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ON THE EVOLUTION OF BEHAVIOUR IN CARABID BEETLES

Report of a symposium, held at the fieldstation Rees-Grietherbusch of the Zoological
Institute of the University of Cologne
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edited by

P. J. DEN BOER, H. U. THIELE and F. WEBER

H. VEENMAN & ZONEN B.V. – WAGENINGEN – 1979

We dedicate these papers to the memory of
Carl H. Lindroth (8.9.1905 – 23.2.1979),
who inspired us all

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PREFACE

At a symposium like this one, in most cases people come together who are engaged in the same field of science, quite independent from the animal species or group from which they derive their insights. In extreme cases, this spectrum may reach from protozoa to mammals.

It is also attractive, however, if scientists meet who, using different methods and having different starting points, are occupied with the same group of animals, as we are with carabids. Of course, a unifying concept and a common interest have to bring us together. It seems that all of us who have gathered here are united by an interest in the question as to how the great variety of species of carabids has come into existence.

If we are convinced that the theory of evolution is the unifying concept of biology par excellence, one feels that it is a most exciting task to trace the evolution of carabids. With something like 40,000 species, they are really a phylogenetic 'success', perhaps the greatest after the Curculionidae.

It seems that the variation in carabid behaviour surmounts that of their external properties. It is not especially difficult to teach a child what a carabid is. You need only exclude a few cases. But the variety in behaviour of the carabids is very great. Those differences in behaviour are the theme of this symposium. Discussing these topics, we must bear in mind the question of whether we are able, with our investigations, to contribute to the better understanding of the evolution and the history of geographical distribution in a great and important group of animals.

Most of the scientists who are concerned with the biology of carabids started investigating the problem of habitat binding or choice of habitat of our beetles. This applies also to most of the participants of this symposium. What binds carabid species to their often narrowly restricted habitats? From the early work of CARL LINDROTH, the founder of experimental ecology of carabid beetles, it became obvious that, in addition to the physiological capability, behaviour is decisive for the adaptation of a species to its special mode of life. Nowadays, we know that besides a preference for special microclimatic conditions, the following complexes of behaviour guarantee the annidation of species: brood care, food choice, mobility, diurnal rhythm of activity, and annual periodicity of development. All of these patterns of behaviour are genetically variable. They were first investigated as if they were stable and unvariable characteristics of the species. But today more and more we investigate the question of how they became altered in the course of the genetic adaptation of populations, the formation of subspecies and species, and in phylogeny. It is the goal of this symposium to gain some insight into these processes.

We are convinced that the value of the individual investigations is increased by a combined publication under a comprehensive heading. It has already become a good tradition that the Landbouwhogeschool Wageningen, The Netherlands, opens its excellently equiped journal 'Miscellaneous Papers' to voluminous papers on carabid ecology. As early as 1971, the Symposium 'Dispersal and Dispersal Power of Carabid Beetles', held at the Biological Station in Wijster, was published, as well as den Boer's work on 'Dispersal Power and Survival' in 1977.

The publication of this volume was made possible by numerous subscriptions from the Deutsche Forschungsgemeinschaft and the participants of this symposium. We are greatly indebted to them all.

H. U. THIELE F. WEBER

INSTEAD OF AN INTRODUCTION

The double role played by modes of behaviour in animal evolution has been pointed out by MAYR (1970).

1. Inborn behaviour is just as much exposed to the influence of evolutionary factors as are physical characteristics and undergoes the same kind of changes in the course of evolution. WICKLER (1970) regards behaviour 'so to say, as the most malleable organ of the organism ... The 'plasticity' of behaviour makes it especially useful as an adaptive feature and is one reason why behaviour often acts as 'pacemaker' in evolution'. This implies 'that, in the process of adaptive evolution, alterations in behaviour precede changes in body structure...'.

2. Considerable emphasis is placed by MAYR (1970) on the role of individual modifications in behaviour as causal factors in evolution. He writes: 'The particular significance of behaviour as an evolutionary factor lies in the possibility offered to the individual of escaping certain environmental influences and of confronting others as they arise'. We mentioned above that this holds true to a particularly high degree for carabids. Thanks to their powers of activity they are readily able to move on to new habitats that present them with changed conditions of selection, initiating new evolutionary processes and the occupation of new ecological niches.

In this connection Mayr considers it to be a 'somewhat unexpected' discovery that 'the aspects of behaviour that have been especially thoroughly studied by ethologists, i.e. inter- and intraspecific relationships... are just those that play a relatively insignificant role in macroevolution... Intraspecific behaviour consists mainly in an exchange of signals, and serves the purpose of communication or of misleading an enemy, or assists escape. *Only rarely does it play a role in the discovery of a new ecological niche or adaptive zone* (present author's italics). There is good reason for the ethologist's reluctance to concern himself with the ecological aspects of behaviour: they are extremely difficult to analyse. On the one hand, they often vary considerably even within one and the same population, and on the other, they always involve a strong, non-hereditary component. This is true of choice of food, choice of biotope and also of certain types of movement. The significance of types of behaviour in the larger evolutionary events becomes obvious when one considers the transition from aquatic to terrestrial life, from tree-life to one on the ground, or from an earthbound life to one involving flight'.

The adaptive role of these types of behaviour in cladogenesis and speciation of any one animal group has seldom been the subject of such extensive investigation as in the carabids, and the studies on this group provide the zoologist with the means of bridging the gaps between ecology, behaviour and evolution.

(This text is derived from THIELE, Carabid Beetles in Their Environments, 1977, p. 326–327)

PARTICIPANTS

J. Althoff: Zoologisches Institut der Universität Münster, Germany
Ir. F. Balk: Biologisch Station Wijster, The Netherlands
Dr. Th. Bauer: Zoologisches Institut der Universität Ulm, Germany
Dr. P. J. den Boer: Biologisch Station Wijster, The Netherlands
Dr. P. Brandmayr: Istituto di Zoologia e Anatomia Comparata, Università di Trieste, Italy
Dr. Th. S. van Dijk: Biologisch Station Wijster, The Netherlands
L. Erbeling: Zoologisches Institut der Universität Münster, Germany
M. Heine: Zoologisches Institut der Universität Münster, Germany
Ing. T. H. P. van Huizen: Biologisch Station Wijster, The Netherlands.
Dr. G. Juberthie: Laboratoire Souterrain, CNRS, Moulis, France
Dipl. Biol. D. Koch: Zoologisches Institut der Universität Köln, Germany
G. Leyk: Zoologisches Institut der Universität Köln, Germany
W. Meisner: Zoologisches Institut der Universität Münster, Germany
Ir. P. J. M. Mols: Biologisch Station Wijster, The Netherlands
Prof. Dr. D. Mossakowski: Zoologisches Institut der Universität Bremen, Germany
J. Müller: Zoologisches Institut der Universität Freiburg, Germany
Dr. P. Nagel: Geographisches Institut, Abteilung Tiergeographie, Universität Saarbrücken, Germany
Drs. N. Nelemans: Biologisch Station Wijster, The Netherlands
Dipl. Biol. H. K. Nettmann: Zoologisches Institut der Universität Bremen, Germany
Dozent Dr. W. Paarmann: Zoologisches Institut der Universität Würzburg, Germany
Dipl. Biol. R. Pospischil: Zoologisches Institut der Universität Köln, Germany
Dozent Dr. P. Sauer: Zoologisches Institut der Universität Freiburg, Germany
Prof. Dr. H. U. Thiele: Zoologisches Institut der Universität Köln, Germany
Prof. Dr. F. Weber: Zoologisches Institut der Universität Münster, Germany

1. Behaviour and body structure

THE CLASSIFICATION OF CARABIDAE

summarized by PETER NAGEL

Abteilung für Biogeographie, Universität des Saarlandes, D-6600 Saarbrücken 11
Federal Republic of Germany

The following summary gives a brief survey of the essential taxonomic characteristics of the various groups of Coleoptera, especially of Carabidae. Mainly the literature listed below was evaluated and interpreted. As there are diverging concepts (some diverging considerably) of the classification of many subfamilies of Carabidae, the cladogram Fig. 2 has been drawn up on the basis of the most confirmed concepts and the authors own evaluation. Fig. 1 shows the position of Carabidae within the system of Coleoptera as accepted today (see also Table 1).

A. SUBORDERS OF COLEOPTERA

1. Archostemata

Family Cupesidae only (Fig. 3); ovarioles polytrophic; notopleural suture visible; alae not folded but with apex spirally rolled; alae still with many transverse veins; hypopharynx of larvae with sclerome (xylophagous); tibia and tarsus of larvae fused to tibiotarsus; four Malpighian tubules only; sister group of Archostemata (after KLAUSNITZER 1975): Pantophaga = Adephaga + Myxophaga + Polyphaga.

2. Adephaga

Ovarioles polytrophic; notopleural suture visible; second to fourth abdominal segment fused; hind coxae completely divide first visible abdominal sternite (second segment); tibia and tarsus of larvae separated; four Malpighian tubules only; sister group of Adephaga (after KLAUSNITZER 1975): Heterophaga = Myxophaga + Polyphaga.

3. Myxophaga

Minute (0.5–1.5 mm); notopleural suture visible; mandible with flexible tooth behind incisivus; galea reduced; tibia and tarsus of larvae fused to tibiotarsus.

4. Polyphaga

Ovarioles telotrophic; notopleural suture missing; tibia and tarsus of larvae melted to tibiotarsus; number of Malpighian tubules (with few exceptions) at least more than four.

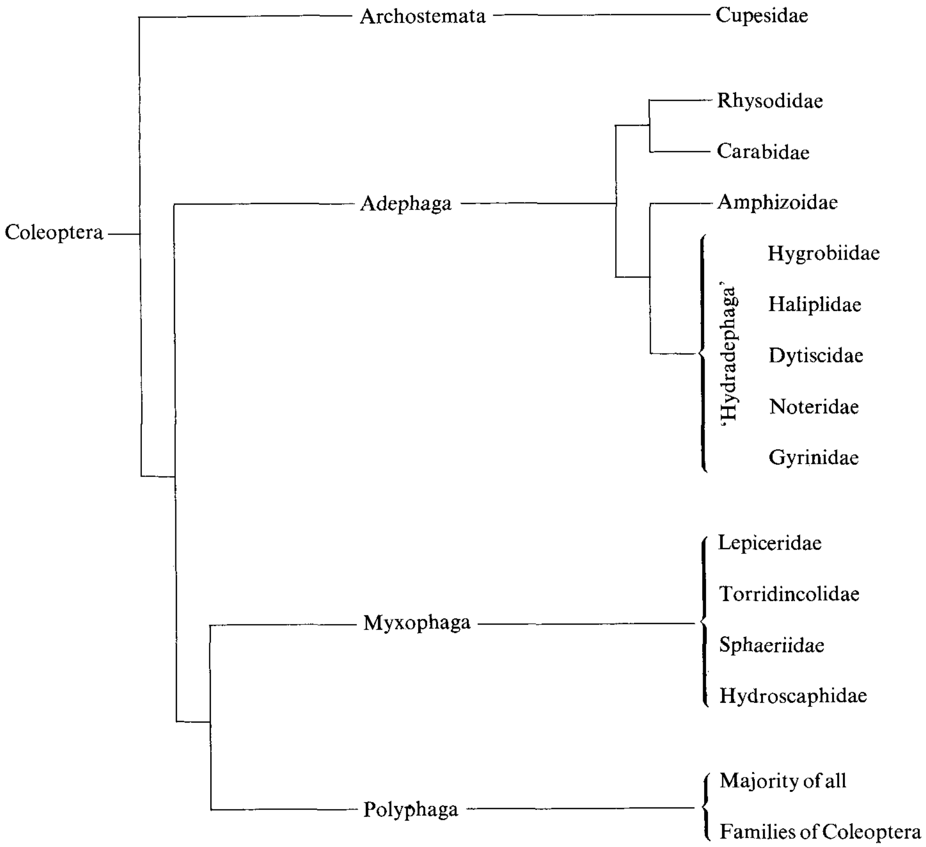


Fig. 1. Cladogram of Coleoptera.

B. FAMILIES OF ADEPHAGA

1. Rhysodidae (Fig. 4)

Protibial comb organ length-wise oriented; first visible abdominal sternite perceptible even between hind coxae; metasternum without transverse suture in front of hind coxae (as in most Hydradephaga); labial palpi of larvae reduced.

2. Carabidae

2.1. Isochaeta (Fig. 13)

Protibial spurs terminal, not associated with the comb organ; mesepimera reach middle coxal cavities (disjunct); metepisterna with distinctively separated metepimera (limbat).

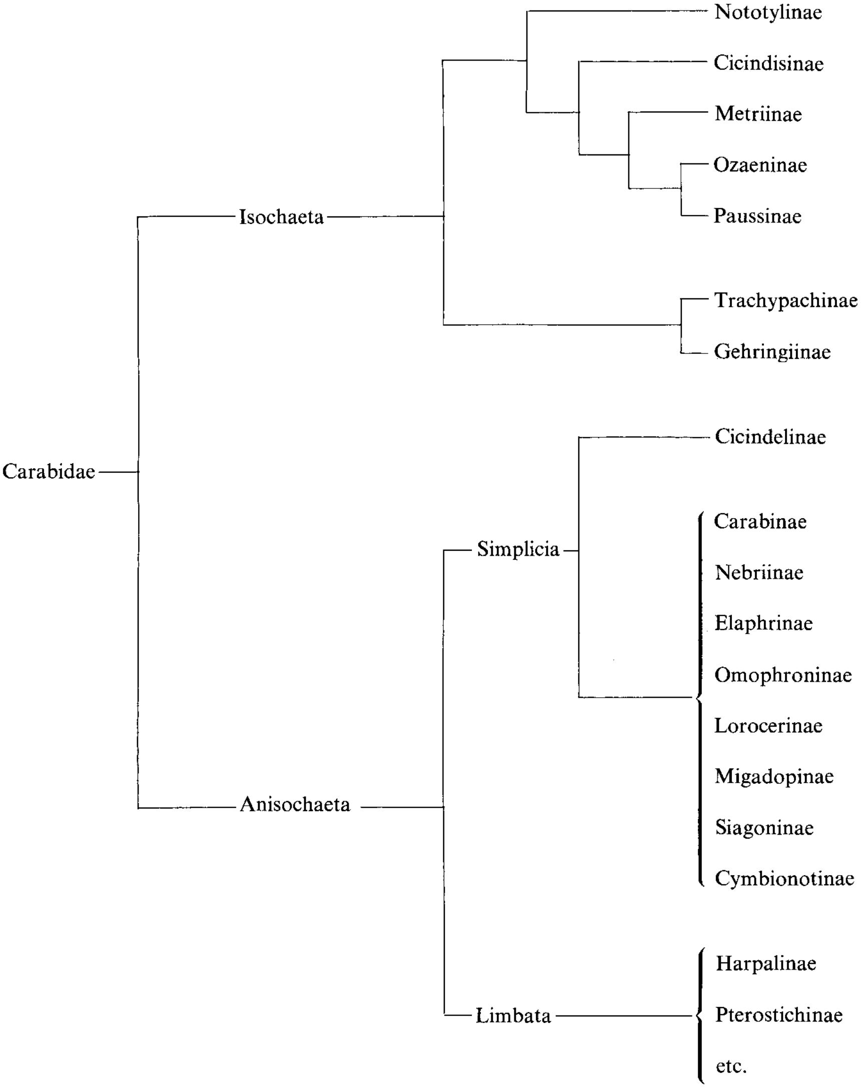


Fig. 2. Cladogram of Carabidae.

2.1.1. Nototylinae (Fig. 5)

Protibia neither with comb organ nor with emargination; front coxal cavities closed; larva unknown.

2.1.2. Cicindisinae (Fig. 6)

Protibia with lengthwise oriented emargination, but without comb organ; front coxal cavities closed; hind coxae not separated; antennae tightly pubescent from fifth segment onwards; without fixed setae; basis of elytron margined.

Tab. 1. Distribution and approximate number of species of Carabidae and some other families of Coleoptera.

	Number of species (ca)	Distribution
Archostemata		
Cupesidae	20	N-& S-America, E-Asia, S-Africa, Madagascar, Australia
Adephaga		
Rhysodidae	125	nearly world-wide, esp. tropical reg.
Carabidae		
Isochaeta		
Nototylinae	1	Brazil
Cicindisinae	2	Argentina, Pers. Gulf
Metriinae	1	West coast of N-America
Ozaeninae	120	nearly world-wide, esp. tropical reg.
Paussinae	450	nearly world-wide, esp. tropical reg.
Trachypachinae	5	N-Holartic Reg., Chile
Gehringiinae	1	western N-America
Anisochaeta		
Simplicia		
Cicindelinae	1500	world-wide
Carabinae	750	world-wide
Nebriinae	320	nearly world-wide (except Ethiop. Reg., Madagascar, Australia)
Elaphrinae	60	Holarctic Reg.
Omophroninae	65	nearly world-wide (except Australia, S-America)
Lorocerinae	15	Holartic Reg.
Migadopinae	30	southern S-America, circumantarctic Isles, Australia, New Zealand
Siagoninae	50	S-America, Africa, Madagascar, India, Mediterranean Reg.
Cymbionotinae	20	Africa, India, Central Asia
Limbata	25000	world-wide
Harpalinae		
Pterostichinae		
etc.		
Amphizoidae	4	N-America, Tibet
'Hydradephaga'	4500	world-wide
Myxophaga		
Lepiceridae	2	Central America
Torridincolidae	12	Africa, Madagascar. S-America
Sphaeriidae	18	nearly world-wide
Hydroscaphidae	11	Holarctic Reg., Madagascar, S-America
Polyphaga	320000	world-wide

2.1.3. Metriinae (Fig. 7)

Protibia with oblique emargination; front coxal cavities closed; hind coxae separated; antennae tightly pubescent from fifth segment onwards; fixed setae present.

