eggs of the queen and produce male offspring that would compete for food, space, and other resources at the nest.

Queens should thus be selected to leave workers in a competitive situation, resulting in a dominance fight and in the production of a dominant worker that controls and reduces the egg-laying tendencies of the rest of the numerous workers. The benefit to the queen is obvious, as her offspring is effectively raised even after her death. But there is still a benefit to the alpha worker, and this study demonstrates for the first time, the selfish fitness advantage to the dominant workers in eusocial insect societies. If workers were selected to maximize their inclusive fitness, they should not sacrifice sisters (new reproductive queens) to produce their own sons.

To maximize her inclusive fitness, the alpha worker should ideally kill off all the male eggs and larvae of a declining queen. This kind of selective fratricide has not been observed, but a worker may not be able to separate brothers from sisters before they hatch.

It is possible to speculate around the presence of worker-produced males in the nest in late summer. The world-wide genus *Bombus* occurs in all zoogeographic regions, with a particularly rich fauna in the Scandinavian peninsula, and some species even reaching the high arctic (Løken 1973). Climatic conditions are unpredictable in northern areas. During periods of bad weather, the sexually mature, young queens could be prevented from swarming. Young queens could then be forced to mate with males that are present in the nest, and mating with a half-brother would be better than not mating at all. This also influences the fitness of the mother queen, as her genetic contribution should be counted for more than one generation. The egg-eating and aggression in a *Bombus hypnorum* colony thus seems to contribute to the maximization of the classical fitness of the queen, as well as the dominant workers.

## ACKNOWLEDGEMENTS

This study is financed by a grant from the Norwegian Research Council for Sciences and Humanities to Torbjörn Järvi. I am indebted to Torbjörn for his support, and to the Dept. of Zoology and the Faculty of Science and Mathematics at the University of Trondheim, for providing me with facilities and additional funding. Finally, I would like to thank Eivin Røskaft and Yngve Espmark for criticizing the manuscript.

## REFERENCES

- Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5: 325—383.  
Andersson, M. 1984. The evolution of eusociality. *Ann. Rev. Ecol. Syst.* 15: 165—189.

- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *J. Theor. Biol.* 7: 1—52.  
Krebs, J. R. & N. B. Davies 1987. *An introduction to behavioural ecology*. Blackwell, Oxford. IX + 389 pp.  
Løken, A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk ent. Tidskr.* 20: 1—218.  
Röseler, P.-F. & Röseler 1977. Dominance in bumblebees. *Proc. VIII Int. Congr. Intl. Union Study Social Ins.*: pp. 232—235.  
Trivers, R. L. & H. Hare 1976. Haplodiploidy and the evolution of social insects. *Science* 191: 249—263.  
Wilson, E. O. 1971. *The insect societies*. Belknap Press, Harvard Univ. Press, Cambridge. X + 548 pp.

Received 25 Oct. 1988.



# Host selection by odorous compounds from host and non-host trees in bark beetles

BJØRN ÅGE TØMMERÅS

Tømmerås, B. Å. 1989. Host selection by odorous compounds from host and non-host trees in bark beetles. *Fauna norv. Ser. B* 36, 75—79.

This paper is a presentation of the first results obtained by having used a new method introduced to find out which compounds of the complex mixtures of bark volatiles are biologically active in the choice of proper host in bark beetles. The method contains linked gas-chromatographical (GC) separation technique to electrophysiological single cell recordings from olfactory receptor cells. The results so far showed that rather few of the volatiles from bark are active on the sensory cells. Furthermore, that there are olfactory cells in the bark beetles able to discriminate between compounds present in host and non-host trees respectively. Most of the cells activated by GC-fractions could be grouped in few groups according to responses to one particular fraction after GC separation. The active fractions were usually of small amounts, which is in accordance with that minor compounds normally are the differences between the volatile substances in the various trees. The new method used has a interesting potential in connection to new progress in chemical separation techniques and better extraction procedures, for finding the chemical compounds responsible for host selection in insects dependent on host volatiles.

Bjørn Åge Tømmerås, Department of Zoology - AVH, University of Trondheim, N-7055 Dragvoll, Norway.

## INTRODUCTION

Most insects probably use several sensory modalities in sequence, or in concert, when finding and accepting a host for feeding, breeding or oviposition (cf. Miller & Strickler 1984). In bark beetles, however, olfaction is considered to be the most important sense for host recognition and acceptance (Birch 1984). The mechanisms by which the pioneer beetles find the host tree are still a matter of debate. Two hypothesis have been extensively discussed; beetles may either detect and select the host by the use of olfactory cues released from the tree or land at random on the tree. After landing, beetles may select or reject the host on the basis of e.g. cues received from feeding (Birch 1984).

Primary attraction has been shown in several species of bark beetles, including the spruce bark beetle, *Ips typographus* (Moeckh 1981). In this species it is furthermore demonstrated that the beetles discriminate between different ages and quality of the trees, and prefer a host of a certain condition (Johann 1986). Whether the insects are using both attractive and repellent olfactory cues

for finding and selecting a proper host remain unclear. Such hypothesis have not been successfully debated (Lanier 1983).

The odours from a possible host are a complex mixture of a lot of different compounds in a specific amount relationship. The question which of these compounds are behaviourally active on the insects, have been tried solved by making chemical extracts of the specific host, using fractions of the extract for behavioural tests or analysing for chemical structure to make synthetic compounds for tests in laboratory and in the field. The results by such methods so far have shown that rather few compounds of the complex mixtures are behaviourally relevant e.g. concerning attraction of elm bark beetles to moribund American elm (Millar et al. 1986) and by Phan-Delegue et al. (1986) concerning the olfactory choices of the honeybee among sunflower aromas.

Another way to find out which of the constituents from the volatiles of the host are of biological relevance is studies of the olfactory system using electrophysiological tech-

niques. In bark beetles (especially the genus *Ips*) studies have revealed numerous receptor cells activated by vapour of bark from host trees (Mustaparta 1979, Tømmerås 1985, Tømmerås & Mustaparta 1987). These cells do not respond to pheromones and the presence of such receptor cells indicates that host odours are significant stimulants for these species of bark beetle.

Already in 1964 Schneider and coworkers reported separate olfactory receptor cells for plant odours and pheromones from a study of single receptor cells in *Antheraea pernyi*. Subsequently, several species from various families and genera have been studied by single cell recording and have demonstrated separate olfactory units for host/food odours and pheromones. In these investigations mainly synthetic compounds have been used as test odours; selected on the basis of prior chemical identification of the constituents of plant and food material. Therefore, it is obvious that the compounds belong to the major

rather than minor components of the volatile substances in a particular plant. As a result numerous minor constituents have not been used as test compounds in previous studies of host plant receptor cells. In the carrot fly, *Psila rosae*, this problem was approached by linking a gas-chromatographic (GC) separation system to the recordings of electroantennogram (EAG) (Guerin et al. 1983). Interestingly, in this study minor constituents of the plant volatiles were found to be the most effective receptor cell stimulants.

Knowing that among bark beetles 30–50% of the identified olfactory receptor cells were strongly activated only by bark vapour, we thought that it was worth trying to identify the effective constituents for these receptor cells by linking the GC-separation system to single cell recordings from cells being activated by natural bark (Tømmerås & Mustaparta 1987). After the separation in the GC-column the fractions reach the detector of the GC and the antenna of the beetle suc-

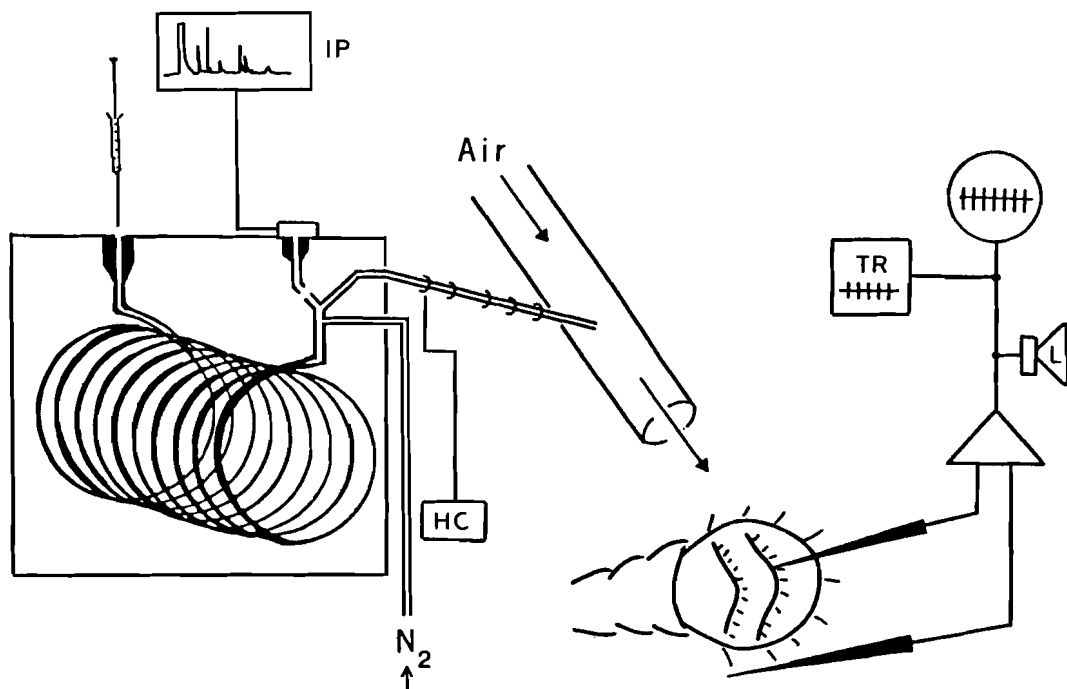


Fig. 1. Diagram of equipment for recording single cell responses to odours applied via the gas-chromatograph (GC) column. Recordings are indicated from olfactory sensilla on the antennal club of bark beetles, using tungsten micro-electrodes. Recording equipment comprises amplifier, audio-amplifier with loudspeaker (L), tape recorder (TR) and oscilloscope. The GC-column is illustrated with a split end for leading the effluent gas equally to the FID-detector and out through the GC-wall. The tube leading gas out of the GC, ends at an air-stream directed onto the antenna. HC, heat control of the effluent gas; IP, integrator and printer; N<sub>2</sub>, make-up gas (after Tømmerås & Mustaparta 1987).

cessively. In this way a simultan recording from both the chemical and the biological detector has been made possible (see Fig. 1). In principle, the method contains the necessary features for solving the question of which constituents of the host volatiles are important for the beetles, and how individual cells receive each compound.