2.1.4. Ozaeninae (Fig. 8)

Protibial emargination slight to distinctively toothed (comb organ slightly developed to highly differentiated); front coxal cavities closed; hind coxae separated; antennae without tight pubescence at least in two genera; fixed setae missing in some species; elytron with subapical fold of the outer edge; some genera myrmecophilous.

2.1.5. Paussinae (Fig. 9)

Same characteristics as Ozaeninae, but elytron without raised external margin, and considerably truncated; all genera presumed to be myrmecophilous (at least larvae).

2.1.6. Trachypachinae (Fig. 10)

Comb organ present, but antennae not pubescent; front coxal cavities open behind; hind coxae separated; hind coxae reach border of elytron; fixed setae present; small (about 4 mm); larvae without ligula; habitat terrestrial but near fresh water; systematic position together with Gehringiinae possibly not far from Hydradephaga.

2.1.7. Gehringiinae (Fig. 11)

Comb organ present; as Trachypachinae, but tiny (2 mm); elytron with lateral portion of disc bent under abdomen; last palpal segment rudimentary; more hydrophilous than Trachypachinae.

2.2. Anisochaeta (Fig. 13)

One protibial spur shifted proximally together with comb organ.

2.2.1. Simplicia (Fig. 14)

Metepisternum without separate Metepimeron; mesepimera reach middle coxal cavities (disjunct) (except: in the genus *Notiophilus* the middle coxal cavities are conjunct).

2.2.1.1. Cicindelinae

Comb organ shows many plesiomorphous characteristics; antennae situated on frons; larvae with characteristical hooks on tergum of fifth abdominal segment; the systematical position and rank of tiger-beetles is controversial even today.

2.2.1.2.–9.

Within this group of Simplicia-Disjuncta it should be noticed that presumably Elaphrinae and Migadopinae as well as Siagoninae and Cymbionotinae are more closely related than others.

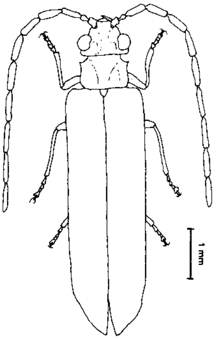
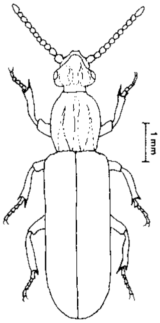


Fig.3 **Cupesidae**
Cupes concolor Westw.
(after ARNETT 1963)



g.4 **Rhysodidae**
Rhysodes sulcatus Fbr.
(after FREUDE 1971)

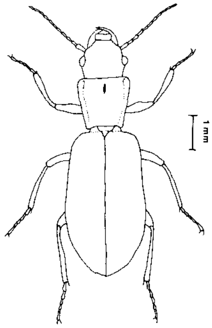


Fig.5 **Carabidae-Nototylinae**
Nototylus fryi (Schaum)
(after SCHAUM 1863)

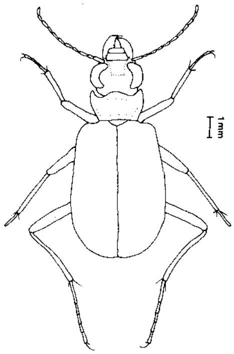


Fig.6 **Carabidae-Cicindisinae**
Cicindis horni Bruch
(after BRUCH 1908)

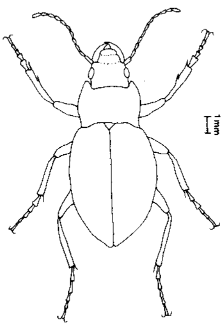


Fig.7 **Carabidae-Metriinae**
Metrius contractus Esch.
(after DUPUIS 1913)

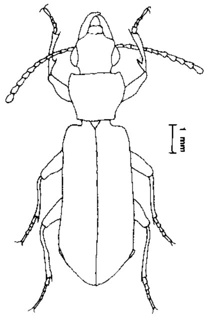


Fig.8 **Carabidae-Ozaeninae**
Pseudozaena (Sphaer.) goryi Cast.
(after JEANNEL 1946)

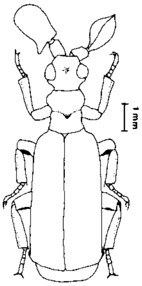


Fig. 9 **Carabidae-Paussinae**
Paussus thomsoni Reiche
(after NAGEL 1979)

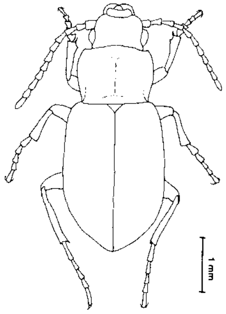


Fig.10 **Carabidae-Trachypachinae**
Trachypachus zetterstedti Gyll.
(after LINDROTH 1961)

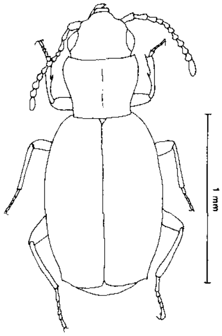


Fig.11 **Carabidae-Gehringiinae**
Gehringia olympica Darl.
(after LINDROTH 1961)

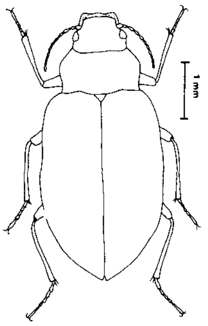
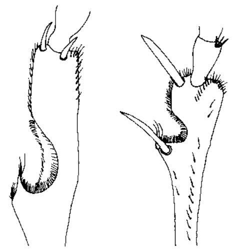


Fig. 12 **Amphizoidae**
Amphizoa lecontei Mathews
(after ARNETT 1963)

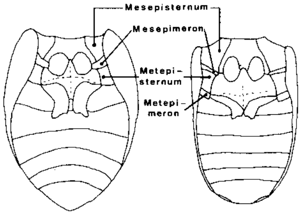


Isochaeta **Anisochaeta**

Pseudozaena(Sphaer.) longipennis Chaud. Broscus cephalotus L.

(after JEANNEL 1941)

Fig. 13



Simplicia **Limbata**
Disjuncta Conjuncta
Cychrus spec. Pterostichus spec.

(after JEANNEL 1941)

Fig. 14

2.2.2. Limbata (Fig. 14)

Metepisternum with distinctively separated Metepimeron; mesepimera do not reach middle coxal cavities (conjunct) (except: Scaritinae and Mormolyce of Thyreopterinae are disjunct); the majority of all Carabid species belongs to this group.

3. *Amphizoidae (Fig. 12)*

Antennae not pubescent; mesepimera reach middle coxal cavities (disjunct); metasternum with transverse suture; larvae without ligula; semi-aquatic.

4. *'Hydradephaga'*

Antennae not pubescent; metasternum with transverse suture present only within Haliplidae family; no indisputable evidence of being a monophyletic group; sometimes Notaridae are considered to be a subfamily of Dytiscidae.

REFERENCES

ARNETT, R. H.: The Beetles of the United States. – Washington, 1963.

BÄNNINGER, M.: Neunter Beitrag zur Kenntnis der Carabinae: Die Nebriini. – Entom. Mitt. **14**: 180–195, 256–281, 329–343 (1925).

BÄNNINGER, M.: Die Ozaenini (Col. Carab.). 10. Beitrag zur Kenntnis der Carabinae. – Deutsche Entom. Z. **1927**: 177–216 (1927a).

BÄNNINGER, M.: Zur Erforschung des Persischen Golfes (Beitrag Nr. 13: *Cicindis john-beckeri* n.sp. (Carabid., Col.). – Suppl. Entom. **16**: 119–121 (1927b).

BELL, R. T.: Does *Gehringia* belong to the Isochaeta? (Coleoptera: Carabidae). – Coleopterist's Bull. **18**: 59–61 (1964).

BELL, R. T.: *Trachypachus* and the Origin of the Hydradephaga (Coleoptera) – Coleopterist's Bull. **20**: 107–112 (1966).

BELL, R. T.: Coxal Cavities and the Classification of the Adephaga (Coleoptera). – Ann. Entom. Soc. Amer. **60**: 101–107 (1967).

BRUCH, C.: Eine neue Carabidengattung aus Argentinien: *Cicindis horni* (Col.). – Deutsche Entom Z. **1908**: 497–500 (1908).

CROWSON, R. A.: The Natural Classification of the Families of Coleoptera. – Hampton, 1955 (Repr. 1967).

CROWSON, R. A.: The Phylogeny of Coleoptera. – Ann. Rev. Entom. **5**: 111–134 (1960).

DARLINGTON, P. J.: Paussid Beetles. – Trans. Am. Entom. Soc. **76**: 47–142 (1950).

DUPUIS, P.: Metriinae et Mystropominae. – in: Genera Insectorum **116**: 1–4, t. 1–2 (1913).

FREUDE, H.: Rhysodidae. – in: Die Käfer Mitteleuropas **3**: 93–94 (1971).

HLAVAC, T. F.: Differentiation of the Carabid Antenna Cleaner. – Psyche **78**: 51–66 (1971).

JEANNEL, R.: Coléoptères Carabiques, 1e Partie (Faune de France 39). – Paris, 1941.

JEANNEL, R.: Coléoptères Carabiques de la Région Malgache (1e Partie) (Faune de l'Empire Français 6). – Paris, 1946.

JEANNEL, R. & R. PAULIAN: Morphologie abdominale des Coléoptères et systématique de l'ordre. – Rev. franç. Entom. **11**: 65–110 (1944).

KLAUSNITZER, B.: Probleme der Abgrenzung von Unterordnungen bei den Coleoptera. – Entom. Abh. Mus. Tierk. Dresden **40** (8): 269–275 (1975).

KRYZHANOVSKIJ, O. L.: An Attempt of Revised Classification of the Family Carabidae (Coleoptera). – Rev. Entom. URSS **55** (1): 80–91 (1976) (russ., latin nomencl., short engl. summary).

LINDROTH, C. H.: The Larvae of *Trachypachus* Motsch., *Gehringia* Darl., and *Opisthius* Kby. (Col. Carabidae). – Opusc. Entom. **25**: 30–42 (1960).

LINDROTH, C. H.: The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 2. – Opusc. Entom. Suppl. **20**: 1–200 (1961).

MACHATSCHKE, J. W.: Bemerkungen zum System der Coleoptera. – Ber. **9**. Wandervers. Dtsch. Entom. (Berlin 1961): 121–137 (1962).

MANDL, K.: Wiederherstellung des Familienstatus der Cicindelidae (Coleoptera). – Beitr. Entom. **21** (3/6): 507–508 (1971).

NAGEL, P.: Metrische Untersuchungen an *Paussus thomsoni* Reiche (Carabidae, Paussinae). – Entom. Blätter **74** (3): 140–144 (1979).

REGENFUSS, H. : Die Antennen-Putzeinrichtung der Adephaga (Coleoptera), parallele Vervollkommnung einer komplexen Struktur. – Z. zool. Syst. Evolut.-forsch. **13**(4): 278–299 (1975).

REICHARDT, H.: A critical study of the suborder Myxophaga, with a taxonomic revision of the Brazilian Torridincolidae and Hydroscaphidae (Coleoptera). – Arq. Zool. (S. Paulo) **24** (2): 73–162 (1973).

SCHAUM, H. R.: Descriptions of four new genera of Carabidae. – J. Entom. (London) **2**: 74–78, t.4 (1863).

SLOANE, T. G.: The Classification of the Family Carabidae. – Trans. R. Entom. Soc. London, 1923: 234–250.

ASPECTS OF THE EVOLUTION OF MYRMECOPHILOUS ADAPTATIONS IN PAUSSINAE (COLEOPTERA, CARABIDAE)

PETER NAGEL

Abteilung Biogeographie, Universität des Saarlandes, D-6600 Saarbrücken 11
Federal Republic of Germany

ABSTRACT

The most characteristic synapomorphous feature of the two sister groups Paussinae and Ozaeninae is a subapical elytral fold (Fig. 4). The cladogram of the Paussinae is given in Fig. 3. It is immaterial to the systematics of the group whether one follows DARLINGTON's (1950) suggestion to acknowledge three tribes of equal rank (Ozaenini, Protopaussini, Paussini) among the subfamily Paussinae (s.l.), or to maintain the original classification. From the cladogram it becomes evident that the Protopaussini are opposed to all remaining Paussinae as a sister group.

The most conspicuous synapomorphous character of the remaining Paussinae (Paussini as described by DARLINGTON 1950) is the reduction of the pedicel, a phenomenon unique among insects as far as I know (Fig. 5, 6, 7). True, there are quite a number of insects (especially beetles) with reduced antennal segments, but this reduction only affects the flagellum, whereas the scapes and pedicels are always preserved. The pedicel, normally the seat of the Johnston's organ acquires a new function: through a wedging ('Einkeilung') it is rigidly connected with the fused flagellum (in species with several separate antennal segments with the basal flagellum segment), a mechanism which enables the heavy club to become directly movable. The reduction in number of the originally 9 flagellum segments (which is independent of the reduction of the pedicel) occurred four times within the Paussini as described by DARLINGTON (1950), viz. in the Pentaplatarthrini (reduction to 5 segments) as well as in the Platyrhopalini, the Ceratoderini and the Paussini (s. str.) (reduction as low as one segment in the most extreme case). The effects of this reduction on the myrmecophilous mode of life are dealt with in connection with the discussion of the two main types of life, i.e. the defiant type ('Trutztypus') and the symphilous type ('Symphilentyp') (cf. chapter 1, Figs, 1, 2). The statement by JANSSENS (1949), that the peculiar antennal formation in Paussinae (and other myrmecophilous beetles) does not constitute newly 'invented' organs, but primarily a necessary intensification of the normal functions of an antenna and in the second place only a deviation from the normal structure favourable to this specific mode of life, is corroborated by our investigations. The lack of tactile setae (fixed setae typical of Carabidae) induced DARLINGTON (1950) to conclude that the Paussinae lead 'relatively non-tactile lives'.

My own SEM investigations of the integument of the antennal club confirm the absence of large tactile setae, it is true, but they also show that at least in terms of the external appearance there exists a great variety of sensilla no less conspicuous than in other Carabidae. In the Paussinae, however, the sensilla are likely to represent chemoreceptors (including hygroreceptors) rather than mechanoreceptors.

An other synapomorphous character, at least of the Paussini as described by DARLINGTON (1950) (Paussinae excluding Protopaussini; *Protopaussus* could not be studied by me concerning this character) is the presence of an apical sensory field on the respective distal antennal segments. It is mainly characterized by a marked increase in the number of sensilla basiconica (Figs. 8–11, 13).

The trichome which shows a marked accumulation of pores of dermal glands (the orifices of the glandular excretory canals are extremely numerous all over the antennae) and is located, in many *Paussus* species, at the base of the distal (third) antennal segment (i.e. the antennal club) (Fig. 12), should in future be called 'antennal symphilous organ', because the term 'Organe pédicellaire' introduced by ANTOINE (1951) is not in keeping with the facts: in all investigated species, this organ is located in the proximal part of the flagellum fused into a club, whereas the pedicel of all Paussinae, except the Protopaussini, is reduced to a chitinous ring. The sexual dimorphism, which for example in most species of the *Paussus armatus* group appears in males as a granulated and in females as a punctate antennal integument under normal stereomicroscopic magnification (up to 100 fold), could be more closely identified with the aid of SEM studies (Figs. 15, 16). It was found that the antennal integument of the males, besides the sensilla chaetica occurring in females, also contains a great number of sensilla basiconica inserting behind small cuticular granules. In females, the latter sensilla are restricted to the sensory field and its immediate surroundings.

1. BASIC FORMS OF MUTUALISM

The antennae of the Paussinae sometimes show bizarre forms; this modification of the normally 11-segmented antenna is directly connected with the development of

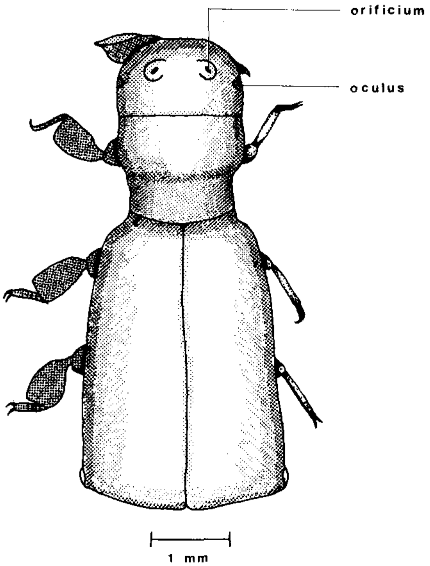


Fig. 1. Defiant type ('Trutztypus'): *Hylotorus hottentottus* Westw. from Pretoria, South Africa. Left antennal club somewhat protruding; apart from the apical tip, the antennal clubs can be hidden completely in a depression of the head; the flattened legs can also be laid close to the ventral surface.

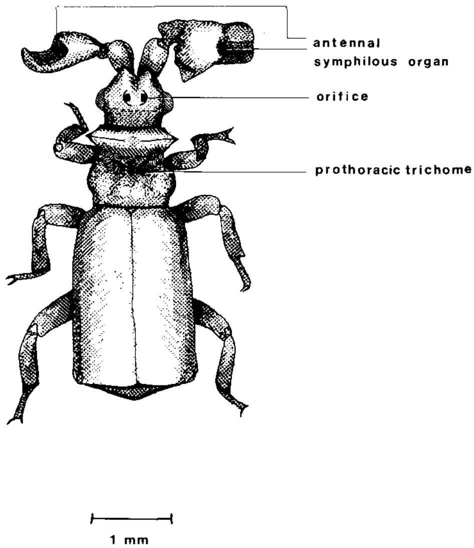


Fig. 2. Symphilous type ('Symphilentypus'): *Paussus linnei* Westw. from Worcester, South Africa.

myrmecophilous life.[1] In many instances, the mere shape of the antennae makes it possible to distinguish whether mutualism represents a case of symphily (true host relationship) or of synechthry (beetles as predatory inquilines).[2] The morphological adaptation to the intensity and nature of mutualism affects the antennae and the prothorax and besides these, also the pygidium, the extremities, the head and the elytra. Two parallel evolutionary series of morphologic-anatomical adaptation can be distinguished, with the body shape being one of the criteria (REICHENSPERGER 1948; cf. WASMANN 1896, 1929). Within the known Paussinae species a series can be set up between two extremes. One of these extremes is represented e.g. by the genera *Hylotorus* and *Platyrhopalopsis.* This so-called defiant type ('Trutztypus') (Fig. 1) is characterized by a heavily 'armoured' body as well as rounded structures leaving the mandibles of the ants hardly any opportunity to attack. The entire body appears 'compact'; orifices with trichomes for releasing exudate are non-existant or only rudimentary. The latter characteristic points to the second parallel evolutionary series, i.e. the development of so-called 'symphilous organs' (external structures of special glandular organs). The external shape of the other extreme is characterized by a much more articulated body. In this type, the antennae sometimes have bizarre ramifications, and the prothorax does not form a compact pronotum, but is more or less strongly structured, as is the pygidium. Moreover, the extremities do not lie close to the body so as to prevent attack, but are rounded transversally (not flattened) and stand off from the body, sometimes being extremely prolonged. In contrast to the first mentioned extreme, the antennae, the head and/or the prothorax as well as the elytra and the pygidium of this so-called 'symphilous type' (Fig. 2) are equipped with active glands usually releasing their exudate through an accumulation of pores which serve at the same time as insertion sites for trichomes. In contrast e.g. to some myrmecophilous Staphylinidae, the exudates of the Paussinae do not exclusively consist of fat and volatile substances (ethereal oils), but represent solid fine foods of unknown chemical composition. The symphilous type is intensively licked in a 'friendly' way by the ant hosts which, in spite of often being smaller, carry them away (usually by the antennae!) as they do their own brood in case of danger or migrations. On the other hand the ants are forced to accept the presence in their nests of the synechthrous type ('Trutztypus') because this type is inassailable.

2. PHYLOGENETIC SYSTEM

The Paussinae, however, are not only interesting because of these types of mutualism which can be found in more or less deviating forms also among other myrmecophilous beetles, but especially because of the extremely great variety of shapes connected with a

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[1] All Paussinae spend at least one phase of their life with ants; a termitophilous mode of life is supposed in a few species (LUNA DE CARVALHO 1977).

[2] All Paussinae however feed on the brood of their hosts.

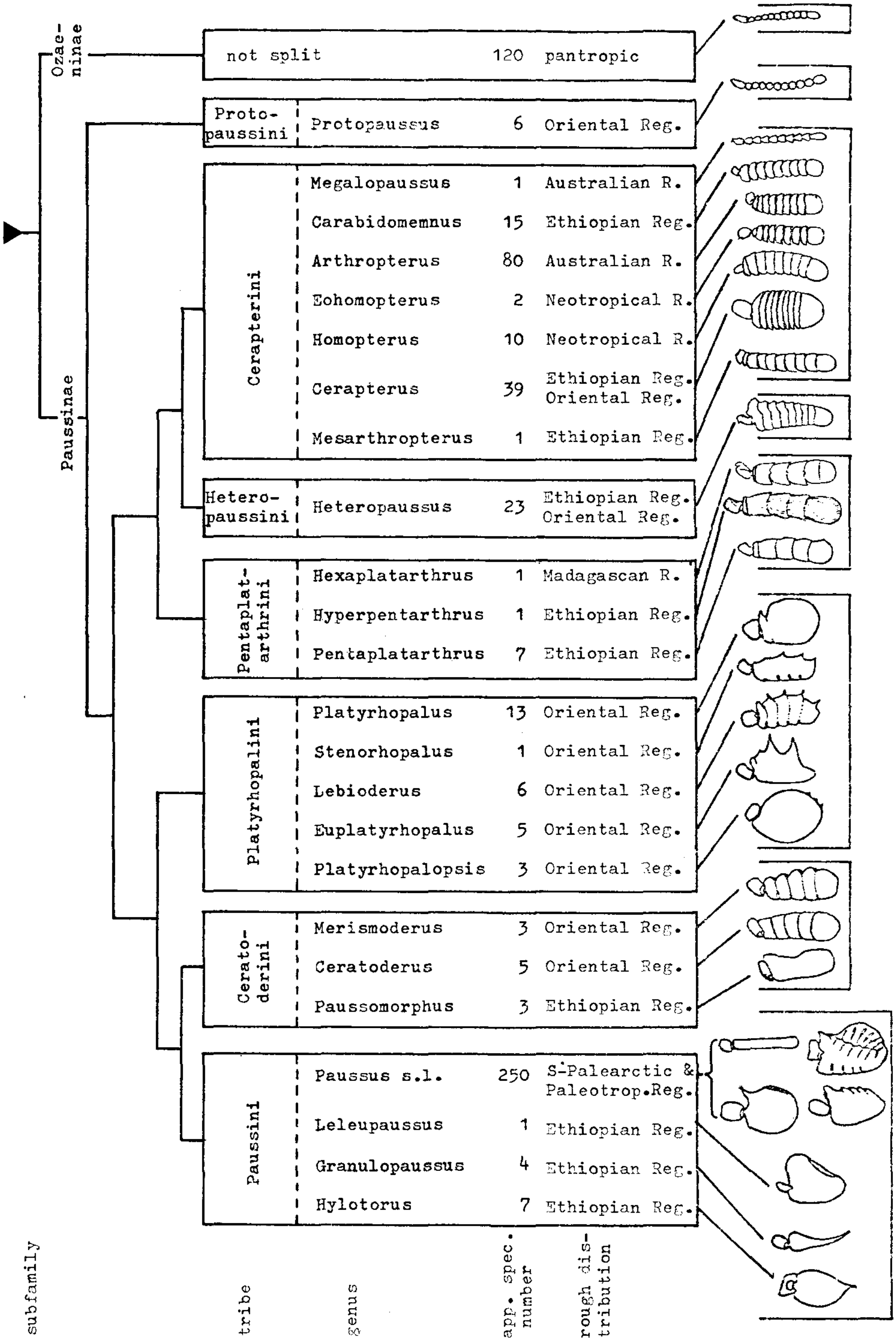

Fig. 3. Cladogram of the Paussinae with illustration of the most common antennal forms, the geographical distribution, and the approximate species number of the different genera (drawings of the antennae mainly after Darlington and Luna de Carvalho).

Fig. 4. Subapical elytral fold of *Paussus armatus* Westw., × 100.

progressive reduction of the number of antennal segments. These two characteristics especially permit us to reconstruct – perhaps better than in other Carabid groups – the phylogenetic system. In addition to this, several Paussinae are known from Baltic amber (Early Oligocene) which enable us to add an absolute time axis to the cladogram (Fig. 3).

The following are some short remarks on the classification of the Paussinae in the system of the Adephaga. As recently as in the first half of the last century, these beetles were looked upon as Clavicornia and sometimes also as 'Xylophaga' due to their unusual antennal shape, and were thus placed in relationship with the genus *Trochoideus* now considered as a member of the family Endomychidae. It is Burmeister (1841) who already recognized that they belonged to the Adephaga, but this idea was only generally accepted after Raffrays (1885–1886) publications.

Among these adephagous beetles they existed as a family of their own until 1950. Darlington (1950) then found the Ozaeninae to be the beetles the most closely related to the Paussinae.[3] Since then the Paussinae have been considered a sub-family of the Carabidae because their body shape, which sometimes diverges so greatly from the Carabid type, is only and exclusively due to their myrmecophilous mode of life. A synapomorphous character both of the Paussinae and of the Ozaeninae can be seen

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[3] A relationship with Ozaeninae had already been supposed by Burmeister (1841) and Kolbe (1927).

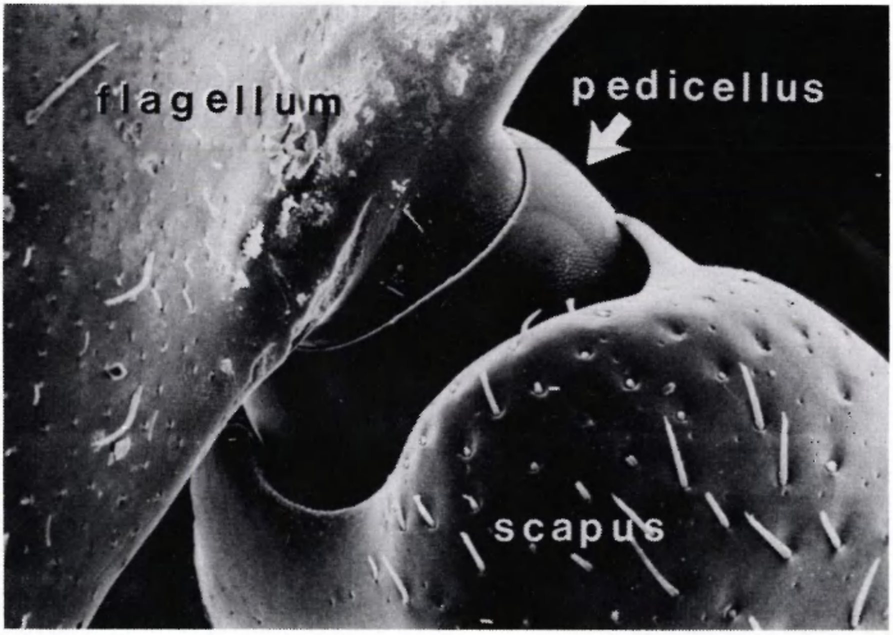

Fig. 5. Base of antennal club of *Paussus procerus* Gerst., male, × 75.

especially in the typical fold in the outer apical corner of the elytron (subapical elytral fold) (Fig. 4).

Let us first have a look at the classification of this subfamily (Fig. 3): The Protopaussini have been separated from all remaining Paussinae. DARLINGTON (1950) even placed the Ozaenini, the Protopaussini and the Paussini (s.l.) at the same level of differentiation. Ozaenini and Protopaussini have above all in common the shape of the antennae, of the front coxae and of the median cell of the wings. The genus *Protopaussus* is the only representative of the Paussinae which still has 11 fully developed antennal segments, its front coxae are separated by the original, wide prosternal process, and the median cell is quadrate rather than triangular as in the remaining Paussinae. The mentioned genus differs from the Ozaeninae by its modified mouth parts, its altogether myrmecophilous mode of life (only the genus *Physea* among the Ozaeninae lives with ants of the genus *Atta*)[4], and its being in possession of prothoracic trichomes.

A comparison with fossil Paussinae is interesting in regard to the development of symphilous characters. WASMANN (1929) could examine the Paussinae embalmed in Baltic amber (Late Eocene to Early Oligocene) and, with one exception, only found representatives of the Cerapterini. His study of the beetles in the amber did not reveal any differences between 10 species (out of 20) and the recent genus *Arthropterus*

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[4] See also footnote 1.

(s.str.), in spite of the age difference of 50 million years. However, *Eopaussus balticus* is also remarkable because of its fused antennal club which is hollow like that of many recent *Paussus* species and also possesses trichomes at the usual sites. This similarity caused WASMANN (1929) to place this species in close relationship with recent species of the genus *Paussus*, the only distinct difference being a different shaped mouth: closed except for a small crack in the case of the active brood predator *Paussus*, and wide open in the case of *Eopaussus* which is fed by ants from their own crops (similar to *Lomechusa*). However, I should like to endorse DARLINGTON's (1950) opinion in assuming that *Eopaussus* belongs to the original Paussinae, i.e. into the Ceraptini relationship, mainly because of the prosternal process which separates the front-coxae. The fact remains, however, that Paussid beetles at the highest symphilous level existed as early as the Early Tertiary.

3. MORPHOLOGICAL ADAPTATIONS TO MYRMECOPHILOUS LIFE

3.1. *Reduction of the antennal segments*

All body parts of all tribes, genera and species need not necessarily be equally affected by morphological adaptations to myrmecophilous life. Thus, in the case of *Pentaplatarthrus* for instance, the flagellum of the antennae is only reduced to five segments, whereas the pronotum is equipped with numerous exudate trichomes and is more structured than that of most of the other known Paussinae. Moreover, the pygidium is densely lined with trichomes. In *Heteropaussus*, on the other hand, only the posterior pronotal corners as well as the humeral parts of the elytra are equipped with small trichomes. Numerous examples of such a separately developed morphological adaptation of various degrees of intensity can be found, especially within the large genus *Paussus* (s.l.).

All Paussinae, with the exception of the Protopaussini, are characterized by a reduction of the pedicellum and of the Johnston's organ (Figs. 5, 6). The reduction of the number of antennal segments therefore does not start in the flagellum, but at one of the basal segments. No matter whether there are still nine free segments in the flagellum (as originally) (cf. Cerapterini, Heteropaussini), or whether the flagellum consists of one segment only, e.g. a spherical one (cf. *Paussus sphaerocerus*), the antennal base is always uniformly shaped (Figs. 2, 3): The scape inserts with a large condyle in the head capsule and is connected with the latter by a highly developed ball-and-socket joint. Functionally, the flagellum and the pedicel form a single entity because the pedicel, which is reduced to a ring, is wedged with the short proximal process of the flagellum, i.e. it is rigidly connected with the latter ('Einkeilung'), thus forming the condyle of the ball-and-socket joint between scape and pedicel (Fig. 7). In view of the fact that in the flagellate antenna muscles always only start from the scape, and insert into the proximal part of the pedicel, thus enabling the flagellum to be moved only indirectly, a direct movement of the flagellate antenna has become possible because of the wedging.