By using this new method considerable amounts of data are achieved from two bark beetle species, *I. typographus* and *Trypodendron lineatum*, while some results are obtained from *Dendroctonus micans*. As can be seen in Tab. 1 where the number of cells responding to the different stimuli sources is summarized, most of the cells responding to natural bark were activated by vapour of both spruce and pine in both species. Furthermore, both species have some olfactory reseptor cells responding exclusively to non-host trees as well, pine and birch. Cells being activated by only spruce bark were only obtained in *I. typographus*. Using the same bark for making extracts by different methods led to the possibility of testing the extracts as stimuli on the same cells stimulated by syrin-

ges. In both species several cells failed to give respons to any extract, indicating that the extraction procedures are not able to catch all of the active compounds from natural bark or the structure of some active compounds have been changed. The next step was to use the same fractions in the separation system of a GC. Again the responses of some cells were lost. Not all of the cells being activated by the whole extract from syringes did respond to any of the fractions when separated in the GC-column. These complications are related to problems previously encountered during analysis of plant odours, and may concern stabilities of the volatiles in the air, low amounts of the particular compounds, absorption in the extraction medium, changes at high temperature in the GC-oven and interaction with the medium in the GC-column. Such problems adhered to a similar study, linking the GC to recording of summated receptor potentials, EAG, in the carrot fly (Guerin et al. 1983). Like in the present bark odour studies, it was shown only a few minor constituents were effective on the antennae. However, while the first analysis showed

Table 1. Number of cells responding to various stimuli from natural bark, bark extracts and fractions of extracts separated by gas chromatograph. Not all the cells responding to natural bark did respond to an extract from the same bark. Nor did all the cells responding to an extract become activated by the separated fractions of the same extract. (Data on *Ips typographus* from Tømmerås & Mustaparta 1987).

Species of host and non-host trees	Number of cells responding to odours from one or two species of host and non-host trees, using three types of stimuli.		
	Vapour of whole bark applied by syringe	Vapour of extracts applied by syringe	Separated fractions applied through GC-column
<i>Ips typographus</i>			
Both spruce and pine	30 a	20	13 b
pine (exclusively)	8	3	2
spruce (exclusively)	2	0	-
birch (exclusively)	11 c	2	0
<i>Trypodendron lineatum</i>			
Both spruce and pine	38	25	11 b
pine (exclusively)	2	0	-
birch (exclusively)	2	0	-

a Ten cells excluded due to recording uncertainties

b Three cells in *I. typographus* and one cell in *T. lineatum* excluded due to unstable recording conditions, making the response unreliable

c Eight cells responded strongly to *exo-brevicomin* also.

three effective fractions, two additional compounds were later found which had initially been lost in the GC-separation system (Städler, pers. comm.). Another explanation for the inefficiency of an extract may be due to a synergistic action by two or more compounds occurring when the receptor is exposed to the whole extract, but absent when each compound is applied separately after GC-treatment. However, existence of synergism on the receptor level has never been shown in insect olfactory systems.

Although it so far has been difficult to find all of the components which activated receptor cells, a lot of cells have shown responses stimulated by fractions separated in the GC-column. In *I. typographus* it always was fractions of small amounts (small peaks in the

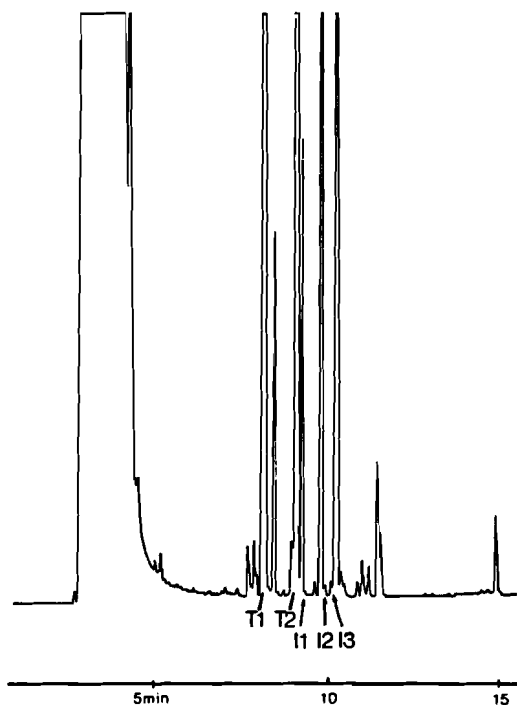


Fig. 2. Showing a chromatogram of a pine extract made by head-space procedure. The fractions marked with arrows, I1, I2 and I3 elicited responses from different olfactory cells in *Ips typographus* while peaks marked with T1 and T2 activated olfactory cells in *Trypodendron lineatum*. Other extracts made from spruce and pine bark by different procedures also contained some of these peaks and in addition other active stimulatory fractions for olfactory receptor cells in both species.

GC-chromatograms) which elicited responses, as example see Fig. 2; peak I1, I2 and I3. Twelve of the 15 cells with GC-responses were activated by two single fractions (I1 and I2; 6 cells each), the large number indicated that these two compounds have a biological meaning to the beetles of this species. The chemical structure of the compounds is not yet established. Concerning *T. lineatum* there were also two fractions (Fig. 2; T1 and T2) which activated most of the cells (8 out of 11), however, here the rule was that both fractions elicited responses on the same cells. These fractions contain  $\alpha$ - and  $\beta$ -pinene and are in large amounts in the extracts. It is difficult to be sure whether the recorded responses were elicited because of the very high concentration of these compounds while the real «key» for these cells were lacking in the tested extracts. Another possibility is that the large peaks were masking smaller peaks which activated the cells. However, this is not to deny that this species in fact can use  $\alpha$ - and  $\beta$ -pinene for orientation. The attractive effect of especially  $\alpha$ -pinene together with own pheromone is well concluded (Bakke 1983) and then this species can diverge from other bark beetle species. *T. lineatum* bores into the wood of the host and should be out of competition from other bark beetles breeding in the bark of the trees.

The results obtained from the bark beetle *D. micans* show the same pattern as in *I. typographus*. The cells are activated by fractions of small amounts, one cell usually by one fraction. If one particular cell were activated by more than one fraction, one small fraction was always most potent (Tømmerås, unpubl.).

## DISCUSSION

Although the new method linking GC-separation to single cell recording so far not was able to detect all active components from bark volatiles, the conclusion must be that rather few constituents of the complex mixtures have biological meaning to the beetles investigated. This make sense considering that most of the compounds present in bark can be found in most tree species, and therefore would be unuseful as orientation cues for searching a proper host. The findings that compounds of small amounts are usually active support this theory. Both in *I. typograph-*



hus and *T. lineatum* cells are obtained responding exclusively to a non-host tree e.g. birch. Such capability can be an evolutionary overhang, however, the possibility for that some compounds from non-host trees are received for biological meaning can not be overlooked. In the choice of breeding material inhibitory input from an unproper tree should be useful for the orientation against a suitable host.

I have discussed the progression obtained about the question which constituents of a host are important for an insect in finding and selecting a host by means of the volatiles. As mentioned above, usually fractions of small amounts (possible exceptions in *T. lineatum*) are active on the olfactory receptor cells. The small amounts cause problems in normal chemical analysis of these compounds. However, in the last years considerable progress has been made making such analysis easier and more certain to perform. The other chemical challenges are in the extraction procedures, additional better methods are not available, making the problem with losing compounds less important. Also in the field of possible changes in the structure of active compounds in the GC-column, the use of different types of columns can minimize the problems of changing structure of interesting compounds in this step.

The new method introduced by linking GC-separation technique to electrophysiological single cell recordings combined with new methods in extraction procedures and GC-separation systems both for analysis and for stimulation of the olfactory receptor cells, will possibly have a big potential in solving which constituents in both host and non-host plants are important for the choice of proper host in insects using host volatiles as the main cue. A breakthrough can give the possibility of manipulating a lot of pest insect species by manipulating the odour of the normal host plant.

## REFERENCES

- Bakke, A. 1983. Dosage response of the ambrosia beetle *Trypodendron lineatum* (Oliver) (Coleoptera, Scolytidae) to semiochemicals. *Z. Angew. Entomol.* 95: 158—161.
- Birch, M. C. 1984. Aggregation in bark beetles, pp. 331—354 in: Bell, W. J. & Cardé, R. T. (eds.) *Chemical ecology of insects*. Chapman and Hall, London.
- Guerin, P. M., Städler, E. & Buser, H. R. 1983. Identification of host plant attractants for the carrot fly, *Psila rosae*. *J. Chem. Ecol.* 9 (7): 843—861.
- Johann, M. 1986. Zur Anlockung des Buchdruckers (*Ips typographus* L.). Die Lockwirkung natürlicher Brutmaterials. *Z. Angew. Entomol.* 101: 332—342.
- Lanier, G. N. 1983. Integration of visual stimuli, host odorants, and pheromones by bark beetles and weevils in locating and colonizing host trees, pp. 161—171 in: Ahmad, S. (ed.) *Herbivorous insects*. Academic Press, New York.
- Millar, J. G., Zhao, C.-H., Lanier, G. N., O'Callaghan, D. P., Griggs, M., West, J. R. & Silverstein, R. M. 1986. Components of moribund american elm trees as attractants to elm bark beetles, *Hylurgopinus rufipes* and *Scolytus multistriatus*. *J. Chem. Ecol.* 12: 583—608.
- Miller, J. R. & Strickler, K. L. 1984. Plant-herbivore relationship, pp. 127—158 in: Bell, W. J. & Cardé, R. T. (eds.) *Chemical ecology of insects*. Chapman and Hall, London.
- Moeckh, H. A. 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* 7: 49—83.
- Mustaparta, H. 1979. Chemoreception in the bark beetles of the genus *Ips*: synergism, inhibition and discrimination of enantiomers, pp. 147—158 in: Ritter, F. J. (ed.) *Chemical ecology: Odor communication in animals*. Elsevier/N. Holland, Amsterdam.
- Phan-Delegue, M. H., Masson, C., Etievant, P. & Asar, M. 1986. Selective choices of the honey bee among sunflower aromas: Studies by combined olfactory conditioning and chemical analysis. *J. Chem. Ecol.* 12: 781—794.
- Schneider, D., Lacher, V. & Kaissling, K. E. 1964. Die Reaktionsweise und das Reaktionsspektrum von Riechzellen bei *Antheraea pernyi* (Lepidoptera: Saturniidae). *Z. Vergl. Physiol.* 48: 632—662.
- Tømmerås, B. Å. 1985. Specialization of the olfactory receptor cells in the bark beetle *Ips typographus* and its predator *Thanasimus formicarius* to bark beetle pheromones and host tree volatiles. *J. Comp. Physiol.* 157: 335—341.
- Tømmerås, B. Å. & Mustaparta, H. 1987. Chemoreception of host volatiles in the bark beetle *Ips typographus*. *J. Comp. Physiol.* 161: 705—710.

Received 17 Sept. 1988



# How does the olfactory system in insects discriminate between odours of own and related species

H. MUSTAPARTA AND T. J. ALMAAS

Mustaparta, H. & Almaas, T. J. 1989. How does the olfactory system in insects discriminate between odours of own and related species. *Fauna norv. Ser. B* 36, 81—86.

Among the various volatiles present in the environment, the insects are able to detect the pheromone blend as well as chemical cues of related species. The mechanism for how the insect olfactory system discriminate pheromones from those produced by related species have been studied both own in respect to receptor cell specificities and central neuron responses. In general the results have shown that pheromones are received by specialist types of cells, transmitting the information to the brain via own axons, labeled for one particular compound. Thus, the pheromone message is a specific ratio of activities in the particular labeled pheromone lines. Odours of related species elicit a different ratio of activity in the same lines or in different lines. This mechanism generally applies to the different effects of pheromone compounds studied so far. The results imply that the membrane receptors are conserved through evolution, resulting in similar cells for the same compound in closely as well as distantly related species. It seems therefore that changes in the olfactory system rather occur in the CNS processing than in the receptors. The CNS studies show a certain integration in the antennal lobe of pheromone information from differently labeled line; as well as maintained separation of pathways to the protocerebrum for the major pheromones and the interspecific inhibitor. The high number of receptor cells and CNS neurons, responding specifically to the major pheromone compounds, favour the component hypothesis that insects are influenced by the various pheromone components in sequences, from long distance attraction by the major component to the use of the whole blend at closer ranges.

H. Mustaparta & T. J. Almaas, Dept. of Zool., University of Trondheim, AVH, N-7055 Dragvoll, Norway.

## INTRODUCTION

Insects have in a very elaborate manner evolved the utilization of chemical signals for finding sex partners, host plants, etc. Partly encouraged by the interest in using such signals (particularly pheromones) in controlling pest species, research on chemical communication in insects has expanded greatly over the last three decades. Chemical analyses of pheromones, as well as physiological and behavioural studies, has resulted in identification of pheromones in numerous insect species. Furthermore, the relatively simple and easily accessible sensory/nervous system, make insects suitable also for basic investigations in olfaction.

Two insect groups of importance are moths and bark beetles. Because of their different biology, it is interesting to compare them in respect to chemical communication and olfactory mechanisms. In the solitary

moth species, the sexual pheromones are produced in the female abdominal gland which is pressed out by the haemolymph and exposed when the females is «calling for males». In the gregarious bark beetle species, the pheromones are produced (either by females or by males) during the boring into the bark. The pheromones are in some cases produced in the beetle intestine from host volatile precursors (Hughes 1973, 1974). The secondary mass attack is then initiated by pheromone attraction of both sexes (aggregation pheromones).

As the research in this field has progressed, it has become evident that pheromones usually consist of several compounds. Furthermore, the ratio between the constituents as well as the configuration of each component are often decisive for the attraction of the species members. The existence of synergistic

effects of the components as well as inhibition (antagonistic effects) was early demonstrated in bark beetles (Silverstein et al. 1966) and subsequently shown to be common both in bark beetles and in moths (Roelofs and Comeau 1971, Roelofs et al 1974, Birch et al 1980). Interspecific interactions are particularly interesting to study in bark beetles, where crowds of beetles, of the same or different species, live together on the same host or in the same area. The use of pheromones of the neighbours for own benefit is one aspect in our studies (Mustaparta 1984). Previous investigations in our laboratory have been focused upon olfactory mechanisms underlying synergistic effect of pheromones on the insect behaviour (Mustaparta et al 1979, 1980), interspecific inhibition (interruption) (Mustaparta et al 1977), interspecific synergism (Tømmerås et al 1984), as well as attractions of predators to prey (Tømmerås and Mustaparta 1985).

### Receptor responses

#### *What is the pheromone message to the brain?*

The ratio between the pheromone constituents is critical for pheromone attraction of the conspecific sex partner in moths as well as for the attraction of both sexes in bark beetles. A problem of interest was therefore, how the information from this particular mixture is received by the olfactory receptor cells located in the insect antennae (Fig. 1). During the last decade, the growing data from electrophysiological investigations of single receptor cells have revealed that pheromone mixtures are received by receptor cells which are each specialized for one particular compound in the blend (cf. Mustaparta 1984). Each cell, responding only to one compound, transmit via its own axon the single compound information to the brain and may therefore be called a «labelled line». Although some contradictory results exist (Payne 1975, Payne et al 1982, O Connel 1975, concerning interaction of pheromone components on the receptor cells), the mechanisms of «labelled line» seem to be general concerning pheromone perception in insects.

Furthermore, the insect antennae contain a certain number of each type of specialist cells; the majority of which are specialized for one or two of the major pheromone components, i.e. the compounds that are produced in largest amounts and seem to be the

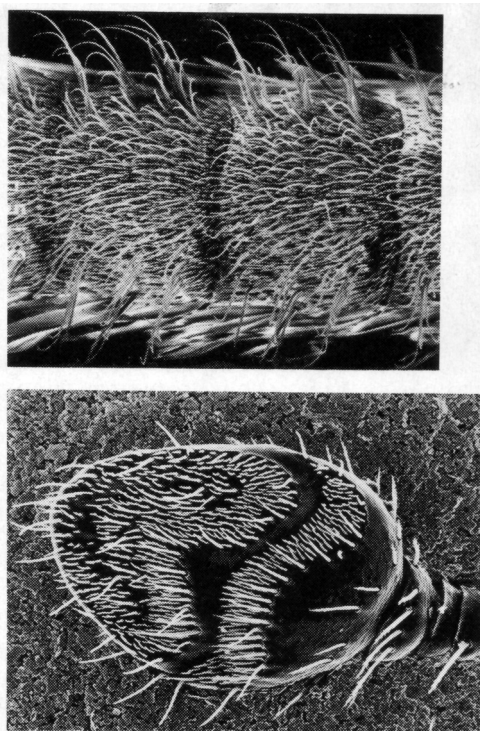


Fig. 1. Scanning electron micrographs of the antennae of A) the Tobacco budworm moth *Heliothis virescens* and B) the bark beetle *Ips typographus*. Pheromone receptor cells in *H. virescens* males are located within the sensilla trichodea (long hairs). In the bark beetle the olfactory sensilla are located both in the two bands as well as on the distal part of the club. Scale bar 100  $\mu\text{m}$ .

most effective on the behaviour (Kaissling 1979, Priesner 1979, 1984, Mustaparta 1979, Almaas and Mustaparta 1988). An alternate hypothesis is that minor components may modulate the receptor cells of the major compounds (O Connel 1975). In a recent study of the tobacco budworm moth *Heliothis virescens* we have tested this hypothesis (Almaas and Mustaparta, unpublished). However, no influence by minor components on the major pheromone cells were found when comparing the responses to the major compound alone and to the mixture of the major and the minor compounds. Furthermore, studies in progress have demonstrated specialist cells for minor constituents (Almaas and Mustaparta, unpublished). The integrated results from our and others studies imply that the pheromone blend is perceived via special-

list types of cells were the proportions of the various types is characteristic for a species. This means that the message from the receptor cells to the brain about the conspecific pheromones consists of a particular ratio between the activities in the pheromone labelled axons.

*The message to the brain about odours of other species.*

Taxonomically related species often use the same compounds as pheromones, however, in a different blend ratio. This means that the message to the brain about own pheromones and the pheromones of the neighbours would differ in respect to the ratio of activities in the respective labelled lines. In principle, this might be sufficient for many species in distinguishing conspecifics from neighbouring species. However, between closely related species, an additional mechanism exists. Here, a particular pheromone component in one species blocks the attraction of the neighbouring species. In early studies it was demonstrated that this inhibition is not due to competitive blocking of the pheromone receptor cells (Mustaparta et al 1977). Instead, the insects have separate cells that are specifically activated by the compound produced by the other species. Thus in this case the brain also get an additional information via activity in particular axons. This additional information may then interact in CNS with the activity in the pheromone pathways, resulting in interruption of the pheromone attraction. This mechanism seem to be an efficient way for isolation between species of the same genus.

In addition to the chemically mediated isolation between species, which is clearly demonstrated both in bark beetles and moths, other interactions by chemical signals might be widely distributed among bark beetles. One observation was that species of different genera have specific receptor cells for the reciprocal genus (Tømmerås and Mustaparta 1985), which was found to be of biological relevance (Tømmerås et al 1984). Thus the pheromone of the reciprocal genus increased the attraction when mixed with own pheromones. It was concluded that species which are not competing may use the reciprocal pheromone to find suitable breeding materials and thus benefit from one another. For this purpose they have evolved particular receptor cells.

Even more surprising was the finding that the predators of bark beetles, being of different families (Cleridae, Rhizophagidae), possess olfactory receptor cells for the prey's pheromones, that are similar to the respective pheromone cells in the prey (Tømmerås and Mustaparta 1985, Tømmerås et al 1984). Both in *Thanasimus formicarius*, being a generalist as well as in *Rhizophagus grandis* being a specialist on bark beetles, the specificities of the olfactory receptor cells could not be distinguished from those of the prey. This implies that the cells of predator and prey possess the same types of membrane receptors.

The integrated results have shown that compounds, produced in an insect group and used by closely or distantly related species, are perceived via the same types of receptor cells which thus seem to be conserved through evolution. What may therefore preferably be changed in evolution is the mechanisms in the CNS processing of information from the olfactory receptor cells.

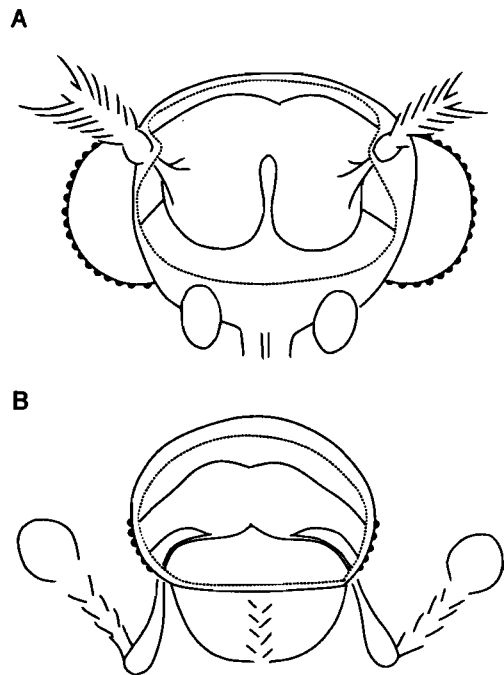


Fig. 2. Drawings, showing the brains of a moth (*H. virescens*) and a bark beetle (*I. typographus*), which are exposed after removing the headcapsule on the frontal side. The antennal nerves entering the antennal lobes are indicated.