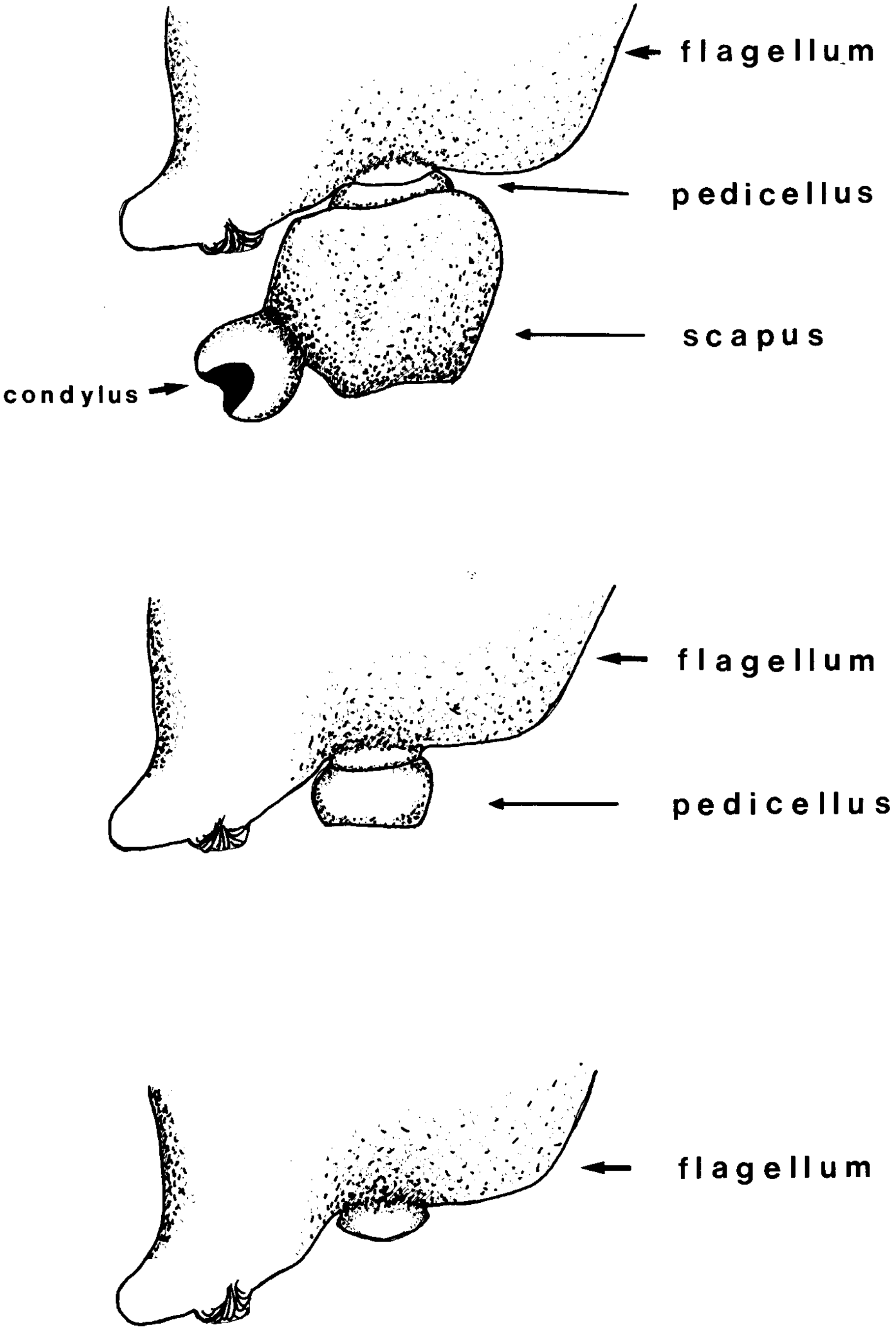

Fig. 6. Base of antennal club of *Paussus humboldti pilosus* Rchsp. with progressive removal of scape and pedicel.

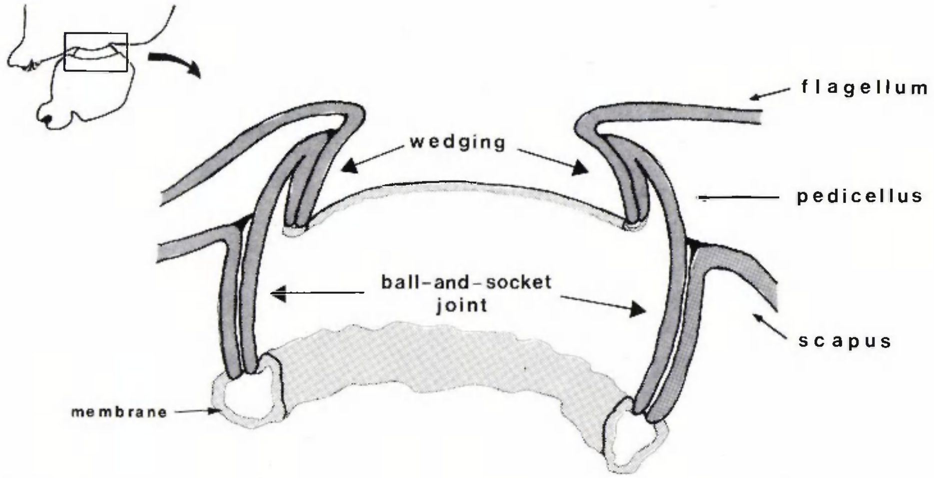

Fig. 7. Dissected base of antennal club of *Paussus humboldti pilosus* Rchsp. to demonstrate articulation types: ball-and-socket joint between scape on the one hand and pedicel and flagellum, on the other, as well as rigid connection (wedging, 'Einkeilung') between pedicel and flagellum; pedicel and flagellum fused into the antennal club form a functional entity.

This, however, caused the Paussini (with the exception of *Protopaussus*) to lose Johnston's organ which, with the scolopidia lacking stimulation, would in any case not function any longer due to the wedging of the proximal part of the flagellum. The Johnston's organ serves as a mechanoreceptor to the Pterygota; i.e. it serves as the seat of the tactile sense as well as e.g. a flight speed indicator. The disappearance of this organ, just as the lack of any fixed setae on the entire body (the Ozaeninae, too, possess none or only few such 'fixed setae' so characteristic of the remaining Carabidae), and the reduction of the tactile function of the maxillary palpi induced Darlington (1950) to say that the Paussinae lead 'relatively non-tactile lives', a statement to be checked in the following.

3.2. Fine structure of the antennal integument

3.2.1. Sensilla types

Even with a slight magnification it can be seen that the antennal club of the Paussinae is equipped with tiny, little bristles. However, only a study with the scanning electron microscope (SEM) enables the individual sensilla to be classified according to their external appearance (cf. Snodgrass 1935, 1956; Dethier 1963; Schneider & Steinbrecht 1968; Harbach & Larsen 1977). The function can only be guessed at present, as there have been no studies with the transmission electron microscope (TEM) or any functional (lead) studies.

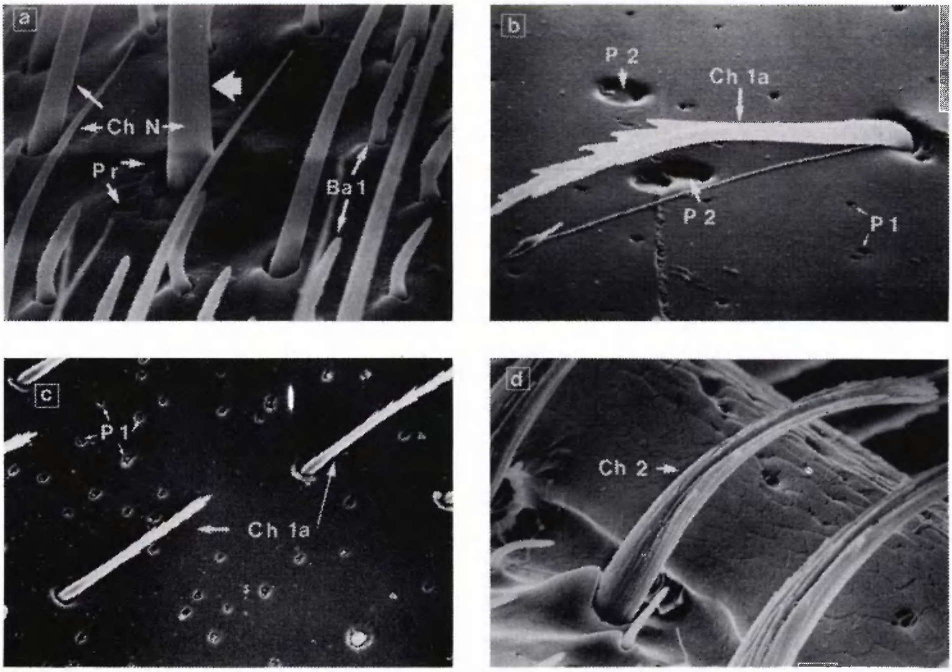

Fig. 8. Sensilla types of the antennae. a) *Molops piceus*, female, 9th antennal segment, apical part (thick arrow pointing to the longitudinal corrugation of the Ch N), × 1000; b) *Paussus humboldti pilosus*, female, × 1000; c) *Paussus procerus*, female, × 250; d) *Paussus armatus*, male, × 500. For abbreviations see Appendix.

a. Sensilla trichodea (hair organs).

So far, only the hairs of the antennal symphilous organs of some species can clearly be found to belong to this type[5] (Fig. 12). They appear to be long and thin, smooth-walled and motile, i.e. not rigid. Without studies with the light microscope or TEM studies it cannot be decided whether these hairs are chemoreceptors or have a tactile function. YUNG (1938) did not discover any hair organs with several sensory cells each (his studies, however, concentrated on glandular cells), it can thus be supposed that the sensilla trichodea of the antennal symphilous organ are hairs with a tactile function. The function of this antennal organ will be discussed further.

b. Sensilla chaetica (bristle organs).

b.1. Type 1

Figs. 8a and 14a + b show different sizes of the obviously 'normal' type of the sensilla chaetica in Carabidae.[6] It could be proved to exist in *Abax parallelus* and *Molops piceus*

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[5] Some species of the *Paussus inermis* group might possibly possess such hairs also on either part of the antennal club.

[6] According to HARBACH & LARSEN (1977) it is the sensillum trichodeum which is often surrounded by the pores of dermal excretory canals.

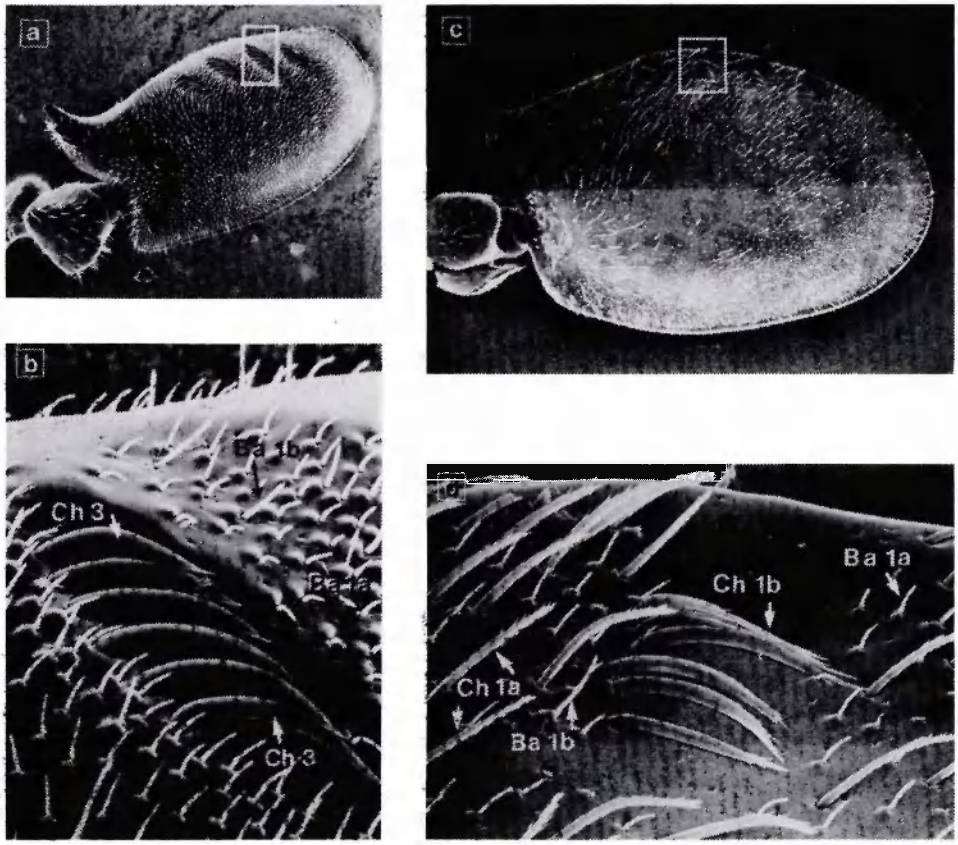

Fig. 9. Sensilla types of grooves of antennal clubs; a) antennal club of *Paussus spinicoxis*. × 25; b) magnified section of a), × 250; c) antennal club of *Paussus procerus*, male, × 20; d) magnified section of c), × 175. For abbreviations see Appendix.

(author's own studies) as well as in *Aphaenops crypticola* (cf. Juberthie & Massoud 1977: 150, f. 3b + d). The surface of these bristles is longitudinally corrugated, which makes them easy to recognize. So far, this normal type could not be shown to be present in any of the investigated Paussinae. A sensillum type frequently found to occur on the surface of the antennal club of the investigated Paussinae, here called type 1a, is distinguished by its dentate margin. The bristle itself can be rounded transversally (e.g. in *Paussus procerus*) (Figs. 8c, 9d, 13) or flattened towards the apex (e.g. in *Paussus humboldti pilosus*) (Fig. 8b). The teeth which might become very long, are exclusively located in the apical part of the bristles. The bristles of the so-called type 1b are located in the region of the antennal grooves of *Paussus procerus* (dorsally). They are essentially similar to type 1a, but differ by being approximately four times as thick as the sensilla chaetica, type 1a, of the surrounding surface of the antennal club (Figs. 9c, d).[7]

[7] Callahan (1975, fig. 3) figures similar 'sicula-sickle-shaped' sensilla on the antenna of the ant (!) *Odontomachus ruginodis* (Wheeler).

b.2. Type 2

The bristles of the carinate posterior margin of some species of the *Paussus armatus* group are characterized by their extraordinary size and thickness (Figs. 8d, 10c, 16a + b). Moreover, their surface is very strongly grooved and looks 'weathered'. These sensilla chaetica, type 2, could be proved to occur in *Paussus armatus*, *cilipes* and *arabicus*. As for other species of this group with a carinate posterior margin, it can be assumed that the respective bristle row is also formed by such Ch 2 (e.g. *thomsoni*, *spinicola*, *aethiops*).

b.3. Type 3

The sensilla chaetica, type 3, could so far only be found in the antennal grooves of *Paussus spinicoxis* (Figs. 9a + b). They are characterized by an extraordinary thickness. Besides, they have a smooth surface, are slightly bent and end in a sharp point. They insert obliquely into the integument and lie close to the surface rather than protruding.

c. Sensilla basiconica

c.1. Sensilla basiconica, type 1

Among the setiform sensilla, the sensilla basiconica of type 1 are distinguished by being small sized and smooth surfaced. Among the *Paussus* species investigated so far,

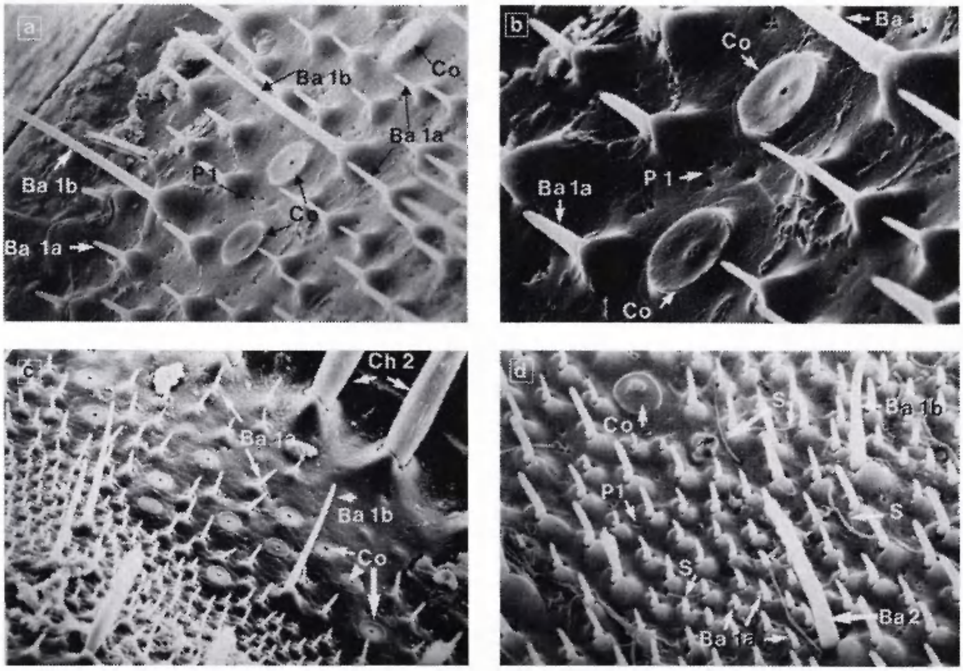

Fig. 10. Sensilla types of antennal clubs; a) *Paussus humboldti pilosus*, female, apex, × 500; b) like a), x 1000; c) *Paussus armatus*, female, ventral apex, × 250; d) *Paussus armatus*, male, apex, × 500. For abbreviations see Appendix.

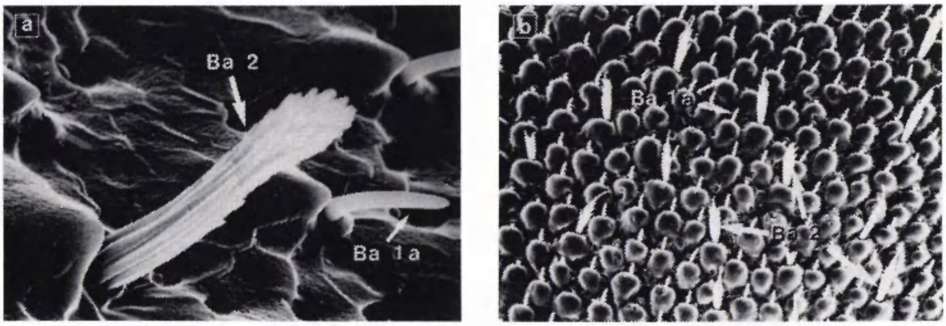

Fig. 11. Sensilla types of antennal clubs; a) *Paussus armatus*, male, × 1000; b) *Paussus c. cilipes*, male, × 175. For abbreviations see Appendix.

this type seems to represent the most frequently occurring sensilla of the antennal club (Fig. 10). They are spread over the entire surface of the antennal club (at least in males; see below) and reach their greatest density in the crescent subapical sensory fields which are discernible even with a minor magnification (approximately 50 fold). This particularly applies to type 1a which is only about half the size of type 1b (Figs. 9, 10, 13). Both types, however, also occur on the disk of the club, where type 1b can be half as frequent as type 1a, whereas in the subapical sensory field the ratio between types 1a and 1b is approximately 8:1.

c.2. Sensilla basonica, type 2

These sensilla seem to differ from the sensilla chaetica of type 2 mainly by their size (Fig. 11). They are characterized by a very strongly grooved, 'weathered' looking surface as well as their brushlike apex. These Ba 2 are to be found in *Paussus armatus*, *arabicus* and *c. cilipes* (the latter species with transitions to a form similar to the sensilla chaetica of type 1a).

d. Sensilla coeloconica

In contrast to the sensilla ampullacea with very large orifices found in *Aphaenops crypticola* (JUBERTHIE & MASSOUD 1977), the corresponding sensilla of the investigated *Abax parallelus*, *Molops piceus* and *Cychrus attenuatus* have orifices with diameters at most as large as the insertion sites of the sensilla basiconica. A common feature of these 'normal' sensilla coeloconica is the fact that their orifices lie at the apex of a small tubercle of the cuticle (Fig. 14). In *Paussus humboldti pilosus* and *Paussus armatus* as well as *Paussomorphus chevrolati* only the subapical region of the antennal club shows a structure strongly suggesting that it also represents sensilla coeloconica (Fig. 10). The orifices, however, are not larger than the surrounding pores of the glandular excretory canals (see below), and this structure can also be considered an inverse formation of the sunken orifices of the glandular excretory canals (see below). Without any histological studies (which are projected) this question must be left open.[8] The structure in question

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[8] CALLAHAN (1975, figs. 14J & 21) figures sensilla ampullacea on the antenna of the ant (!) *Odontomachus ruginodis* (WHEELER), which are obviously identical to the sensilla coeloconica described here from Paussinae.

consists of a disk-like, raised, round plate with a central orifice, with the disk itself being a little sunken, yet the orifice in it lying at the apex of a flat elevation.

3.2.2. Glandular excretory canals

In *Abax parallelus*, but also in *Molops piceus*, the pores of the glandular excretory canals are both individually distributed over the surface and arranged in a semicircular to circular way round the base of the largest type of the sensilla chaetica (Ch N), (Figs. 8a, 14). The orifices are tiny, i.e. much smaller than the orifices of the sensilla coeloconica, whereas the antennal integument of the studied Paussinae is densely strewn with pores of dermal glands, i.e. they are very numerous. At least two different structures appear to occur in the various species (cf. also chapter 3.2.1.d), on the one hand the plain pores known from other Carabidae (P 1), and on the other hand the plate-like sunken disk with central or somewhat eccentric pores (P 2), (Figs. 8, 10, 16).

According to the investigations of YUNG (1938), these two forms do not differ essentially. Both constitute the orifices of the excretory canals of dermal glands. It is striking that besides the antennae almost the entire body of the Paussinae (so far examined) is covered with these pores and platelike pits. Even the small lumen of the elytra contains almost exclusively such dermal gland cells which excrete their secretory

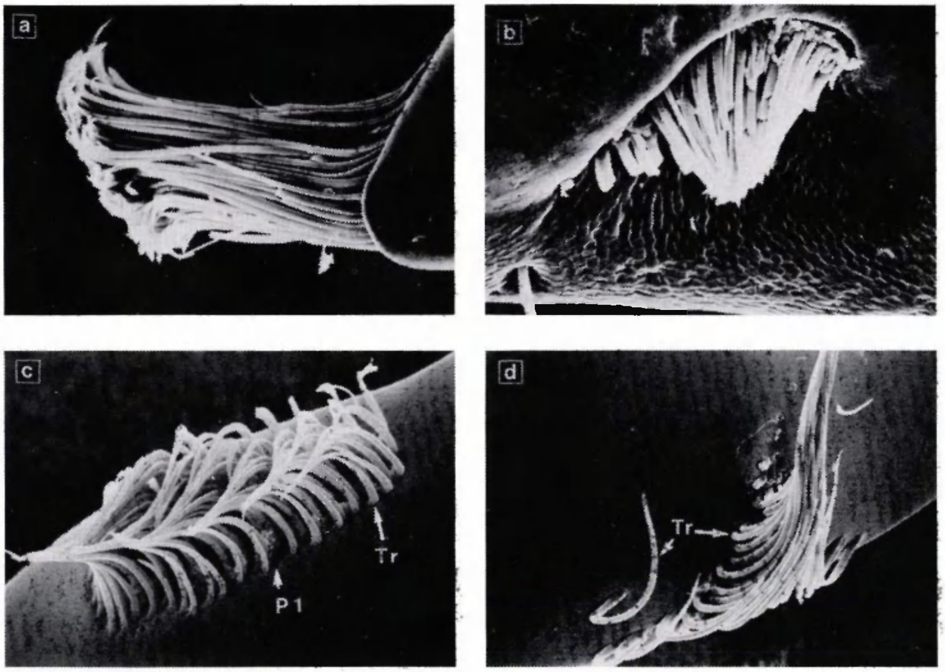

Fig. 12. Antennal symphilous organs in Paussinae; a) *Paussus sphaerocerus*, female, × 250; b) *Paussus arabicus*, male, × 250; c) *Paussus favieri*, × 375; d) *Paussus humboldti pilosus*, × 175. For abbreviations see Appendix.

product through the orifices to the outside. The fact that we are dealing here with a true solid secretory product rather than gaseous or slightly volatile substances becomes clear from Fig. 10d: the string-like structures which start from the pores represent a solidified secretory product. The main secretion sites of the 'symphilous secretory product' are characterized by cribriform cuticular sites. From the outside these sites appear as the position of the usually yellowish trichomes (Fig. 12). Here again, we observe the phenomenon of the parallel development of such a symphilous organ at corresponding body parts in different phylogenetic lines. The symphilous organ at the antennal club is only developed within the large genus *Paussus*, where it shows a great variety of shapes (cf. however *Eopaussus*). Yet, the basic structural plan is always the same: the hairs of the trichome appear to be rigidly connected with the cuticle, between the insertion sites of these trichomes the excretory canals of the glands end.

Due to capillary attraction the viscous secretory product rises between the densely arranged bristles, where it is then eagerly licked off by the ants. The state of development of the trichome depends on the degree of intensity of the myrmecophilous life. The *Paussus armatus* group, one of the *Paussus* groups with the highest degree of myrmecophilous evolution, might serve as an example of this (cf. NAGEL 1977): In this group, there are two species with no trace of a symphilous organ (*rusticus*, *chappuisi*), five species with more or less equal trichomes (some species already showing a bipartition of the trichome) (*dissimulator*, *sphaerocerus*, *humboldti*, *antinorii*, *cornutus*), eight species with double, distinctly separated trichomes (upper and lower sides of the antennal club) (*spinicola*, *thomsoni*, *arabicus*, *somaliae*, *aethiops*, *moltonii*, *armatus*, *bayoni*), and four species in which the dorsal trichomes have disappeared again (*cilipes*, *pseudosetosus*, *setosus*, *woerdeni*). If we look into the function of this symphilous organ, it becomes obvious that the possession of a trichome as large as possible is certainly an advantage to a species of the symphilous type. The reduction or partial loss of the trichome (in connection with a reduced number of pores of the dermal glands) must either be compensated for by morphological structures developed in the direction of the defiant type ('Trutztypus'), or by the development of new symphilous organs in other parts of the body, a working hypothesis which can basically be confirmed at least in this group of species. Since ANTOINE (1951; cf. also ANTOINE 1950) the trichome in the proximal part of the last antennal segment (i.e. at the base of the flagellum fused into a club), has been called 'Organe pédicellaire'. DARLINGTON (1950) and also LUNA DE CARVALHO (1959) have shown very clearly that this antennal segment is identical with the third antennal segment and that, therefore, the trichome in question is not located on the pedicel, which is the second antennal segment. Because these trichomes can also be located on the scape and even at different sites of the flagellum (not necessarily at its base), I suggest naming it 'antennal symphilous organ'.

3.2.3. Sexual dimorphism

Fig. 13 shows the general arrangement of the setiform sensilla in all Paussinae with lenticular or spherical antennal clubs: the middle of the disk is relatively sparsely

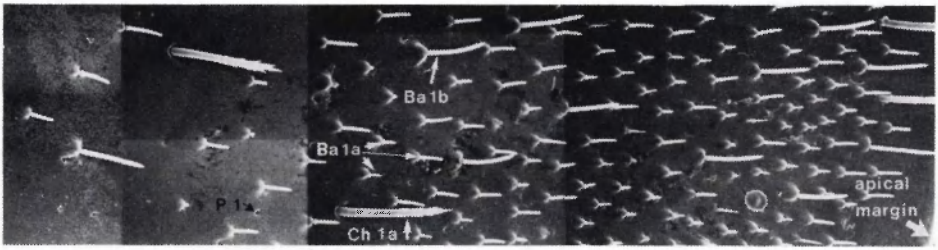

Fig. 13. Section of the surface of the antennal club (dorsally) of *Paussus procerus*, male, × 250: on the left is the disk centre, on the right the apical margin. For abbreviations see Appendix.

covered with hair organs, with the latter increasing somewhat in density towards the margin of the vaulted surface. The sensory field is situated where the antennal club slopes towards the flatter apical carinate margin. The sensory field is at least crescent shaped and can extend as far as the flagellum base in species with a carinate or edged posterior margin. Even in 'primitive' genera such as *Cerapterus* this sensory field can be seen in the subapical part of the last antennal segment. SEM studies showed this field to result from a markedly increased number of especially sensilla basiconica. However, the setiform sensilla do not spread as far as the apical margin of the antennal club, but leave a marginal strip bare.

As far as the antennal sensilla are concerned, the sexual dimorphism can express itself in an unequal number of identical sensilla in males and females (e.g. *Aphaenops crypticola*, cf. JUBERTHIE & MASSOUD 1977) or in a sex-linked occurrence of a certain type of sensillum (e.g. spatulate bristles only in males of *Tenebrio molitor*, cf. HARBACH & LARSEN 1977). *Abax parallelus* has not been subjected to complete quantitative and stereotactic investigations of the antennae; nevertheless, it was striking that the sensilla basiconica are distinctly larger in number in males than in females (Fig. 14).

In all investigated Paussinae species with antennal clubs it could be observed that the disks of the males are always set with numerous sensilla basiconica (Ba 1a), whereas in

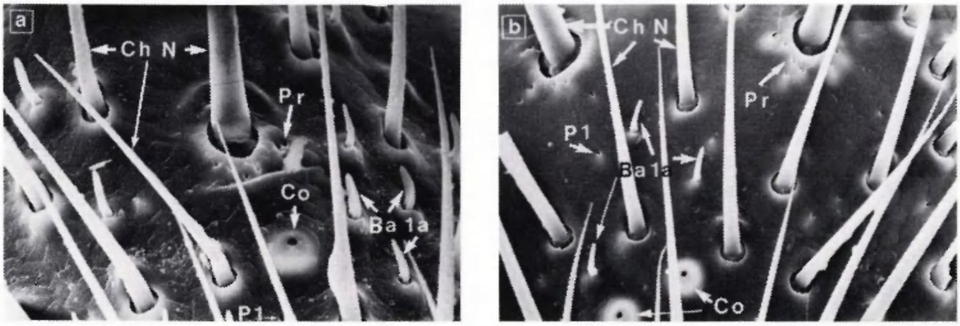

Fig. 14. Sensilla forms and sexual dimorphism in *Abax parallelus*; a) male, 8th antennal segment, apical part, × 500; b) female, 6th antennal segment, apical part, × 375. For abbreviations see Appendix.

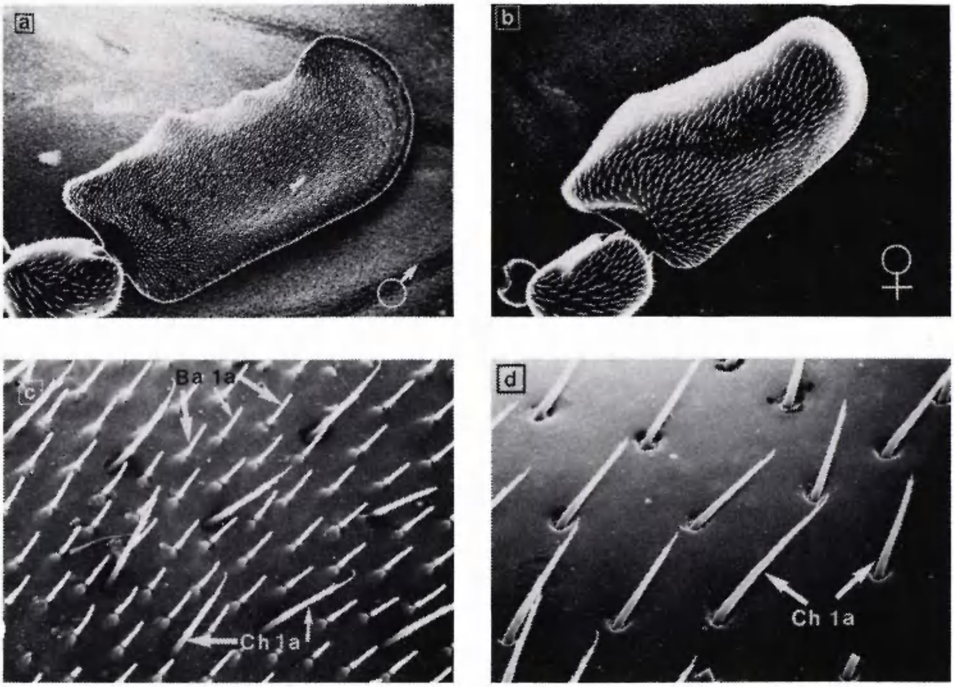

Fig. 15. Sexual dimorphism in the antennal clubs of *Paussus centurio* Dohrn (syn.: *P. bennigseni* Wasm.); a) male, × 20; b) female, × 20; c) magnified section of a), × 250; d) magnified section of b), × 250. For abbreviations see Appendix.

females they occur only in the region of the subapical sensory field and are not present on the disk. The shape of the antennal club itself can likewise differ greatly between males and females (cf. *Paussus centurio*, Fig. 15), or it can be practically identical (cf. *Paussus arabicus*, Fig. 16). In previous studies (Nagel 1977) the antennal club of males was described as granular and that of females as punctate. The reason for this becomes evident from the SEM investigation: the sensilla basiconica, type 1a, each inserted behind a cuticular granule, give the surface of the antennal club a granular appearance.

Whether or not this sexual dimorphism constitutes an adaptation to myrmecophilous mode of life, cannot yet be answered. Usually, the sensilla basiconica are chemoreceptors and might in this case help the males to spot the females. The probability that they have an olfactory function is supported by the observation that males tend to be caught at light much more frequently than females, thus appearing to be more active than females in searching for their sexual mates. On the other hand, Schneider, Lacher & Kaissling (1964) (cf. also Schneider 1963) found the sensilla basiconica of *Antheraea pernyi* (Asiatic silk-moth, Saturniidae) responded to food odours, but not to the sex attractant (pheromone).

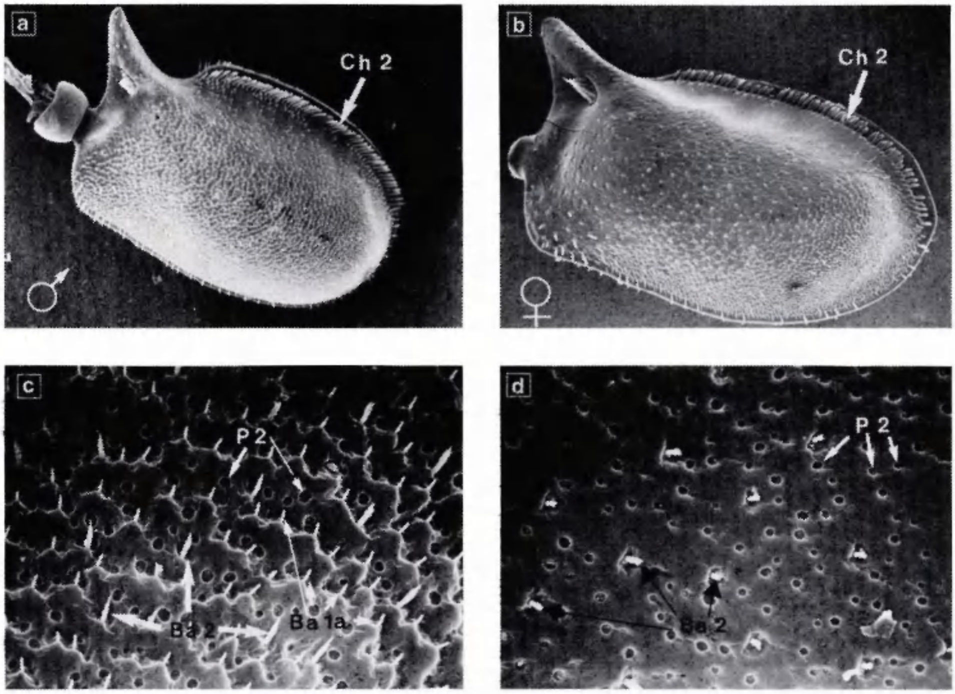

Fig. 16. Sexual dimorphism in the antennal clubs of *Paussus arabicus*; a) male, × 20; b) female, × 25; c) magnified section of a), × 175; d) magnified section of b), × 175. For abbreviations see Appendix.