## Central neuron responses

**The antennal lobe** The primary axons, forming the antennal nerve, terminate in the antennal lobe which is much more pronounced in moths than in bark beetles (Fig. 2). In the latter, the thin antennal nerve penetrate the lobe which appear at the frontal side of protocerebrum, being anatomically more integrated in this part of the brain. The terminals of the primary axons make connections (synapses) with the secondary antennal lobe (AL) neurons within special structures, glomeruli. Of special interest is one particular glomerulus or glomerulus complex, called macroglomerulus or macroglomerulus complex (MGC), which is present in the male moths (Fig. 3) as well as in males of other species (Jawloski 1954, Boeckh and Boeckh 1979, Sanes et al 1977). Here, all pheromone information is transmitted to the AL neurons, while the other glomeruli are concerning with plant odour information (Matsumoto and Hildebrand 1981). In the antennal lobe are two morphologically distinct types of neurons; one local without axons and widely distributed arborizations in many or all glomeruli, and the other (projection neurons) with one axon projecting in protocerebrum (mushroom bodies and lateral lobe). The latter arborize only in one glomerulus; only those responding to pheromones in MGC. Thus it is

only the projection neuron that carry information from the antennal lobe to higher orders of neurons. While the AL pathways are studied fairly well in some species of moth, similar studies in bark beetles have not yet revealed clear results as concerns special glomeruli for pheromones and host odours. So far the results have shown numerous glomeruli which are small and appear not as distinctly separated as in the moths. It has not yet been recorded from neurons of these small beetle brains. However, it is challenging to find out whether a sexual dimorphism exists in these antennal lobes, whether pheromone and host three volatile pathways are separated, and furthermore how the pheromone information from the specialist receptor cells are sorted out in the bark beetle brains.

In the moth species of *Heliothis*, utilizing multicomponent pheromones which interspecific effects, it has been possible to study the olfactory pathways in the CNS by intracellular recordings combined with Lucifer Yellow staining (Christensens et al 1988). Furthermore, the extensive anatomical and physiological studies of the AL in the sphinx moth *Manduca sexta* (Christensen and Hildebrand 1987) has formed the basis for the interpretations of the results in *Heliothis*. In the studies of the antennal lobes of *Heliothis* it has been focused upon how the neurons discriminate the pheromone blend of conspecifics and related females, which include the mechanism for behavioural synergism and inhibition.

The intracellular recordings from pheromone projection neurons in the AL of both *H. zea* and *H. virescens* showed that numerous neurons were almost equally activated by the fresh odour of female glands from own and related species. Since many of these cells were not tested for single compounds, two main interpretations can be given. It is possible that all these neurons were triggered by the major pheromone compound which is the same in both species. Another explanation is that these neurons are generally triggered by the pheromones of related species (blend generalists). The two explanations implies respectively that there is either a convergence of only the major pheromone labelled lines into these AL neuron or that all types of pheromone cells converge on these neurons. Other neurons were tested for single syntetic pheromone compounds as well as the mixture

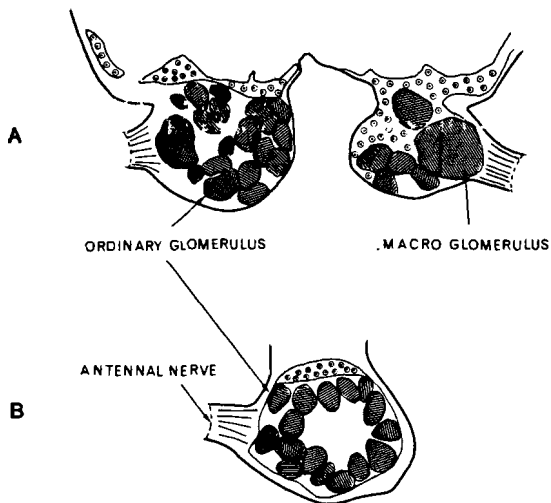


Fig. 3. Drawings from sections of the *H. virescens* brain, demonstrating the sexual dimorphism of the antennal lobes in females and males. The macroglomerulus is present only in males, at the entrance of the antennal nerve.

of compounds in the natural ratio (pheromone blend) produced by the two respective species. These results demonstrated the presence of neurons distinguishing the two blends (pheromone specialists). Furthermore the results of single component tests showed that numerous AL cells were triggered by the major pheromone components. Similar findings have previously been found in *Antheraea* (Boeckh and Boeckh 1979). Some of them responded specifically to the major compound, while others were also excited by the secondary constituent. It was occasionally found neurons that were primarily excited by the secondary component with weaker response to the major constituent. Synergistic effect by some pheromone constituents were also found in a few cells. Furthermore, particular cells in *H. zea* were selectively activated by the compound produced by *H. virescens* and causing interruption of the pheromone attraction in *H. zea*. No AL neurons activated by pheromones, were clearly blocked when this inhibitor was added. The results from these studies of the antennal lobe neurons have led to the conclusion that the information from the differently labelled lines are partly integrated in the AL neurons, resulting in blend generalist and blend specialists (Christensen et al, 1988). In addition information both from the major pheromone compounds and the interspecific inhibitor, leave the antennal lobe through separate pathways. This implies that a further important processing of the information take place in protocerebrum. Similar results was demonstrated in *Manduca sexta* (Christensen and Hildebrand 1987).

The sensitivity of the AL neurons are much higher than that of the receptor cells, and can be explained by the strong convergence from numerous (tens of thousands) receptor cells on fewer (ca. 250) AL neurons. It is thus possible that the convergence, taking place in the AL, to a large extent is concerned with convergence of similarly labeled lines. In addition, some AL neurons seem clearly to carry information about the whole pheromone blend.

These results are interesting in connection with the two main views, the component hypothesis and the blend hypothesis (cf. Linn et al 1987), about species-specific influence of pheromone blends. According to the component hypothesis, the major pheromone compounds play the role as long-distant attrac-

tant, whereas the minor constituents are important at short ranges, mediating particular behaviours as landing and mating. In accordance with this are the electrophysiological results that the majority of the pheromone pathways (receptor cells and AL neurons) are addicted to the long range pheromone information. Furthermore, the fewer olfactory pathways mediating the short range pheromone information may then influence the attraction behaviour to finally result in mating. In *H. virescens* it is possible that two compounds are involved in the long-distance attraction.

The blend hypothesis states that the complete blend is necessary to elicit any pheromone orientation behaviour at long or close distances. The electrophysiological results do not exclude this hypothesis. It is still possible that integration in protocerebrum might result in numerous blend specialists. However, because of the dominating number of pheromone pathways for the major component information, the component hypothesis seems favourable.

## REFERENCES

- Almaas, T. J. & Mustaparta, H. 1988. Pheromone reception in the tobacco bud worm moth *Heliothis virescens* (Submitted).
- Almaas, T. J. & Mustaparta, H. Unpublished.
- Birch, M. C., Light, D. M., Wood, D. L., Browne, L. E., Silverstein, R. M., Bergot, B. J., Ohloff, G., West, J. R., & Young, J. C. 1980. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. *J. Chem. Ecol.* 6: 703—717.
- Boeckh, J., Boeckh, V. 1979. Threshold and odour specificity of pheromone-sensitive neurons in the Deutocerebrum of *Antheraea pernyi* and *A. polyphemus* (Saturniidae). *J. Comp. Phys.* 132: 235—242.
- Christensen, T. A., & Hildebrand, J. 1987. Male-specific, sex pheromone-selective projection neurons in the antennal lobes of the moth *Manduca sexta*. *J. Comp. Phys. A* 160: 553—569.
- Christensen, T. A., Mustaparta, H., & Hildebrand, J. 1988. Discrimination of sex pheromone blends in the olfactory system of the moth. *Chemical Senses* (in press).
- Hughes, P. R. 1973. *Dendroctonus*: Production of pheromones and related compounds in response to host monoterpenes. *Z. Angew. Entomol.* 73: 294—312.
- Hughes, P. R. 1974. Myrcene: A precursor of pheromones in *Ips* beetles. *J. Insect Physiol.* 20: 1271—1275.

- Jawłowski, H. 1954. Über die struktur des Gehirns bei Saltatoria. *Ann. Univ. Curie-Skłodowska, Lublin* 8C, 403—434.
- Kaissling, K.-E. 1979. Recognition of pheromones by moths especially in Saturniids and *Bombyx mori*. In: Ritter FJ (ed) *Chemical ecology: Odour communication in animals*. Elsevier/North Holland, Amsterdam, pp 43—56.
- Linn, C. E., Campbell, M. G., & Roelofs, W. L. 1987. Pheromone components and active spaces: what do moths smell and were do they smell it? *Science* 237: 650—652.
- Matsumoto, S. G., & Hildebrand, J. 1981. Olfactory mechanism in the moth *Manduca sexta*: response characteristics and morphology of central neurons in the antennal lobes. *Proc. R. Soc. B* 213, 419—428.
- Mustaparta, H. 1979. Chemoreception in bark beetles of the genus *Ips*: synergism, inhibition and discrimination of enantiomers. In: Ritter, F. J. (ed.); *Chemical ecology: Odour communication in animals*. Elsevier/North Holland, Amsterdam, pp. 147—158.
- Mustaparta, H. 1984. Olfactory. In: Bell W. A., & Carde, R. T. (eds.). *Chemical ecology in insects*. Chapman and Hall, pp 37—70.
- Mustaparta, H., Angst, M. E., & Lanier, G. N. 1977. Responses in single receptor cells in the pine engraver beetle *Ips pini* (Say) Coleoptera: Scolytidae) to its aggregation pheromone ipsdienol and the aggregation inhibitor, ipsenol. *J. Comp. Physiol.* 121: 343—347.
- Mustaparta, H., Angst, M. E., & Lanier, G. N. 1979. Specialization of olfactory cells to insect- and host produced volatiles in the bark beetle *Ips pini* (Say) *J. Chem. Ecol.* 5. 109—123.
- Mustaparta, H., Angst, M. E. & Lanier, G. N. 1980. Receptor discrimination of enantiomers of the aggregation pheromone ipsdienol, in two species of *Ips*. *J. Chem. Ecol.* 6: 689—701.
- O Connell, R. J. 1975. Olfactory receptor responses to sex pheromone components in the red-banded leafroller moth. *J. Gen. Physiol.* 65: 179—205.
- Payne, T. L. 1975. Bark beetle olfaction III. Antennal olfactory responsiveness of *Dendroctonus frontalis*, Zimmermann and *D. brevicomis*, Le Conte (Coleoptera: Scolytidae) to aggregation pheromones and host tree terpenes hydrocarbons. *J. Chem. Ecol.* 1: 233—242.
- Payne, T. L., Richerson, J. V., Dickens, J. C., Berisford, C. W., Hedden, R. L., Mori, K., Vite, J. P., & Blum, M. S. 1982. Southern pine beetle: olfactory receptor and behaviour discrimination of enantiomers of the attractant pheromone frontalin. *J. Chem. Ecol.* 8: 873—881.
- Priesner, E. 1979. Specificity studies on pheromone receptors of noctuid and tortricid lepidoptera. In: Ritter F. J. (ed.) *Chemical ecology: Odour communication in animals*. Elsevier/North Holland, Amsterdam, pp 57—71.
- Priesner, E. 1986. Correlating sensory and behavioural responses in multichemical pheromone systems of lepidoptera. In: Payne, T. L., Birch, M. C., & Kennedy, C. E. J. (eds.): *Mechanisms in insect olfaction*. Oxford University Press, pp 225—233.
- Roelofs, W. L., & Comeau, A. 1971. Sex pheromone perception: synergists and inhibitors for the red-banded leaf roller attractant. *J. Insect Physiol.* 17: 435—448.
- Roelofs, W. L., Hill, A. S., Carde, R. T., & Baker, T. C. 1974. Two sex pheromone components of the tobacco budworm moth, *Heliothis virescens*. *Life Sciences* 14: 1555—1562.
- Sanes, J., Prescott, D. J., & Hildebrand, J. 1977. Cholinergic neurochemical development of normal and deafferented antennal lobes during metamorphosis of the moth, *Manduca sexta*. *Brain Res.* 199: 389—402.
- Silverstein, R. M., Rodin, J. O., & Wood, D. L. 1966. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* 154: 509—510.
- Tømmerås, B. Å., Mustaparta, H., & Gregoire, J.-Cl. 1984. Receptor cells in *Ips typographus* and *Dendroctonus micans* specific to pheromones of the reciprocal genus. *J. Chem. Ecol.* 10: 759—769.
- Tømmerås, B. Å., & Mustaparta, H. 1985. Olfactory receptor cells of *Thanassimus formicarius* specialized to single prey pheromone compounds. *Naturwiss* 72: 74—75.



## ABSTRACTS

### *Borrelia burgdorferi* i skogflått *Ixodes ricinus* i Norge

REIDAR MEHL, TOVE BJERKNES, PER SANDVEN OG BODVAR VANDVIK

Mehl, R., Bjerknæs, T., Sandven, P. & Vandvik, B. 1989. *Borrelia burgdorferi* in the tick *Ixodes ricinus* in Norway. *Fauna norv. Ser. B* 36, 87.

A short review is given of tick borne borrelioses in man. In Norway this disease is reported from the whole distribution range of the tick *Ixodes ricinus*. Preliminary results indicate that the prevalence of *Borrelia burgdorferi* in tick nymphs is 20—30% and 40—60% in adults *I. ricinus*. *Borrelia* was not found in larvae. *Borrelia*-like spirochets were also found in the tabanid fly *Haematopota pluvialis*. *B. burgdorferi* was isolated five times from ticks from different locations and from one wood mouse *Apodemus sylvaticus*.

I Norge overfører skogflåtten *Ixodes ricinus* (L.) de viktige husdyrsykdommene piroplasmose hos kyr og sjodogg hos sau. Piroplasmose skyldes den malariaparasitt-lignende hemosporidien *Babesia divergens* og sjodogg skyldes den lille rickettsiabakterien *Ehrlichia phagocytophila*.

Man har lenge visst at skogflåtten også overførte sykdommer til mennesker her i landet, både hudsykdommer og sykdommer i nervesystemet. Hvilke mikroorganismer som forårsaket sykdommene var ukjent.

I forbindelse med en epidemi av en flåttoverført sykdom på østkysten av USA i 1975 ble det satt igang undersøkelser for å finne mikroorganismen som flåtten overførte. I årene 1981 til 1983 lyktes det. Det var en bakterie av ordenen spirochæter som ble isolert både fra pasienter og flåtten *Ixodes dammini*. I samme periode ble bakterien også funnet i *Ixodes pacificus* på vestkysten av USA og i *I. ricinus* i Europa. Bakterien ble gitt navnet *Borrelia burgdorferi* etter oppdageren.

Det ble nå klart at denne spirochæten var ansvarlig for flere tidligere beskrevne sykdommer: Erythema chronicum migrans, Acrodermatitis chronica atrophicans, Lymphadenitis benigna cutis, Bannwarths syndrom og Lyme sykdom. Dette er sykdommer med infeksjoner og reaksjoner i hud, ledd, hjerte og nervesystem. En person kan ha sykdom i ett eller flere av disse organer, og en

tilstand kan gå over i en annen. Det er alle grader av sykdommen fra et kløende utslett til alvorlige tilfeller med lammelser, deformering av ledd, store smerter og invaliditet.

Flere publikasjoner de siste årene i *Tidsskrift for den Norske Lægeforening* viser at sykdommen er vanlig og følger flåttens utbredelsesområde i Norge. I 1986 startet vi feltundersøkelser over *Borrelia*-økologi hvor hovedformålene var å påvise bakterien, utrede infeksjonshyppigheten i vektorer og vertsdyr, og isolere bakterien i laboratoriet (Mehl, Sandven & Braathen 1987). Til påvisning av *Borrelia* i flått brukte vi mikroskopering av tarminnhold med fasekontrast-utrustning ved 500x forstørrelse. Ved isoleringsforsøkene ble det brukt metoder og medier som beskrevet fra USA.

De foreløbige resultatene tyder på at det er vanlig at 20—30% av nymfene og 40—60% av de voksne *I. ricinus* er infiserte med spirochæten både på Vestlandet, Sørlandet og Østlandet. Det ble ikke funnet spirochæter i larver. Vi har lyktes å få isolert bakterien i laboratoriekultur fra fem flått fra forskjellige lokaliteter og en skogmus *Apodemus sylvaticus*.

Det ble også funnet *Borrelia burgdorferi*-lignende spirochæter i klegg av arten *Haematopota pluvialis* (L.). I USA er slike spirochæter funnet både i klegg og stikkmygg av flere arter (Magnarelli, Anderson & Barbour 1986), men det er ikke registrert i Europa tidligere. Det er uvisst om disse insektene kan overføre bakterien til mennesker.

## LITTERATUR

- Magnarelli, L. A., Anderson, J. F. & Barbour, A. G. 1986. The etiologic agent of Lyme disease in deer flies, horse flies, and mosquitoes. *J. Infect. Dis.* 154: 355—358.
- Mehl, R., Sandven, P. & Braathen, L. R. 1987. Skogflåtten *Ixodes ricinus*. Vektor for spirochætose. *Tidsskr. Nor. Lægeforen.* 107 (19-20-21); 1642—1644.

Received 15 Nov. 1988

Reidar Mehl, Tove Bjerknæs og Per Sandven, Statens institutt for folkehelse, 0462 Oslo 4, Norway. Bodvar Vandvik, Neurologisk avdeling, Rikshospitalet, Oslo 1, Norway.

**Water balance and osmotic regulation in the East African tenebrionid beetle *Rhytinota praelonga***

RAGNAR BJERKE, ROLF LUNDHEIM, JAN OVE REIN, JOHN ALEXANDER STRØMME AND KARL ERIK ZACHARIASSEN

Bjerke, R., Lundheim, R., Rein, J. O., Strømme, J. A. & Zachariassen, K. E. 1989. Water balance and osmotic regulation in the East African tenebrionid beetle *Rhytinota praelonga*. *Fauna norv. Ser. B* 36, 88.

The water balance and osmotic regulation of the Tenebrionid *Rhytinota praelonga* from dry areas in Kenya were investigated. *R. praelonga* has a restrictive water balance which makes it possible for the beetles to survive in dry areas for long periods without a dietary water intake. The beetles survived for 2 1/2 months in the laboratory without water and food, at 20°C inside a desiccator, where the relative air humidity was kept at 0–5%.

The beetles lost up to 42% of their body weight before they died. During the experimental dehydration, the beetles displayed no osmotic regulation. The extracellular concentrations of sodium and the free amino acids, were regulated.

Ragnar Bjerke, Rolf Lundheim, Jan Ove Rein, John Alexander Strømme and Karl Erik Zachariassen, University of Trondheim, Department of Zoology, N-7055 Dragvoll, Norway.

Received 12 Oct. 1988

**The distribution and habitat choice of the family Pythidae in Sweden**

ROGER B. PETTERSSON

Pettersson, R. B. 1989. The distribution and habitat choice of the family Pythidae in Sweden. *Fauna norv. Ser. B* 36, 88.

The tree-living beetles of the family Pythidae are represented by three species in Europe. The present distribution shows two patterns; the common *Pytho depressus* is present in all of Sweden, whereas *P. kolwensis* and *P. abieticola* are found only in the northern parts. The latter species are restricted to spruce, only *P. depressus* can use both pine and spruce for its development. According to the core species hypothesis by Ilka Hanski (1983) I suggest that *P. depressus* is a core species and the other two satellite species. This may explain the distribution and difference in abundance between the species.

The absence of *P. kolwensis* and *P. abieticola* in the southern part of Sweden is probably a result of the distribution of spruce forests. The distribution between spruce forests and these two tree-living species of beetles shows a striking resemblance. It is harder to explain why these species are less common, more restricted to nature forests, and more patchily distributed in comparison with *P. depressus*. The possibility for *P. depressus* to use other tree species than spruce as food, gives it an advantage compared to the other two species. In years when there are few or no suitable spruce logs, *P. depressus* can survive in a forest area on pine logs or dead, standing pines. Therefore it can colonize the habitat of spruce logs faster than the other two species, and maintain a more or less stable population, even in areas where the food resource are so limited that the other two species can not survive.

Roger B. Pettersson, Dept. of Wildlife Ecology, The Faculty of Forestry, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden.

Received 28 May 1988

***Parnassius mnemosyne* ssp. *argiope* (Lep.) in Blekinge 1984–1988**

OLLE HAMMARSTEDT

Hammarstedt, O. 1989. *Parnassius mnemosyne* ssp. *argiope* (Lep.) in Blekinge 1984–1988. *Fauna norv. Ser. B* 36, 88.

*Parnassius mnemosyne* ssp. *argiope* has been studied in Blekinge, SE Sweden, 1984–1988. The fate of about ten small to very small populations has been followed by marking-recapture technique. At two managed sites, the populations have increased in number, while at unmanaged sites, population numbers have fluctuated. Four very small colonies have gone extinct. One reintroduction at an old site has been successful. Oviposition behaviour studies have shown that the majority of eggs are attached to some kind of dead organic material, low in the vegetation, often in the edges of bushes where most of the foodplants are growing. Dispersal and migrations have been observed to occur more frequently in sunny and warm years, as in 1986, when the majority of stated migrations took place. Mating success, indicated by the frequency of sphragis put on to the female by the male copulation, has been «normal» only in the two largest colonies. Predation of adult individuals was studied only occasionally. The minimum amount of foodplant needed to support a very small population was found to be 3 m<sup>2</sup> *Corydalis* spp., if growing in a suitable habitat. There are

localities of *Corydalis* with an area of more than 20 m<sup>2</sup> of foodplants, but without any butterflies.

Olle Hammerstedt, Svärmarvägen 28, S-240 17 Söndra Sundby, Sweden.

Received 19 July 1988.

### Phenological variability and distribution of Fennoscandian carabid beetles

DAGFINN REFSETH

Refseth, D. 1989. Phenological variability and distribution of Fennoscandian carabid beetles. *Fauna norv. Ser. B* 36, 89.

The life cycle patterns of 10 carabid species of western and northern Europe were found to vary considerably within the species' geographical ranges. The times of breeding and of adult emergence are seasonally displaced in accordance with variations in the initial and final dates of the growing season. Such a displacement is required if the larvae are to attain optimal conditions for feeding and growth also in areas with cool climates.