REFERENCES

ANTOINE, M.: A propos de *Paussus favieri* Fairm. – Entomologiste **6** (6): 170–171 (1950).

ANTOINE, M.: Notes d'Entomologie Marocaine. LV. Additions et Remarques Taxonomiques. – Bull. Soc. Sci. Nat. Maroc. **31**: 103–119 (1951).

BURMEISTER, M. H.: Observation sur les affinités naturelles de la famille des Paussidae. – Mag. Zool. 1841, Insectes, note **76**: 1–15, planche 76 (1841).

CALLAHAN, P. S.: Insect antennae with special reference to the mechanism of scent detection and the evolution of the sensilla. – Int. J. Insect Morphol. & Embryol. **4** (5): 381–430 (1975).

DARLINGTON, P. J. : Paussid Beetles. – Trans. Am. Entom. Soc. **76**: 47–142 (1950).

DETHIER, V. G.: The Physiology of Insect Senses. – London, New York, 1963.

HARBACH, R. E. & J. R. LARSEN: Fine Structure of Antennal Sensilla of the Adult Mealworm Beetle, *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). – Int. J. Insect Morphol. & Embryol. **6** (1): 41–60 (1977).

JANSSENS, E.: Sur la Massue antennaire de *Paussus* LINNÉ et Genres voisins. – Bull. Inst. Roy. Sci. Nat. Belg. **25** (No. 22): 1–9 (1949).

JUBERTHIE, C. & Z. MASSOUD: L'Equipement sensoriel de l'Antenne d'un Coléoptère troglobie, *Aphaenops cryticola* LINDER (Coleoptera: Trechinae). – Int. J. Insect Morphol. & Embryol. **6** (3/4): 147–160 (1977).

Kolbe, H.: Die Einstammigkeit der Paussiden und die primitiven Gattungen dieser myrmekophilen Coleopterenfamilie. – Zool. Anz. **72** (5/8): 205–218 (1927).

Luna de Carvalho, E.: Notas sobre Paussideos (Col. Carab. Isochaeta). – Publ. Cult. Comp. Diam. Angola **48**: 47–90 (1959).

Luna de Carvalho, E.: Are there Termitophilous Paussid Beetles? (Coleoptera Carabidae Paussinae). – Sociobiology **3** (1): 67–70 (1977).

Nagel, P.: Revision der *Paussus armatus* – Gruppe (Coleoptera, Carabidae, Paussinae). – Stuttgarter Beitr. Naturk., Ser. A, Nr. **293**: 1–95 (1977).

Raffray, A.: Matériaux pour servir à l'étude des Coléoptères de la famille des Paussides. – Nouv. Arch. Mus. Hist. Nat., 2^e sér., **8**: 307–359, t. 15–19 (1885) & **9**: 1–52 (1886).

Reichensperger, A.: Die Paussiden Afrikas. – Abh. Senckenb. Naturforsch. Ges. **479**: 3–33 (1948).

Schneider, D.: Vergleichende Rezeptorphysiologie am Beispiel der Riechorgane von Insekten. – Jb. Max-Planck-Ges. 1963: 150–177 (1963).

Schneider, D., V. Lacher & K.-E. Kaissling: Die Reaktionsweise und das Reaktionsspektrum von Riechzellen bei *Antheraea pernyi* (Lepidoptera, Saturniidae). – Z. vgl. Physiol. **48**: 632–662 (1964).

Schneider, D. & R. A. Steinbrecht: Checklist of Insect Olfactory Sensilla. – Symp. Zool. Soc. London **23**: 279–297 (1968).

Snodgrass, R. E.: Principles of Insect Morphology. – New York, London, 1935.

Snodgrass, R. E.: Anatomy of the Honey Bee. – Ithaca, 1956.

Wasmann, E.: Vergleichende Studien über Ameisengäste und Termitengäste. – Tijdschr. Entom. **33**: 27–97 (1890).

Wasmann, E.: Die Myrmekophilen und Termitophilen. – C.-R. Séances 3^{eme} Congr. Int. Zool. 1895: 410–440 (1896).

Wasmann, E.: Zur näheren Kenntnis des echten Gastverhältnisses (Symphilie) bei den Ameisen- und Termitengästen. – Biol. Zentralblatt **23**: 63–72, 232–248, 298–310 (1903).

Wasmann, E.: Die Paussiden des Baltischen Bernsteins und die Stammesgeschichte der Paussiden. – Bernstein-Forsch. **1**: 1–110, t. 1–7 (1929).

Yung, C. Mou: Morphologische und histologische Studien über Paussidendrüsen. – Zool. Jb. (Anat.) **64**: 287–346 (1938).

APPENDIX

Abbreviations used in figures and text.

Ba 1a	Sensilla basiconica type 1a
Ba 1b	Sensilla basiconica type 1b (app. twice as long as Ba 1a)
Ba 2	Sensilla basiconica type 2 (strongly grooved surface)
Ch N	Sensilla chaetica 'normal type' (faintly and longitudinally corrugated surface)
Ch 1a	Sensilla chaetica type 1a (dentate)
Ch 1b	Sensilla chaetica type 1b (app. 4 times as thick as Ch 1a)
Ch 2	Sensilla chaetica type 2 (strongly grooved surface, large)
Ch 3	Sensilla chaetica type 3 (very thick, smooth, pointed)
Co	Sensilla coeloconica

P r	Pores circularly arranged round the base of sensilla (outer orifices of the glandular excretory canals)
P 1	Pores simple, in level with the surface
P 2	Pores at the base of flat pits
S	solidified glandular secretion
Tr	Sensilla *trichodea*

THE EVOLUTION OF PARENTAL CARE PHENOMENA IN PTEROSTICHINE GROUND BEETLES, WITH SPECIAL REFERENCE TO THE GENERA *ABAX* AND *MOLOPS* (COLEOPTERA, CARABIDAE)

Pietro Brandmayr – Tullia Zetto Brandmayr

Istituto di Zoologia, Università di Trieste, via Valerio, 32, I-34100 Trieste, Italia

Abstract

A first synthesis is given of presocial evolution in Pterostichini. As far as is known, in this group of Carabidae brood care behaviour does not go beyond the 'Brutfürsorge' stage (sensu Melber and Schmidt), and true mother-larvae families have not developed. Starting from a direct pushing of the eggs into the soil (Brutvorsorge Ia), as is observed in most Carabidae, a higher specialized 'moulding use' of the ovipositor apparatus leads to the formation of 'loamy ovigerous capsules' for single eggs (Brutvorsorge Ib). This behaviour seems to be connected with a preadaptative value of the laterocaudal lobe of the valvifer (hemisternite IX, lateral tergum part IX), which is present in many tribes of 'higher' Carabidae, including Pterostichini.

An evolutionary development from both kinds of 'Brutvorsorge' has evolved into a more complex postnatal 'Brutfürsorge', in which eggs are laid at the bottom of subterranean nests and the mother sits on them till they are hatched and the larvae are pigmented. As a result of the inactivity of the ovipositor, rudimentation phenomena have been observed in this apparatus. The older the behaviour (geologic age of appearance), the more advanced are the phenomena.

The relations between behaviour and evolution have been studied in great detail in the genus *Abax*, for which a phyletic tree is given, showing the distribution of the three types of maternal habits within this taxon and their relationship with the adaptive radiation. The selective pressures involved and the adaptive value of 'watch' on eggs have been discussed in detail, especially within the genus *Molops*, where a further specialization of behaviour was attained by coinciding with an imaginal aestivation, perhaps as a consequence of a cold-moist geological period.

Finally, some of the current views on the relationships between behaviour and evolution in connection with taxonomy have been examined. A superiority of morphological characteristics over behavioural ones is emphasized. Moreover, reproductive behaviour may also play a role as 'pacemaker' in evolution, at least at generic or subtribe level: in fact, *Molops* must be considered the result of a cladogenesis induced by parental care.

Introduction

In this paper we have tried to give a first synthesis on the possible evolution of behaviour connected with parental care in Pterostichine ground beetles, with special emphasis on the best studied genera *Abax* and *Molops*. Phenomena of this nature are considered by socio-biologists as first steps in the social evolution ('Soziogenese') of an animal group. Instead of merely considering our beetles as 'presocial', or even as 'subsocial' (WILSON, 1971), we prefer the more detailed classification proposed by MELBER and SCHMIDT (1977) for Heteroptera, another group where, as in Carabidae, typical eusocial behaviour has not been detected. Based on real connections between the female and its larvae, these authors modify the classical difference between 'Brutfürsorge' (behaviour patterns up to egg laying) and 'Brutpflege' (parental care after egg laying; see WEBER, 1930; v. LENGERKEN, 1939). They recognize three steps of complexity among the behaviour types which together are generally called 'presocial', i.e. characteristic of insects showing specific activities for the survival of the offspring:

1. Precautionary measures for the development of the eggs (Brutvorsorge), i.e. all activities which will result in a lower death rate of eggs and larvae, but only up to oviposition (it is even possible to distinguish between a nutritional care, 'Nahrungsvorsorge', and protective care, 'Schutzvorsorge').

2. Brood care in a strict sense (Brutfürsorge), i.e. those cases in which activities favouring the survival of the offspring are continued after egg-laying, by both parents or the female only. Nevertheless, no direct contact takes place between eggs or larvae and adults, there is only passive protection ('passive Brutpflege' of DINGLER, 1932).

3. The nursing of the offspring (Brutpflege), consisting of a direct care of eggs and larvae, such as cleaning and turning over the eggs, or breeding the larvae by secreting substances ('trophallaxis'), this could be called 'aktive Brutpflege'.

Hereafter for the sake of brevity we shall use the German terminology, which permits the greatest concision. This classification by MELBER and SCHMIDT (1977) seems to apply very aptly to Carabidae, predator Coleoptera whose presocial behaviour, as far as is known, does not go much beyond that of Heteroptera. In fact, all parental care observed among Pterostichini does not surpass the level of 'Brutfürsorge'. The level of 'Brutpflege', according to the previous terms, was reached in the Ditomina subtribe of Harpalini: for *Carterus calydonius* BRANDMAYR and BRANDMAYR-ZETTO (1974) were able to describe the rearing up to pupation of eyeless larvae that were almost not able to walk, in a subterranean nest supplied with plant seeds. A direct interaction can be supposed between female and larvae since they must live together in a limited space for some months. We may perhaps assume that olfactory and/or tactile stimuli will induce the mother to release the food for the larvae.

We will first describe each kind of parental behaviour in the Pterostichini. Next we will discuss links between morphological features and behaviour, the possible phylogeny of behaviour patterns, and the selective pressures that might have played a part in the origin of the phenomena described. Finally, in the cases of the genera *Abax* and *Molops* we will attempt to estimate the geological age of parental care and speculate about its relationship in the general course of evolution.

I – Brutvorsorge

Ia – The most widespread and less complex type of parental behaviour in Pterostichini is the direct pushing of the eggs into the earth, as in the other Carabidae. This occurs by means of the ovipositors digging work, especially by the two-jointed appendages of the IX abdominal segment (called styli by most authors, gonocoxae by BILS, 1976). KIRCHNER (1927) and STURANI (1962) have given a more or less detailed description of the oviposition sequence for the genus *Carabus*. BAUER (1971, 1974) was able to observe this behaviour in *Asaphidion* and *Elaphrus* and to recognize some fixed motor patterns. During a first phase, the abdomen – after a tactile exploration of the soil surface – is pushed into the earth and a hole is both dug and widened by moving the abdomen to and fro. At the same time the gonocoxae move up and down together forming a small hole in which the egg is deposited. After the abdomen has retreated, the opening is covered with soil by oscillating movements of the apex (this last phase has not been observed in *Elaphrus*, an inhabitant of very wet soils).

Although we have no detailed notes about the digging use of the gonocoxae in Pterostichini, we think that it is not very different from the description by BAUER and STURANI. However, oviposition frequently occurs deeper (about 2–3 cm below the soil surface), therefore this or similar behaviour is probably only shown by the female after she has crawled into the soil. The eggs of *Poecilus koyi*, for example, were found in small holes 2–3 cm deep in our terrarium (BRANDMAYR, 1973). In other species the eggs simply adhere to a little humus clot, without any well-formed hole (e.g. *Calathus glabricollis*, pers. obs.).

Ib – The second level of complexity of 'Brutvorsorge' in the Pterostichini concerns the construction of mud cells for single eggs ('ovigerous capsules'), which are attached to stones, mosses or other litter components. Such behaviour was observed for the first time by BARGAGLI (1874) in *Percus* (a Molopine genus). Afterwards the same was found for several tribes of Carabidae: for Chlaeniini (RILEY, 1884; CLAASSEN, 1919); Galeritini (KING, 1919); Brachinini (KING, cit., ERWIN, 1967); Lebiini (CHABOUSSOU, 1939; in *Tecnophilus*, according to LARSON's observations, the females also construct a silk-like string).

Such behaviour seems to be very common among Pterostichini, having been observed not only in *Percus*, (see also the recent data by LUMARET, 1971), but also in many species of *Abax* (LÖSER, 1970; 1972; BRANDMAYR and BRANDMAYR-ZETTO, 1974; BRANDMAYR, 1977) and *Pterostichus* (BRANDMAYR, 1977, on *Pt. justusi*), in *Platynus* (syn. *Agonum*) *dorsalis* (DICKER, 1951 and KRECKWITZ, 1978), *Calathus melanocephalus* (VAN DIJK, pers. communication), finally in *Lesticus magnus* (HABU and SADANAGA, 1969, see photo at p. 121).

In *Abax* this behaviour can be described as follows (according to observations by LÖSER, 1972 and BRANDMAYR, 1977):

a. The gravid female reaches the dampest place in the terrarium, stretches the invaginated abdominal segments and, moving the styli around, gathers more and more little particles of loam around the ovipositor till the end of the abdomen is completely covered with a thin coat of soft mud, even under the elytra.

b. Afterwards the female walks about with the muddy loam stuck to the abdominal apex. This part of behaviour lasts longest, sometimes 15 minutes.

c. The female approaches the selected substrate and presses the abdomen against it. The egg is thus laid in a cylindrical transverse hole shaped in the earth by the styli, the posterior lobes of the valviferi and the membraneous sternal area of segment IX (sternum X of BILS, cit.). During this time a repeated swelling of the loamy sheath has been noticed. When the egg has been laid, the cell is closed by the dorsal flap which sticks like a lid to the ventral one. Finally, the apex of the abdomen seals the capsule by horizontal sideway movements. This third phase is very short, not more than two minutes.

Platynus dorsalis often dips the abdomen into little droplets of water during the a. phase, in order to make the construction of the muddy bowl easier (KRECKWITZ, 1978).

Percus navaricus previously prepares (i.e. makes soft) the loam with the help of intensive mandible movements (LUMARET, 1971).

The structure of the earth sheaths is described in detail by BRANDMAYR (1977).

The significance of the above behaviour is probably a protection not so much from desiccation as from fungal attacks (LÖSER, 1972; BRANDMAYR, 1977). The location of the cases differs according to the habitat preferences of the species of *Abax* concerned. Forest-dwelling representatives of the genus (e.g. *Abax exaratus*) put the ovigerous capsules arbitrarily on the lower or the upper side of stones, on contrary to the species from the upper montane and alpine open formations, which put the egg-capsules only on the lower side, thus protecting them from strong radiation and dry atmosphere.

II – Brutfürsorge (sensu MELBER *and* SCHMIDT; *Brutpflege of other authors)*

Symbol II represents the phenomenon described for the first time by BOLDORI (1933) in *Pterostichus (Oreophilus) multipunctatus*, and apparently restricted to Pterostichini (subtribes Pterostichina and Molopina). The females dig out a cell into the soil or in logs, just like the cell made for hibernation or aestivation, they deposit their eggs in it and rest upon them until the larvae have hatched and become pigmented. Two to three days after hatching the first instar larvae disperse. During the time they remain in the nest, the females do not take food, living of the body fat. The embryonic development is rather long, from about 14 days in *Pt. anthracinus* (at 18°C) to 30 (*Abax ovalis*, 15°C) or even more (*Molops*). In spite of the long stay in the nest, close to the eggs, most students are convinced that the beetles neither clean the eggs with their mouths or manage them in any other way (except KOMAREK, 1954, in *Molops piceus*). On the contrary, the female's movements often cause a casual mixing of the eggs, which get more and more covered with loam particles. Very interesting is also the total lack of any escape or defence reaction by the mother (except in *Tanythrix senilis:* RAVIZZA in

Leonardi, 1969, mentions egg protection by biting males of the same species).