Eventually the growing season becomes too short for the life cycle to be completed in one year, and further extension of the range may be prohibited. However, in some species climatic adaptation has involved a shift from univoltine to semivoltine life cycles, resulting in an increased dispersability. Widely distributed species may therefore consist of both univoltine autumn-breeding populations and semivoltine spring-breeding populations. In northern and alpine areas semivoltinism seems to be an optimal strategy. In any case the geographical ranges of the species seem to be closely associated with some critical length of the growing season. Apparently some species also have a potential of further dispersal in Fennoscandia.

Dagfinn Refseth, Department of Zoology, The University of Trondheim, N-7055 Dragvoll, Norway.

Received 11 Nov. 1988

### Vingframkantens chaetotaxi hos Syrphidae

WALTER HACKMAN

Hackman, W. 1989. Vingframkantens chaetotaxi hos Syrphidae. *Fauna norv. Ser. B* 36, 89.

I en tidigare undersökning av costal chaetotaxi inom Diptera i allmänhet (Hackman, W. & Väisänen, R. 1985: *Ann. Zool. Fenn.* 22) behandlades

även ett antal arter bland blomflugorna. Härvid konstaterades behåringstyperna A<sub>1</sub> (homomorf, oregelbunden fördelning), B<sub>1</sub> (homomorf, 2-radig), samt intermediära typer mellan A<sub>1</sub> och B<sub>1</sub>. I en mer detaljerad undersökning av rikare material av Syrphidae (Hackman, W. & Hippa, H., ej ännu publicerad), beaktades även costalnervens basala avsnitt, av Séguy benämnd «epalette» och särskilt tydligt avgränsad hos Syrphidae. Epålattens behåring uppvisar tvenne typer, bägge heteromorpha, den ena (X) med mer eller mindre jämnt fördelade borst på den mediana ytan, den andra (Y) med en bred submedian srimma utan macrotrichia. Resultaten av undersökningen bekräftade tidigare slutsatser att en övergång från A<sub>1</sub> till B<sub>1</sub> tydligt skett på flere utvecklingslinjer inom familjen. Inom Syrphinae synes typen B<sub>1</sub> höra till grundplanen, men en trend med avsnitt av oregelbunden behåring proximalt (*Eriosoma*, *Leucozona*, *Didea* m.f.) förekommer och leder över till *Chrysotoxum* som även på andra grunder kan placeras inom *Syrphini*. Microdentinae ansluter sig i fråga om costal chaetotaxi närmare till Eristalinae (= Milesiinae), men en specialkaraktär för gruppen (undantag: *Argentinomyia*) utgör att epålätten har ett skarpt ventralhorn. Inom *Milesiini* anträffas allt från A<sub>1</sub> till B<sub>1</sub>. I några triber av Eristalinae finner man hos genera och arter med typen B<sub>1</sub> i det distala avsnittet av costa att den ventrala raden närmar sig den dorsala och försvagas. Inom *Volucellini* och *Cheilosini* dominerar typen A<sub>1</sub> i åtminstone något längre avsnitt. Den costala chaetotaxin hos Syrphidae uppvisar mycket parallelism och man måste vara mycket försiktig med slutsatser beträffande tribernas fylogenetiska sammanhang.

Walter Hackman, Johannesvägen 2 B 10, SF-11020 Helsingfors 12, Finland.

Received 25 May 1988

### Populationsstruktur och genetisk differentiering av subpopulationer hos *Formica truncorum*

LISELOTTE SUNDSTRÖM

Sundström, L. 1989. Populationsstruktur och genetisk differentiering av subpopulationer hos *Formica truncorum*. *Fauna norv. Ser. B* 36, 89.

Polydomi och polygyni förekommer allmänt hos stackmyror av släktet *Formica*. Denna polygyni förefaller strida emot kinselektionens principer, genom att graden av släktskap inom en koloni sjunker från det höga värde som betingas av Hymenopterernas haplodiploidi. *Formica truncorum* som det förestående arbetet berör uppvisar bägge

typerna av kolonier. Arten förekommer allmänt på öar i den finska skärgården, varvid 'spatiellt skilda subpopulationer bildas.

Genetiska studier kan alltså utföras på två plan: dels kan man studera en arts spridningsekologi utgående från en genetisk differentiering av spatiellt skilda subpopulationer, dels kan man studera den sociala organisationen, som reflekteras av släktskapsförhållande inom kolonier och mellan närliggande kolonier.

Provar från både mono- och polydoma kolonier insamlades längs hela skärgårdsregionen från 5 separata ögrupper, samt från en population på fastlandet. Fyra olika polymorfa enzymer analyserades elektroforetiskt från arbetare i alle kolonier. Dessutom analyserades avkomma från enskilda gamla drottningar hållna i kultur för att kontrollera antalet parningar.

Resultaten av denna analys ger vid handen att det finns dels monodoma monogyna, dels polydoma polygyna nästen. Mycket få av de monodoma nästena var polygyna. Denna avsaknad av mellanstadier kunde tyda på avvikande kolonistrategier hos olika typer av kolonier hos *Formica truncorum*. Vad som styr valet av strategi är dock fortfarande oklart. Hos de polygyna nästena varierar graden av släktskap mellan  $B = 0.13$  och  $0.44$ , där  $B$  är regressions-koefficienten som uttrycker den genotypiska korrelationen mellan individer i samma näste. Resultaten från kulturerna tyder på att 20% av drottningarna parat sig två gånger, detta ger i medeltal 1.2 parningar per drottning. Med beaktande av dessa resultat kan antalet obesläktade drottningar per näste uppskattas till 1.5—4.8 ifall dessa parat sig i medeltal 1.2 gånger. Eftersom man vet att det kan finnas inomot 100 drottningar inom et polygynt näste, skulle detta tyda på att dessa är nära besläktade med varandra, troligen syskon.

Den gentiska differentieringen uttryckt med Wrights  $F$ -koefficienter baserade på graden av heterozygoti inom subpopulationerna, visar ingen signifikant differentiering mellan subpopulationerna. Det finns alltså en tillräcklig migration för att hindra en differentiering av allelfrekvenserna i subpopulationerna.

Liselotte Sundström, Helsingfors Universitet, Zoologisk institutt, N. Järnvägsgt. 13, SF-00100 Helsingfors, Finland.

Received 1 June 1988

## Nasjonale meldinger om videreføring av det entomologiske vernearbeidet i Norden i forhold til den nordiske rapporten av 1988

### Entomologisk fredningsarbejde i Danmark

JENS BÖCHER, Zoologisk Museum, København

I 1986 fik Entomologisk Fredningsudvalg, der repræsenterer samtlige 6 entomologiske foreninger i Danmark, en ny struktur. Det blev udvidet til 24 medlemmer, der bor nogenlunde jævnt fordelt over landet. Samtidig repræsenterer de så forskellige interesseområder, at insektsystemet er godt dækket. Udvalget mødes en gang årligt. En bestyrelse på tre medlemmer tager sig af de løbende sager. Bestyrelsen støtter sig til et forretningsudvalg, der foruden bestyrelsen omfatter 4 erfarne medlemmer af fredningsudvalget. Siden 1987 udsender fredningsudvalget et internt meddelelsesblad, «Bladloppen».

I de seneste år har Entomologisk Fredningsudvalgs aktiviteter været i hastig vækst, utvivlsomt i forbindelse med en stadig mere udbredt erkendelse af, hvor betydningsfuld en del af naturen, insekterne utgør. Dette er senest kommet til udtryk igennem Europarådets, og i Danmark Skov- og Naturstyrelsens forslag om fredning af en række invertebrater, hovedsagelig insekter.

Entomologisk Fredningsudvalg bliver i stigende omfang involveret som konsulent og i besigtigelser vedrørende fredningssager, og i samarbejde med Skov- og Naturstyrelsen har vi rådgivet i forbindelse med revisioner af driftsplanerne for statskovene.

Af større projekter indenfor de sidste par år skal nævnes:

1. Udarbejdelse af en oversigt over entomologisk sårbare/bevaringsværdige naturtyper i Danmark.
2. Arbejde i projektgruppen vedrørende de entomologiske interesser i gamle træer og naturskov.
3. Udarbejdelse af rapport om insektlokaliteter i Hovedstadsområdet.
4. Udredning af metodik vedrørende overvågning af insekter og deres levesteder.
5. Arbejde i udvalget vedrørende truede dyr og planter i Danmark («røde lister») under Skov- og Naturstyrelsen.
6. Forarbejde til opbygningen af en database omfattende alle oplysninger om lokalt insektliv i Danmark, hovedsagelig baseret på publicerede faunalister etc.

## Entomologisk naturvernarbeid i Norge

SIGMUND HÅGVAR, NISK, ÅS OG KAARE  
AAGAARD, NINA, Trondheim

Vernearbeidet i Norge befinner seg fremdeles på utredningsstadiet. Det er i 1987 utarbeidet flere rapporter om sjeldne eller truede insekter i Norge. De mindre insektordnene er behandlet i del I av en «rød-data» bok serie. En vurdering av sjeldne blomsterfluer er under arbeid. Verneverdige øyestikkerlokaliteter i Trøndelag og på Sørøst-landet er undersøkt. Sommerfuglerundersøkelser med tanke på vern er foretatt i kystområder i Østfold og Vestfold, dessuten på de kalkrike øyene i Oslo-fjordene og i reservater i Aust-Agder.

Norsk Entomologisk Forening (NEF) har uttalt seg om gode insektlokaliteter i forbindelse med en oversikt over «grønne» områder rundt Oslo, og støttet et forslag om fredning av et verdifullt våtmarksområde (Redalsvann, Aust-Agder). Statens naturvernråd har bedt Miljøverndepartementet om å verne et område i Finnmark med mange nordlige Lepidoptera som naturreservat. NEF har også bedt Direktoratet for Naturforvaltning å ta i bruk naturvernloven for fredning av godt dokumenterte insektlokaliteter. Direktoratet har til nå ikke villet gjøre dette, men henviser i stedet til de lokale myndigheter (fylkesmannen) for andre typer vern ved informasjon etc.

NEF er ikke tilfreds med dette og kan bare beklage at Norge fremdeles ikke har noen vernete områder hvor insektfaunen har vært en viktig del av motivasjonen for vernet.

NEF har også støttet initiativet fra Europarådet om vern av verdifulle saprolytiske invertebrater og deres biotoper. Det ble på det nordiske entomologmøtet ikke lagt frem noe forslag om nye resolusjoner. Det praktiske, målrettede vernearbeidet prioriteres i tiden fremover.

## Entomologisk fredningsarbeid i Sverige

Den nordiske rapporten om vern av insektfaunaen av 1988 er såvidt ajour for Sverige at tilleggsopplysninger ikke er nødvendig.