For two days after hatching the group shows the appearance of a loose mother--larvae 'family', however unstable it may be (Melber and Schmidt, cit., for terminology). The individuals neither recognize each other (i.e. their being conspecific), nor is there any apparent aggregation between the larvae. The possibility of the existence of such a 'family' is due to the transitional lack of cannibalism in the mother and between the larvae, whose predatory motivations are apparently inhibited by the last yolk supplies. The relationship ends when the larvae become pigmented and begin to move, these movements probably stimulate the mother to desert the nest.

While in many mother-larvae families of Heteroptera the reference point for the mother is the group of eggs or larvae, for the nest-building Pterostichini it seems to be the cell itself. As a matter of fact, females of *Molops striolatus* go on guarding the empty nest for a long time, after having devoured their eggs because they had been short of water. On the other hand, when females of *M. ovipennis* were taken from their nest and put into another cell together with their own eggs, they devoured them and abandoned the artificial nest. Oviposition concentrated in a subterranean nest, lack of escape behaviour and of predatory motivation in the mother, embryonic supplies and the absence of defensive reactions by the larvae are the main characteristics of this phenomenon. The matter requires further experimental attention.

The significance of such brood care has probably to be found in a protection of the eggs from fungal attacks (Komarek, 1954; Löser, 1970) during a rather long embryonic development (Brandmayr and Brandmayr-Zetto, 1974). In fact, Lampe (1975) has observed a higher death-rate for eggs of *Abax ovalis* kept away from the maternal cell, and some nests of *Pterostichus morio samniticus* holding eggs forsaken by the mother, were invaded by a thin mould layer (pers. obs.).

IIa – In the least complex stage of this behaviour, the life cycle of the adults is not yet influenced. On the contrary, the adults are constantly active during the whole favourable season, although with oscillations due to meteorological events (see phenology of *Pt. (Cheporus) metallicus*, Weidemann, 1971, and of *Abax ovalis*, Lampe, 1975). It has been observed that the eggs were watched over without remarkable modifications of the annual pattern of locomotory activity of the imaginal population in some species of the following genera: *Abax*, 2 spp.; *Pterostichus* (subgen. *Oreophilus*, 3 spp.; *Cheporus*, 2 spp.; *Pseudomaseus*, 1 sp.). For the authors, see Brandmayr, 1977, table II; Thiele, 1977, table 17, p. 78.

IIb – In the genus *Molops** (5 species studied in all, see table II in Brandmayr, 1977) the guarding of the eggs in subterranean nests has become integrated completely into the life cycle of the adults. During the summer the beetles have withdrawn under deep stones and not even the juveniles show surface activities: pitfall data (Brandmayr,

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*For the closely related genus (or subgenus) *Tanythrix* no pitfall data are available.

1977). At the same time the reproductive females dig their nests and lay a small number (from 5–12) eggs. In the IIa group the number of eggs is generally much higher (between 15 and 30 per nest), little is known of the possible occurrence of a second reproduction.

II(Ib) – This is the isolated case of *Pterostichus (Oreophilus) morio samniticus*, found guarding its eggs (usually over 20) covered with an earth layer in a subterranean cell on the alpine prairie of Mt. Terminillo (Lazio, Italy, central Apennine). The egg cases were not fixed to the bottom of the nest and were thinner than those described in Ib, consisting of a simple, not continuous layer of finest humus particles around the chorion. Sometimes the cases were broken, perhaps as a consequence of the female's movements. Such ovigerous capsules possibly should be considered as remnants from a phylogenetically older behaviour, homologous to the 'Brutvorsorge' Ib, that is observed in a IIa kind of Brutfürsorge'.

THE EVOLUTION OF BEHAVIOUR PATTERNS IN RELATION TO MORPHOLOGICAL FEATURES AND POSSIBLE SELECTION PRESSURES

Our knowledge of intermediate stages of parental care other than that described is poor and incomplete. Also information from the study of possible homologies in behavioural elements is scanty, because there are few direct records of behaviour (especially concerning the fixed motor patterns). Nevertheless, we can try and outline a first impression of the limited presocial evolution of the Pterostichine Carabids. Morphological studies on the ovipositor apparatus of the above species appeared to be of great help for the better understanding of these phenomena. Firstly we can consider the 'Brutvorsorge' Ia as a starting point, taking into account its wide diffusion in all the Carabidae (see fig. 1). A more complex use of the ovipositor marks the transition to the 'Brutvorsorge' Ib, in which the earth is not so much dug out but moulded after having been collected as a muddy bowl on the abdominal apex. We observe a moulding use of the egg-laying apparatus, that is very different from the digging one. Nevertheless, some fixed patterns may be considered homologous, such as the sealing by transverse movements of the abdominal apex. The occurrence of such a behaviour in some groups of Carabidae, other than Pterostichini, might possibly be described in terms of morphological preadaptations. All the tribes quoted on pag. 37 show well formed laterocaudal lobes at the valviferi ('lateraler Tergalteil IX' of Bils, hemisternites IX of the other authors), which probably facilitate the formation of the transversal hollow into the earth case in which the egg is laid. The comparison between the digging ovipositor of *Carabus* and the moulding one of *Abax* is dealt with in more detail by Brandmayr (1977). We can infer the ability to make a hole in more compact substrates, not only from the greater sclerification and the lack of a posterior membranous lobe of the valvifer, but also from the 'rami' (according to Bils, loc. cit.), i.e. the residues of the VIII segment's genital appendages, which moreover could be a better protection of the genital opening.

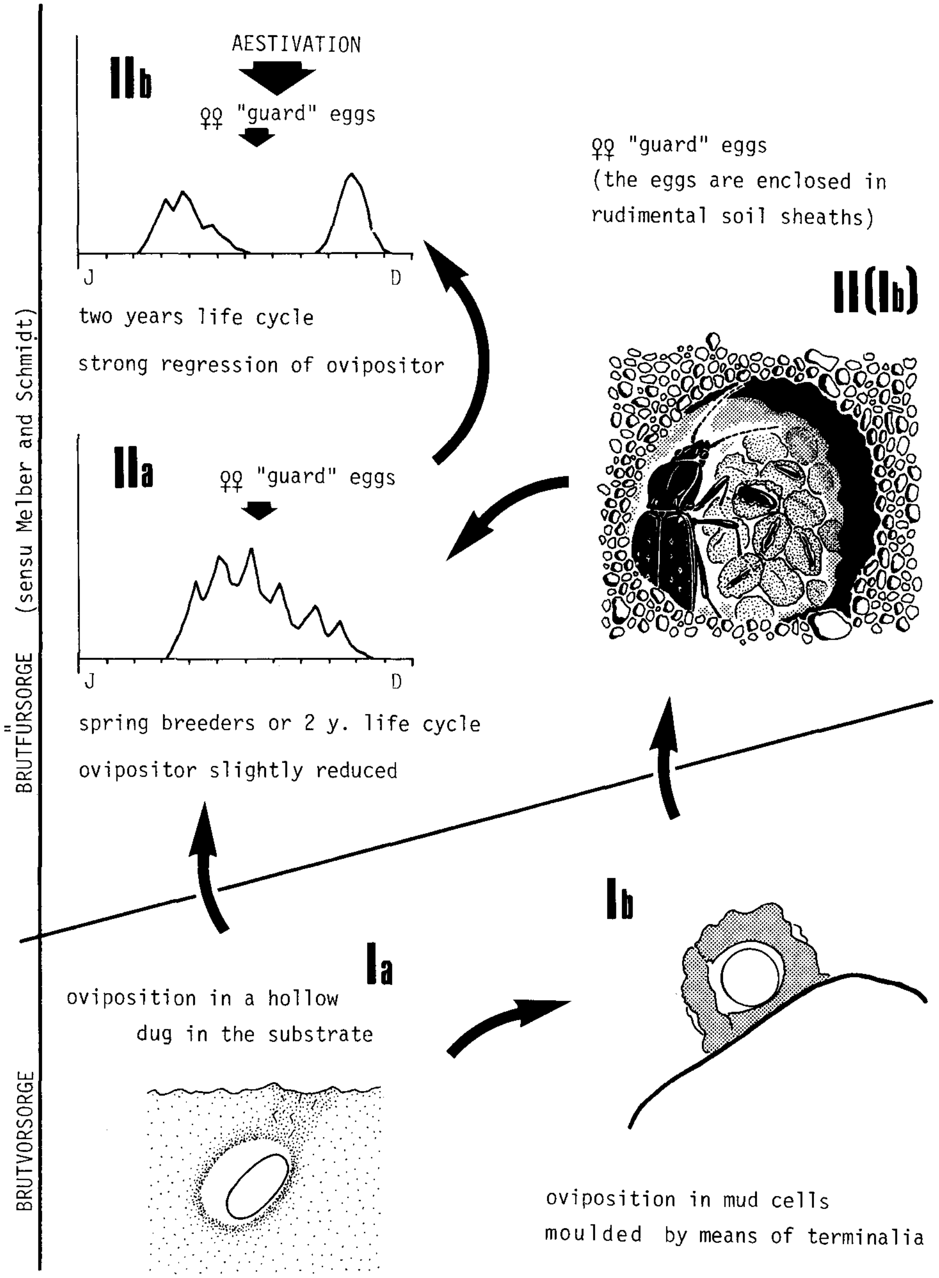

Fig. 1. Synthetic outlines of parental care evolution in Pterostichini. For each behaviour type the main evolutionary features are given. Arrows show the hypothesized routes from one to another. Ib shows a cross section of an ovigerous mud cell. II (Ib) is redrawn from a photo.

A posterior lobe at the valvifer is present in a group of more advanced tribes, including Conchifera and Balteifera of JEANNEL (1941–42), with also some lines of the Stylifera, as Bembidiini. The best overlapping can be found with the phyletic group '2.4.1.' of the Adephaga system suggested by BILS on the basis of female genitalia, which includes all the tribes mentioned on pag. 37. Support for this assumption is the almost complete absence of the genital appendage VIII, one of the newly evolved (synapomorphic) features of this group (see BILS, cit., pag. 158 and table 1).

The next transition to the 'Brutfürsorge' has quite different morphofunctional implications. It consists of a disuse of the ovipositor itself, for the eggs are simply laid on the nest floor. All the species involved show a regression of this apparatus, ranging from a little simplification of the sensorial equipment (as in *Pt. metallicus*), through a dimensional reduction of the styli-valviferi complex (*Abax ovalis*, *parallelus*), to a complete rudimentation (*Molops*, *Tanythrix senilis*, see figs. VII, VIII, XV and XVII in BRANDMAYR, cit.). Highly significant, we observe that the maximum reduction in terminalia has been noted in group IIb (*Molops*), where the Brutfürsorge takes place during the imaginal aestivation.

The evolutionary lines of behaviour patterns could be hypothesized as in fig. 1. We can deduce from it that post-natal brood care II may be reached in two different ways. It may be attained starting from both levels of 'Brutvorsorge', Ia and Ib, as testified by the possible homology of the rudimental earth sheaths of *Oreophilus morio samniticus*.

According to all authors the significance of the parental care should be a lower death rate of the offspring. Thus, parental care may result in less eggs and possibly also in conservation of energy. The smallest egg numbers (5–12) are noticed in *Molops*, the genus with more specialized behaviour.* At the same time we can observe in these Carabidae a reduction in the number of the ovarioles (4 per ovary in *Molops ovipennis*). A smaller number of eggs has been noted also in the presocial evolution of Heteroptera by MELBER and SCHMIDT, 1977: from a maximum of 500 it is decreasing to 50–20 in species with Brutfürsorge (even 8–12 in the Phloecidae *Phloephana longirostris*).

The occurrence of all the adaptations correlated with the guarding of eggs in subterranean cells is very interesting. Some authors (HORION, 1956; THIELE, 1977) had already emphasized that they usually appear in species with a montane distribution (except *Pt. anthracinus*). A more detailed study of many of their biological characteristics (BRANDMAYR, 1977) has led to the following conclusions:

a. The species comprise mainly micropterous beetles (except *Pt. anthracinus*, dimorphic).

b. The species were originally forest-dwellers.

c. The species have a two-year life cycle (with the exception of *Pt. anthracinus* and *Abax parallelus*, spring breeders).

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*The problem of the egg number in Carabidae is dealt with in LAMPE (1975) and THIELE (1977). See also: VAN DIJK in this volume.

d. The species embryonic development is relatively longer than in other Carabidae, reaching a maximum in *Molops*.

This last feature could be an adaptation to the cool-fresh humus layers of montane soils, inducing a selective pressure which has favoured the development of the 'Brutfürsorge' as a protection against fungal attacks the risk of which was increased by prolonged embryonic periods. Such parental behaviour probably arose during wet-cold geological periods, when this kind of selective pressure will have been strongest. The aestivation in *Molops* could also mean an adaptation to a cooler climate. As a matter of fact these ground beetles show activity peaks displaced towards the winter, and are the only Carabidae, that are to be found frequently under stones in December and January (many observation-years in the Triestine Karst).*

Moreover, at this stage of our investigations, we cannot omit the possible relationship of this behaviour to the 'life tactics' that many authors refer to as the dualism of 'K- and r-selection'. The pattern of adaptation mentioned above should collocate the Pterostichini with post-natal brood care on the K-extreme of a possible 'r-K continuum' of the Carabidae. This could mean a change in reproductive strategy of species living in stable environments (montane forests!). A small number of eggs may concur with a low intrinsic growth-rate, a two-year life cycle and a low dispersal power (monomorphic brachypterous state), which are typical for 'K-selected species (for the main features of this type of selection see for example Remmert, 1978).

BEHAVIOUR AND PHYLOGENESIS. THE PROBLEM OF THE HISTORIC AGE OF BROOD CARE

To elucidate the relationships between presocial behaviour and evolution in Pterostichini it was necessary to investigate an entire genus displaying as wide a variety of parental behaviour as possible. We chose the genus *Abax*, and have first submitted it to a taxonomic revision (still in progress, Brandmayr, 1976) on a morphological and biogeographical basis. *Abax* as a whole is an euroanatolic taxon with 17 species, part of them inhabiting Central Europe, most of them, however, showing small distribution areas on the southern border of the Alps. These are often limited to the so called 'massifs de refuge', i.e. the ice-free areas of the glacial periods.** A phyletic tree has been constructed employing the cladistic method of Hennig (1966) as slightly modified by Noonan (1973). A distinction has been made at first between the primitive (plesiomorphic) and derivative (apomorphic) state of characteristics and this was followed by identification of relationships by synapomorphy (searching the common derivative characteristics), taking into account the most evident morphoclines. Finally, a clarifi-

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*More recent pitfall data confirm these observations: *Molops ovipennis* individuals have been found in February on the surface of the formol, which had been frozen six weeks previously.