## Skydd av insekter i Finland; Tillägg t.o.n. 1988

KAURI MIKKOLA och HANS SILFVERBERG,  
Zoologisk Museet, Helsingfors Universitet

### 1. Kommentarer till översikten 1986

1.1. *Runsala* (fi. *Ruissalo*) i Åbo. Officiell fredning kom år 1983, då *Runsala* ekskog på 55.8 ha och skogen i Marjaniemi på 29.0 ha fredades. *Runsala* har en rik ekskogsfauna, bland fjärilar kan nämnas *Ennomos erosarius*, *Amphipyra berbera* och *Catocala promissa*, bland skalbaggar *Ca-*

*losoma inquisitor*, *Dendroxena quadrimaculata*, *Osmoderma eremita*, *Pentaphyllus testaceus*, *Mesosa myops* och *Orsodacne cerasi*. För många skalbaggar är *Runsala* den enda, eller åtminstone den viktigaste fyndorten i Finland.

1.2. *Lenholm* i Pargas. 25.5 ha ekskog har nu fredats, 2.2 ha av denna har staten inköpt.

### 2. Ytterligare skyddsåtgärder där insekterna spelar väsentlig roll

2.1. *Katrinedal* (fi. *Katariinanlaakso*) i Åbo; Åbo och Björneborgs län. 17.1 ha ekskog på en sydsluttning fredades 1983. Här har bl.a. *Mesosa myops* påträffats.

2.2. *Pomponrahka* i Åbo; Åbo och Björneborgs län. En myr på 77.8 ha, känd för sin rika fjärlifauna, fredades år 1983.

2.3. *Harparskog Storträsket* i Tenala; nylands län. Ett eutroft kärr, där bl.a. mätararten *Scopula corvivalaria* har sin enda kända fasta förekomst i Finland. Fredades 1987.

2.4. *Svarta backen – Borgarstrandviken* (fi. *Mustavuori – Porvarinlahti*) i Helsingfors; Nylands län. Ett lund- och vassområde på 36.0 ha, av fjärilar förekommer här bl.a. *Apeira syringaria*, *Eupithecia selinata* och *Senta flammea*. Fredades 1987.

2.5. *Hirvihaara* i Mäntsälä; Nylands län. Ett skogsområde på ca. 30 ha har köpts av staten och skall fredas, här har noterats flere urskogsskalbaggar, bl.a. *Liodopria serricornis*, *Cucujus cinnabarinus* och *Leptura thoracica*.

2.6. *Omenapuumaa* i Raumo; Åbo och Björneborgs län. Ett lundområde på 111.8 ha, med förekomst av bl.a. *Parnassius mnemosyne*. Fredat år 1978.

2.7. *Kitkanniemi* i Kuusamo; Uleåborgs län. Ett urskogsområde på 5900 ha, som förenades med Oulanka nationalpark hösten 1988. Vid inventeringen av området har bl.a. nattflyn, skalbaggar och svampmyggor beaktats.

2.8. *Fjällen Saana och Annjalonji* i Enontekis, Lapplands län. Två dolomitområden på 165 resp. 175 ha, vilka fredades 15.6.1988, särskild på grund av sin fjärlifauna. På det förre flygor t.ex. *Pyrgys andromedae*, *Agriades glandon* och *Symphistis zetterstedtii*, på det senare *Hesperia comma catena* och *Entephria flavicinctata*.

### 3. Åtgärder av administrativ natur

3.1 *Betänkande avgivet av kommissionen för skydd av hotade djur och växter*. Betänkandets

allmänna del har utkommit på svenska (1986, ISBN 951-46-7897-4, 123 ss.) och på engelska (1987, ISBN 951-46-7961-X, 82 ss.).

3.2. *Skyddsprogrammen.* Av sådana skyddsprogram som blivit godkända eller är under arbete innehåller speciellt basprogrammet för myrskydd (godkänt av statsrådet 1979 och 1981) och lundskyddsprogrammet (blir troligen godkänt 1989) områden som är viktiga för skyddet av insekter.

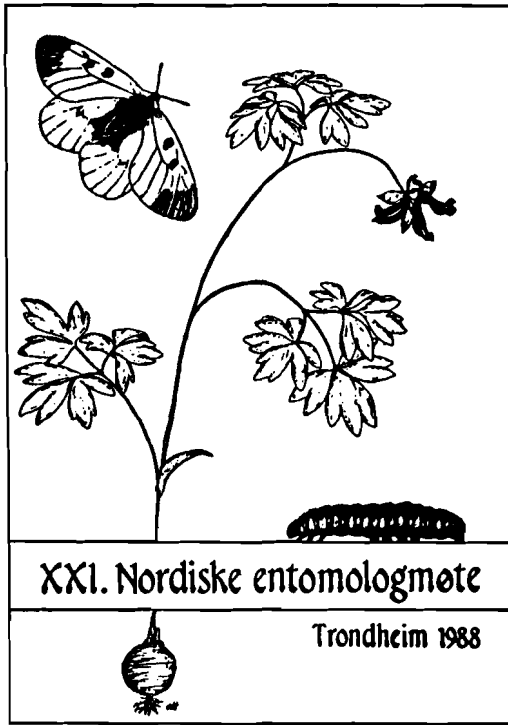
3.3. *Inventeringar.* Miljöministeriet håller på med inventering av områden som är viktiga för hotade insekter. Här kan nämnas Hangö udd, där det finns värdefulla sanddyner och torra änger. Monitoring är på gång rörande bestånden av hotade dagfjärilarter i Finland, likaså rörande några andra viktiga indikatorgrupper.

#### 4. Landskapet Åland

4.1 *Allmänna bestämmelser.* Ålands självstyre innefattar också egna bestämmelser om naturskyddet (Landskapslagen om naturvård, 41/77). För insektskyddet är speciellt skäl att notera förbudet att använda ljus- eller doftfällor. Flere av naturskyddsområdena är viktiga för insekter, men insekterna har inte spelat in vid dessas bildande.

4.2. *Fredade arter.* Enligt landskapsstyrelsens beslut av den 6 februari 1986 är följande fjärilarter fridlysta på Åland: Apollofjäril (*Parnassius apollo*), Liten apollofjäril (*Parnassius mnemosyne*), Båtspinnarfly (*Bena prasinana*), Olvonguldmal (*Phyllonorycter lantanellus*), Liten spinnmal (*Scythropia crataegella*), Krisslesäckmal (*Coleophora inulae*), Safferotsplattmal (*Depressaria libanotidella*), Ängsrutemal (*Ethmia pyrausta*), Spåttelmal (*Metzneria aestivella*), Sällsynt käringtandmal (*Syncopacma taeniolella*) och Stinksyckevecklare (*Endothenia nigricastana*).

# Deltakere til det 21. Nordiske Entomologmøtet i Trondheim 1988



Ståhls, Gunilla, Zoologiska Museet, Entomol. avd., Helsingfors Unversitet, N. Järnvägsg. 13, SF-001 00 Helsingfors.

Sundström, Liselotte, Zoologisk institutt, Helsingfors Universitet, N. Järnvägsg. 13, SF-001 00 Helsingfors.

Westman, Kristian, Zoologiska museet, N. Järnvägsg. 13, SF-001 00 Helsingfors.

## FRANKRIKE

Voisin, Jean-François, 13 Cité Naryse Bastié, F-91220 Bretigny.

## ISLAND

Gislason, Gisli Mar, Biologisk Institut, Islands Universitet, Reykjavik, Island.

## SVERIGE

Andersson, Göran, Naturhistoriska Museet, Box 7283, S-402 35 Göteborg.

Bengtsson, Bengt Å., Box 71, S-380 74 Löttorp.

Carlberg, Ulf, Atlasvägen 53, S-131 34 Nacka.

Gullefors, Bo, Forsed 2109B, S-873 00 Bollsta-  
bruk.

Gustafsson, Bert, Naturhistoriska Riksmuseet,  
Box 50007, S-104 05 Stockholm.

Hammarstedt, Olle, Svärmarvägen 28, S-240 17  
Södra Sandby.

Larsson, Torbjörn, Statens naturvårdsverk, Forskningssekretariatet, Box 1302, S-171 25 Solna.

Nilsson, Ingvar, Ekologihuset, S-223 62 Lund.

Pettersson, Roger B., Institut för Viltekologi,  
Skogshögskolan, S-901 83 Umeå.

Svensson, Ingvar, Vivedalsvägen 10, Österlöv, S-291 94 Kristianstad.

## NORGE

Andersen, Trond, Zoologisk Museum, Muséplass 3, N-5007 Bergen.

Bakke, Sigurd, Starrmyra 16, N-7075 Tiller.

Mehl, Reidar, Statens institutt for folkehelse,  
Geitmyrsv. 75, 0462 Oslo 4.

Bjerke, Ragnar, N-7064 Bratsberg.

Bollingmo, Tor, Zoologisk inst., AVH, Universitetet i Trondheim, N-7055 Dragvoll.

Hanssen, Oddvar, Rønningsvn. 36, N-7045 Trondheim.

Jensen, Lita Greve, Zoologisk Museum, Muséplass 3, N-5007 Bergen.

## DANMARK

Andersson, Jane, Steen Billes Torv 8, DK-8200 Århus N.

Böcher, Jens, Zoologisk Museum, Universitetsparken 15, DK-2100 København Ø.

Jørum, Palle, Nørremøllevej 84, DK-8800 Viborg.

Mahler, Viggo, Steen Billes Torv, DK-8200 Århus N.

Pritzl, Gunnar, Damgårdsvej 1, DK-4671 Strøby.

## FINLAND

Bagge, Pauli, Biol. Inst. Jyrášhylá Univ, Yliopistonk. 9, SF-401 00 Jyrashyla.

Hackman, Walter, Johannesvägen 2 B 10, SF-001 20 Helsingfors 12.

Nummelin, Matti, Tvärminne Zool. Stat., SF-109 00 Hanko.

Silfverberg, Hans, Zoologiska Museet, Helsingfors Universitet, N. Järnvägsg. 13, SF-001 00 Helsingfors.

Lundheim, Rolv, Alexander Kiellandsgt. 3, N-7015 Trondheim.  
Refseth, Dagfinn, Zoologisk inst., AVH, Universitetet i Trondheim, N-7055 Dragvoll.  
Rein, Jan Ove, Yggdrasilveien 1d, N-7033 Trondheim.  
Solem, John O., Universitetet i Trondheim, Vitenskapsmuseet, Zoologisk avd., N-7004 Trondheim.  
Strømme, Alex., Zoologisk inst., AVH, Universitetet i Trondheim, N-7055 Dragvoll.

Söli, Geir E.E., Zoologisk Museum, Musépllass 3, N-5007 Bergen.  
Sømme, Lauritz, Universitetet i Oslo, Zoologisk inst., Postboks 1050, N-0316 Oslo 3.  
Tømmerås, Bjørn Åge, Allforsk avd. 2, AVH, Universitetet i Trondheim, N-7055 Dragvoll.  
Zachariassen, Karl Erik, Zoologisk inst., AVH, Universitetet i Trondheim, N-7055 Dragvoll.  
Aagaard, Kaare, Økoforsk, Vitenskapsmuseet, Universitetet i Trondheim, N-7004 Trondheim.  
Aarvik, Leif, Nyborgv. 19A, N-1430 Ås.

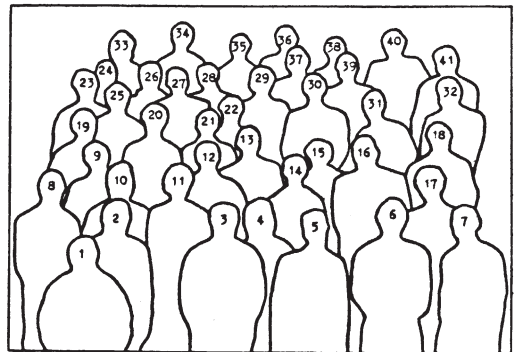




1. Elsa Svensson, 2. Hans Silfverberg, 3. Gisli Mar Gislason, 4. Liselotte Sundstrøm, 5. Ulf Carlberg, 6. Rolv Lundheim, 7. John O. Solem, 8. Ingvar Svensson, 9. Lita Greve Jensen, 10. Kristian Westman, 11. Gunilla Ståhls, 12. Reidar Mehl, 13. Walter Hackmann, 14. Bengt Å. Bengtsson, 15. Anne Marie Hackmann, 16. Jean Francois Voisin, 17. Lauritz Sømme, 18. Bo Gullefors, 19. Pauli Bagge, 20. Palle Jørum, 21. Oddvar Hanssen, 22. Karl Erik Zachariassen, 23. Jens Bøcher, 24. Jane Andersson, 25. Bert Gustafsson, 26. Viggo Mahler, 27. Göran Andersson, 28. Gunnar Pritzel, 29. Bjørn Åge Tømmerås, 30. Dagfinn Refseth, 31. Alex Strømme, 32. Kaare Aagaard, 33. Tor Boltingmo, 34. Olle Hammarstedt, 35. Matti Nummelin, 36. Ragnar Bjerke, 37. Sigurd Bakke, 38. Jan Ove Rein, 39. Leif Aarvik, 40. Torkill Løvli, 41. Jon Suul.

Ikke med på bildet: Trond Andersen, Geir E.E. Søli, Roger B. Pettersson.

Foto: Per Fredriksen



# **INTERNATIONAL CONGRESS OF COLEOPTEROLOGY**

**European Association of Coleopterology  
Barcelona, September 18-23, 1989**

**Faculty of Biology                      University of Barcelona**  
**Avda. Diagonal, 645                      08028 Barcelona (SPAIN)**

**Telephone 93-3308851 ext 165 - Telefax 93-3307157**

**Asociación Europea de Coleopterología**  
**Departamento de Biología Animal (Invertebrados)**  
**Facultad de Biología**  
**Universidad de Barcelona**  
**Avda. Diagonal, 645**  
**08028 Barcelona (SPAIN)**

## GUIDE TO AUTHORS.

FAUNA NORVEGICA Ser. B publishes papers in English, occasionally in Norwegian, with an extensive English abstract. When preparing manuscripts for submission, authors should consult current copies of *Fauna norvegica* and follow its style as closely as possible. Manuscript not conforming to the guide to authors will be returned for revision.

**Manuscripts** should be submitted to the Editor-in-Chief. Send two copies. Separate sheets should be used for the following: 1) Title page, with author's name. 2) An abstract, with the name and full postal address of the author underneath. 3) Tables with their headings. 4) Legends to figures.

Dates should be referred to as 10-20 Aug. 1970.

Underline all generic and species names. Approximate position of figures and tables in the text should be indicated in the margin. All Acknowledgements should be given under a single heading in the end of the text, immediately before the references.

**Figures and Tables.** Send two copies. All illustrations should be identified lightly with the author's name and the figure number.

The placing of figures and tables should be indicated in the margin. If the article is in Norwegian, the figures and tables should have both Norwegian and English text. Write Table and Fig. both in running text and over/under tables and figures.

Take care that all text in the figures is *large enough* for a format of column or page width, c. 7 or 14 cm. Never let odd words or numbers go outside the breadth of other elements of the figure. Figures with cross-hatching (bar charts) must not be drawn so large that it is difficult to judge the result of a considerable size reduction. When a dense cross-hatching is greatly reduced it will coalesce and thereby lead to confusion with an entirely black area. Choose contrasting patterns. Authors with access to a machine able to type Latin species names in italics should utilize this in all tables instead of underlining. We will then be more free to photograph tables without the underlining of Latin names detracting from the appearance of the tables.

**Nomenclature.** The first time a binomen is used in the text the name of its author should be included. Author names should be written in full, except L. for Linnaeus. Dates can be included when considered necessary, i.e. *Rhyacophila nubila* (Zetterstedt, 1840).

**References.** *In the text:* Black (1979), Black & Blue (1973:100), or «as noted by Green (1978) and Black (1979)». Multiple references should be given in chronological order, i.e. (Black & Blue 1973, Green 1976, 1979, Black 1978).

List of references are to be unnumbered and in international alphabetical order (i.e. Å = AA, Æ and Ä = Ae, Ø and Ö = Oe). Titles of journals should be abbreviated according to the World List of Scientific Periodicals. Do not refer to papers «in prep.» among the references.

Examples:

*Journal:*

Løken, A. 1962. Social wasps in Norway (Hymenoptera, Vespidae). *Norsk ent. Tidsskr.* 12: 191—218.

*Book:*

Mayr, E. 1913. *Animal species and evolution*. Harvard University Press. Cambridge, Mass.

Fittkau, E.J. 1962. Die Tanytopodinae (Diptera, Chironomidae). Die Tribus Anatopyniini, Macropeloponi und Pentaneurini. *Abh. Larvalsystem. Insekten* 6: 453 pp.

*Chapter:*

Whitman, I. 1951. The arthropod vectors of yellow fever, pp. 229—298 in: Strode, K. (ed.) *Yellow Fever*. Mc. Graw - Hill, New York & London.

**Proofs.** Two copies of the first proof will be sent to the author. One corrected copy should be returned to the editor without delay. Alterations should be limited to correcting typesetting errors. Extensive alterations will be charged to the author.

**Reprints.** Twentyfive reprints are supplied free (fifty with multiple authorships). Additional reprints can be ordered at a charge (an order form is sent with the proofs).

---

## FAUNA NORVEGICA Serie A, B, C utkommer med tilsammen 5 hefter i løpet av én årgang.

For at heftene skal komme inn under Postverkets regler for billig serie-utsendelse, forlanges det at heftene i de tre seriene av *Fauna norvegica* i hvert kalenderår gis fortløpende nummer fra 1 til 5. Det vil kunne bli noe tilfeldig hvilke hefter som blir gitt de respektive nummer på grunn av uregelmessigheter med rekkefølgen i løpet av året.

Referansemessig skal vi *aldri ta hensyn til nummeret i øvre hjørne på omslaget* (inne i firkanten). Det vi skal ta hensyn til er de oppgitte data for de respektive serier. Det er disse data som gir den korrekte litteraturreferansen, og det er disse forkort-

elsene som står oppført i *Abstract* til hver artikkel og på særtrykkene.

Post-office regulation necessitate numeration of all five issues in the three Series (A, B, C) in the order of their publication. This number is printed in the top right-hand corner of the front cover (in the square). *This number should be ignored when citing issues or papers. The relevant data are given in connection with the number of each series. These numbers provide the correct literature reference and it is these that are given in the abstract of individual papers.*

# Content

Fauna norv. Ser. B. Vol. 36, No. 1.

This number contains papers presented at the 21st Nordic Entomology meeting held in Trondheim, Norway 1988.

## Invated papers

- Sømme, L.: Insektenes tilpasning til høyfjellet (Adaptations in insects and other terrestrial arthropods to the alpine environment) ..... 1  
Gislason, G. M. & Olafsson, E.: Entomology in Iceland ..... 11

## Submitted papers

- Nummelin, M.: Seasonality and effects of forestry practices on forest floor arthropods in the Kibale forest, Uganda ..... 17  
Zachariassen, K. E. & Maloiy, G. M. O.: Water balance of beetles as an indicator of environmental humidity ..... 27  
Bjerke, R., Lundheim, R., Rein, J. O., Strømme, J. A. & Zachariassen, K. E.: Water balance and osmotic regulation of the East African scorpion *Lychas burdoi* (Simon) ..... 33  
Böcher, J.: Boreal insects in the northernmost Greenland: palaeo-entomological evidence from the Kap København Formation (Plio-Pleistocene), Peary Land ..... 37  
Bagge, P.: Abundance and vertical distribution of watermites in the lakes of Finnish Lapland (Acari, Hydrachnellae) ..... 45  
Silfverberg, H.: The problem of arctic Chrysomelidae (Coleoptera) ..... 53  
Strømme, J. A.: Metabolic rates of alpine and high arctic *Amara quenseli* (Col. Carabidae) beetles ..... 57  
Gullefors, B.: The egg-laying behaviour of *Glyphotaelius pellicidus* (Retzius) (Trichoptera: Limnephilidae) ..... 59  
Carlberg, U.: Group Effect during Postembryonic Development in *Eurycantha calcarata* Lucas (Insecta: Phasmida) ..... 65  
Carlberg, U.: Aspects of Evolution and Ecology in Relation to Defecation and Oviposition Behaviour of *Extatosoma tiaratum* (MacLeay) (Insecta: Phasmida) ..... 67  
Bollingmo, T.: Worker — queen conflict and fitness consequences in a colony of *Bombus hypnorum* L. (Hymenoptera) ..... 69  
Tømmerås, B. Å.: Host selection by odorous compounds from host and non-host trees in bark beetles ..... 75  
Mustaparta, H. & Almaas, T. J.: How does the olfactory system in insects discriminate between odours of own related species ..... 81

## Abstracts

- Mehl, R., Bjerkenes, T., Sandven, P. & Vandvik, B.: *Borrelia burgdorferi* i skogflått *Ixodes ricinus* i Norge (*Borrelia burgdorferi* in the tick *Ixodes ricinus* in Norway) ..... 87  
Bjerke, R., Lundheim, R., Rein, J. O., Strømme, J. A. & Zachariassen, K. E.: Water balance and osmotic regulation in the East African tenebrionid beetle *Rhytinota praelonqa* ..... 88  
Pettersson, R. B.: The distribution and habitat choice of the family Pythidae in Sweden ..... 88  
Hammarstedt, O.: *Parnassius mnemosyne* spp. *argiope* (Lep.) in Blekinge 1984—1988 ..... 88  
Refseth, D.: Phenological variability and distribution of Fennoscandian carabid beetles ..... 89  
Hackman, W.: Vingframkantens chaetotaxi hos Syrphidae ..... 89  
Sundstrøm, L.: Populationsstruktur och genetisk differentiering av subpopulationer hos *Formica truncorum* ..... 89  
Nasjonale meldinger om videreføring av det entomologiske vernearbeid i Norden i forhold til den nordiske rapporten av 1988 ..... 90  
List of participants of the 21 Nordic Entomology meeting held in Trondheim 1988 ..... 93