**Holdhaus (1954) gives a detailed description of the faunal features of the 'massifs de refuge'.

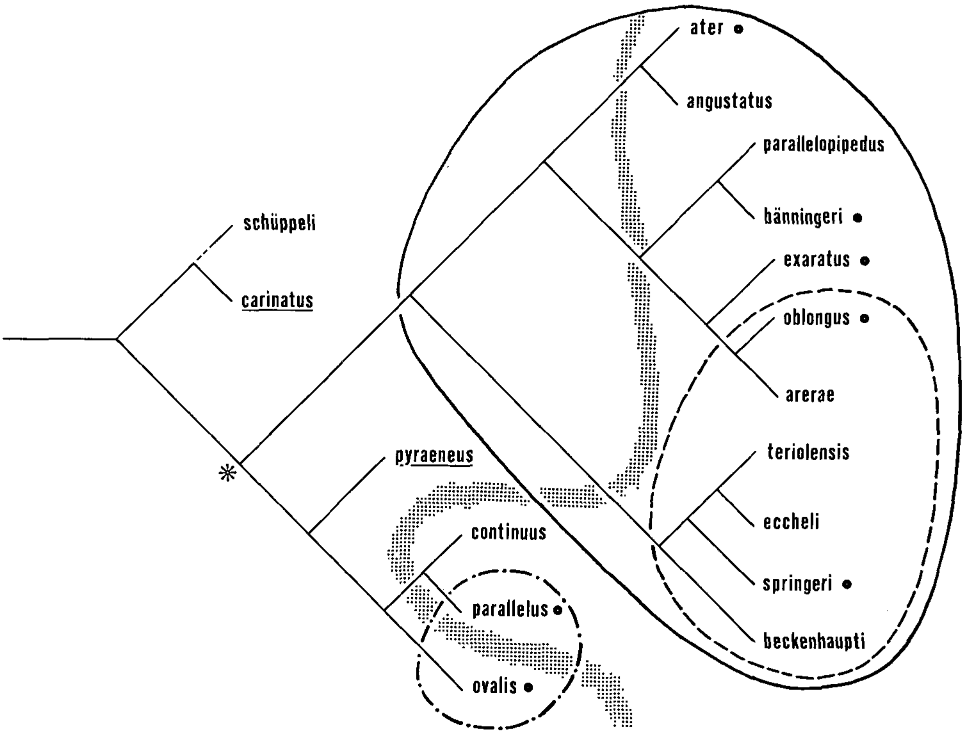

Fig. 2. Distribution of the parental behaviour kinds in the phyletic tree of the genus *Abax*. The asterisk marks the main divergence of the Pliocenic period, (see the text). The continuous line encloses the phyletic group showing behaviour Ib (mud cells). The broken one encloses the species of alpine open formations. Dots and dashes surround the paraphyletic group of 'egg watchers' (IIa). The underlined names belong to the species with the primitive behaviour Ia. Black circles mark all other taxa whose parental behaviour is known. The dotted stripe means the isochronic line separating pliocenic from quarternary divisions.

cation was sought on a chorological basis. Ethological data on parental care were added, obtained by rearing specimens, from the literature or by extrapolation from ovipositor morphology (see table I in BRANDMAYR, 1977). Fig. 2 shows the distribution of presocial behaviour within the *Abax* phyletic tree. The genus may have originated from a prequarternary taxon of continental Europe. The separation of two species from Eastern Europe – for one of which primitive 'Brutvorsorge' Ia has been ascertained (*A. carinatus*) – may be dated back to the Pliocene. In the same period possibly the most significant bifurcation of the genus occurred, when the *pyraeneus-parallelus-ovalis*-group became independent (with the derivative feature: last tarsal joint without a double range of spines). 'Brutvorsorge' Ib probably appeared at this point in the sister group of the above, the so called *ater*-group, because all the species studied so far show the same behaviour and normal genitalia. In this group the greatest variety of environmental preferences are to be found. Upper-montane or alpine meadow-dwelling taxa have twice separated within the *ater*-group during a mainly quarternary evolution (*beckenhaupti*- and *oblongus*-subgroups). On the contrary, no cases of 'Brutvorsorge' are recorded for the exclusively forest-dwelling *ovalis*-group, but only two cases of 'watch on eggs' in subterranean nests of the less specialized IIa type (*ovalis*, *parallelus*). These two species are the only ones showing some reduction of the styli-valviferi complex, but their ethological group is probably paraphyletic (phenetic), in spite of their remarkable morphological likeness. The greatest morphological affinity can be found, in fact, between *parallelus* and *continuus**, whose allopatric distributional areas show a strictly complementary shape (*parallelus* and *ovalis* are largely overlapping). *Continuus* will have originated during a glacial period from *parallelus*-populations isolated in the Po Valley, and shows well-shaped gonocoxae without reduction. This can be considered good evidence not only of the very recent origin of the IIa behaviour, but also of its secondary development in both species. This correlates very well with the moderate reduction level of ovipositors in the above *Abax* species.

There is evidence indicating that in *Molops* the presocial behaviour has primary features. The large number of species of this genus (about 35, if we follow the new revision of MLYNÁR, 1977) show localized distributions in the Balkans (with few exceptions) and have evolved probably from brood care displaying ancestors. All their representatives show strongly reduced ovipositors (noticeable as external features in the rounded hind margin of abdominal sternite VII) and the same life cycle specialization, i.e. aestivation. This supports the likely hypothesis that the genus *Molops* as a whole has to be considered the result of an evolutionary shift induced by the very parental behaviour which might have subjected the original taxon to new selective pressures. The ancestor might have been a Molopine ground beetle with non-specialized life cycle, but already characterized by 'Brutfürsorge' IIa, which shifted to the behaviour IIb as a result of a cold-damp geological period and which was followed by a remarkable allopatric speciation.

The first event may have occurred as a consequence of the progressive cooling down of the climate in the Tertiary era, which reached its climax 2–3 million years ago when, according to SCHWARZBACH (1974), the first climatic oscillations with very cold phases appeared. Important support for the geologically recent origin of the more evolved presocial behaviour in Pterostichini is supplied by the comparative morphological study of the oldest Molopina. They were mainly stenotopic soil-dwelling (endogeous) or cave-dwelling (troglobitic) ancient genera with only one or few species, the relics of oligocenic or at least prae-miocenic forms, which were once living on the land masses around the Thetis, (see JEANNEL, 1924; 1950; FIORI, 1961). As a matter of fact, neither *Speomolops sardous* (from a cave in Sardinia) nor *Typhlochoromus* (from the Carnic Prealps), or *Stenochoromus montenegrinus* (from Yugoslavia) show reduced terminalia (BRANDMAYR, 1977; for the question concerning the possibility of a quarternary evolution in Carabidae, see THIELE, 1977).

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* Supported by a remarkable morphocline of internal sacs.

CONCLUSIONS

The most striking fact of the Pterostichine social evolution is the polyphyletic origin of behaviour. Brood care II, for example, on the basis of the present poor information, must have originated independently at least eight times (*Pt. anthracinus*; subg. *Cheporus; Abax ovalis; A. parallelus; Tanythrix edurus; T. senilis; Molops;* subg. *Oreophilus?*). This assumption is, however, certainly an underestimation. MELBER and SCHMIDT (1977) suppose that the 'Brutfürsorge' in the Heteroptera originated separately at least seven times.

On the basis of evidence concerning the genus *Abax*, we emphasize that it is very difficult to give general rules about the superiority of behavioural or morphological characteristics respectively for the construction of phyletic trees. Therefore at this as well as at a microevolutionary level, the idea of EIBL-EIBESFELDT (1976, p. 244) has not been confirmed: ethological characters are subordinated to morphological ones. This applies particularly to behavioural modifications involving the complete disappearance of some fixed motor patterns and their replacement by quite different ones. In the case of *Abax parallelus* and *ovalis*, concerning some recent behavioural elements, which hardly have affected morphological features, we were able to make a distinction between convergence and monophyletism by means of a morphologic-zoogeographical notion only. STARCK's rule of the superiority of morphology maintains therefore its validity at any taxonomic level.

However, the utmost importance is to be ascribed to behaviour as a causal factor of evolution. THIELE (1977, p. 330) concludes: 'The great wealth of species encountered in the carabid family is closely connected with the manifold modes of behaviour and physiological properties of its species.' In the genus *Abax* a great morphological uniformity coincides with a wide range of presocial behaviours which apparently exerted a certain influence upon the amplitude of adaptive radiation: the greatest variety of environmental preferences are to be found in the group with 'Brutvorsorge' Ib.

According to MAYR (1970) there is a two way connection between behaviour and evolution: 'Behaviour patterns often evolve in the course of phylogeny, but behaviour can also set up new selection pressures...'. With regard to the last phenomenon, the authors distinguish between:

1. Reproductive behaviour such as courtship and parental behaviour, which might be involved especially in the stabilization of the specific isolating mechanisms, and in the production and possible protection of offspring.

2. Environmental behaviour, such as preference for certain kinds of food and/or physical conditions, and the possibility of certain forms of locomotion.

This second type of behaviour, more than the reproductive type, may set up new selection pressures, acting therefore as a 'pacemaker' for the major evolutionary shifts. In his book THIELE (1977) shows a wide range of experimental or inductive indications of the importance of behaviour with respect to environment as a macro- and microevolutionary factor in ground beetles. Our data, however, support the idea that the insects' parental behaviour is a factor in cladogenesis that cannot be neglected in Carabidae, at least at genera or subtribes level. We think that, once selection has fixed parental care in a balanced genotype, such parental care itself leads to the formation of 'a new type of organism', which will then undergo new selective pressures, reacting in different ways to habitat modifications or to different kinds of food. The ancestor of *Molops*, for example, after reaching 'Brutfürsorge' IIa, not only acquired improved survival, but a new way of life, by coupling the guarding of eggs with an imaginal aestivation. During this process (i.e. a transpecific evolutionary separation, or cladogenesis) the ovipositor apparatus became rudimental, and geographic speciation apparently occurred in the course of time.

Reproductive behaviour patterns may thus also act as pacemakers, as we see in eusocial insects. The family Termitidae, for example, by far the greatest among the present Isoptera, stands out not only by the regressive character 'loss of symbiotic flagellates', but also by the derivative condition 'well defined worker caste' (WILSON, 1971, p. 110).

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REFERENCES

BILS, W.: Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung für die Phylogenie. Zoomorphologie, **84**: 113–193 (1976).

BAUER, TH.: Zur Biologie von *Asaphidion flavipes* L. (Col., Carabidae). Ent. Z., **81**: 154–164 (1971).

BAUER, TH.: Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). Oecologia, **14**: 139–196 (1974).

BOLDORI, L.: Appunti biologici sul *Pterostichus multipunctatus*. Studi Trent. Sci. nat. Trento, **14**: 222–233 (1933).

BRANDMAYR, P.: Allevamento di *Pterostichus (Poecilus) koyi goricianus* Müll. e descrizione dei suoi stadi preimmaginali. Boll. Soc. ent. It., **105**: 91–105 (1973).

BRANDMAYR, P.: Revisione del genere *Abax* Bonelli (Coleoptera, Carabidae) su base morfofunzionale, etologica ed ecologica. Atti XI Congr. naz. It. Entomol. (Portici-Sorrento), pp. 65–72 (1976).

BRANDMAYR, P.: Ricerche etologiche e morfofunzionali sulle cure parentali in Carabidi Pterostichini (Coleoptera: Carabidae, Pterostichini). Redia, Firenze, **60**: 275–316 (1977).

BRANDMAYR, P. and T. BRANDMAYR-ZETTO: Sulle cure parentali e su altri aspetti della biologia di *Carterus (Sabienus) calydonius* Rossi, con alcune considerazioni sui fenomeni di cura della prole sino ad oggi riscontrati in Carabidi (Coleoptera, Carabidae). Redia, Firenze, **55**: 143–175 (1974).

CHABOUSSOU, T.: Remarques sur *Lebia grandis* Heutz. Rev. Zool. agric. appl., Bordeaux, (1938), **37**: 163–171 (1939).

CLAASSEN, P. W.: Life history and biological notes on the *Chlaenius impunctifrons* Say. (Coleoptera, Carabidae). Ann. ent. Soc. Amer., **12**: 95–100 (1919).

DICKER, G. H. L.: *Agonum dorsale* Pont. (Col., Carabidae): an unusual egg-laying habit and some biological notes. Ent. mon. Mag., **87**: 33–34 (1951).

DINGLER, M.: Brutpflege bei Insekten. Z. Naturforsch., **9**: 281–287 (1932).

EIBL-EIBESFELDT, I.: Grundriss der vergleichenden Verhaltensforschung. Ethologie, Italian edition, Adelphi ed., Milano, pp. 667, 1976.

ERWIN, T. L.: Bombardier beetles (Coleoptera, Carabidae) of North America: Part II. Biology and behaviour of *Brachinus pallidus* Erwin in California. Coleopt. Bull., **21**: 41–55 (1967).

FIORI, G.: Alcuni appunti sull'entomofauna cavernicola sarda e sui problemi concernenti 11 popolamento delle caverne della Sardegna. Atti Acc. naz. it. Entom., Rendic., **8**: 307–316 (1961).

HABU, A. and K. SADANAGA: Illustrations for identification of Larvae of the Carabidae found in Cultivated Fields and Paddy-fields (Suppl. I). Bull. natl. Inst. agr. Sci. (Japan), S. C, **23**: 113–137 (1969).

HENNIG, W.: Phylogenetic systematics. University of Illinois Press, Urbana, Ill., pp. 263, 1966.

HOLDHAUS, K.: Die Spuren der Eiszeit in der Tierwelt Europas. Abhandl. zool.-bot. Ges. Wien, XVIII, pp. 493, 1954.

HORION, A.: Brutpflege bei montanen und alpinen Carabiden. Nachrichtenbl. bayr. Entomol., **5** (6) (1956).

JEANNEL, R.: Coléoptères nouveaux de Catalogne. Publ. Junta Cjènc. nat. Barcelona, **4** (8): 3–11 (1924).

JEANNEL, R.: Coléoptères Carabiques. Faune de France, 39, 40. Paris, 1941–'42.

JEANNEL, R.: Sur deux Ptérostichides cavernicoles de Majorque. Rev. Franç. d'Entom., **17**: 157–165 (1950).

KING, J. L.: Notes on the biology of the Carabid genera *Brachinus*, *Galerita* and *Chlaenius*. Ann. Amer. ent. Soc., **12**: 382–388 (1919).

KIRCHNER, H.: Biologische Studien über *Carabus cancellatus* Illig. Z. Morph. Ökol. Tiere, Berlin, **7**: 489–534 (1927).

KOMAREK, J.: Mateřská péče u *Molops piceus* Panz. Acta Soc. ent. Čechoslov., **51**: 132–134 (1954).

KRECKWITZ, H.: Untersuchungen zur Fortpflanzungsbiologie und zum jahresperiodischen Verhalten in Temperatur- und Feuchtigkeitsgradienten an Wildfängen und Laborzuchten des Carabiden *Agonum dorsale* Pont. Dissertation, Köln, 1978.

LAMPE, K. H.: Die Fortpflanzungsbiologie und Ökologie des Carabiden *Abax ovalis* Dft. und der Einfluss der Umweltfaktoren Bodentemperatur, Bodenfeuchtigkeit und Photoperiode auf die Entwicklung in Anpassung an die Jahreszeit. Zool. Jb. Syst., **102**: 128–170 (1975).

LARSON, D. J.: A revision of the genera *Philophuga* Motschoulsky and *Tecnophilus* Chaudoir with notes on the North American Callidina (Col. Car.). Quaest. entomol., **5**: 15–84 (1969).

LENGERKEN, H. v.: Die Brutfürsorge und Brutpflegeinstinkte der Käfer. Leipzig, 1939.

LEONARDI, C.: Descrizione delle larve di *Molops senilis* Schaum e *Typhlochoromus* tolzi (Mocz.) e note sulla sistematica larvale di questi due generi di pterostichini (Coleoptera, Carabidae). Ann. Mus. civ. St. nat., Genova, **77**: 609–625 (1969).

LÖSER, S.: Brutfürsorge und Brutpflege bei Laufkäfern der Gattung *Abax*. Zool. Anz. Suppl. **33**, Verh. Zool. Ges., 358–364 (1970).

LÖSER, S.: Art und Ursachen der Verbreitung einiger Carabidenarten im Grenzraum Ebene-Mittelgebirge. Zool. Jb. Syst., **99**: 213–262 (1972).

LUMARET, J. P.: Cycle biologique et comportement de ponte de *Percus (Pseudopercus) navaricus* (Col. Carabique). L'Entomologiste, **27**: 49–52 (1971).

MAYR, E.: Evolution und Verhalten. Verh. Deut. zool. Ges. Köln, **1970**: 322–336 (1970).

MELBER, A. and G. H. SCHMIDT: Sozialphänomene bei Heteropteren. Zoologica, Wien, **43** (127): 19–53. Schweizerbartsche Verlagsbuchh. Stuttgart (1977).

MLYNÁŘ, Z.: Revision der Arten und Unterarten der Gattung *Molops* Bon. (s. str.) (Col. Carabidae). Folia ent. Hung. Budapest, **30** (Suppl. 1977): 3–150 (1977).

NOONAN, G. R.: The Anisodactylines (Insecta: Coleoptera: Carabidae: Harpalini). Classification, evolution and zoogeography. Quaest. entomol., **9**: 266–480 (1973).

REMMERT, H.: Ökologie. Springer Verlag, pp. 269, 1978.

RILEY, G. V.: Annual Address of the President. Proc. ent. Soc. Wash., **1** (1884–89): 23–24 (1884).

SCHWARZBACH, M.: Das Klima der Vorzeit. Third. ed., Enke Verlag, Stuttgart, pp. 380, 1974.

STARCK, D.: Neuere Ergebnisse der Vergleichenden Anatomie und ihre Bedeutung für die Taxonomie. J. Ornith., **100**: 47–59 (1959).

STURANI, M.: Osservazioni e recerche biologiche sul genere *Carabus* LINNAEUS. Mem. Soc. ent. It., **41**: 85–202 (1962).

THIELE, H. U.: Carabid Beetles in Their Environments. Zoophys. and Ecol., **10**. Springer-Verlag, pp. 369, 1977.

WEBER, H.: Biologie der Hemipteren, Berlin, 1930.

WEIDEMANN, G.: Zur Biologie von *Pterostichus metallicus* F. (Coleoptera, Carabidae). Faun.-ökol. Mitt., **4**: 30–36 (1971).

WILSON, E. O.: The Insect Societies. Belknap Press. of Harvard Univ. P., Cambridge, Mass., pp. 548, 1971.

2. Behaviour and ecophysiological functions

INTRASPECIFIC DIFFERENCES IN PHOTOPERIODISM AND MEASUREMENT OF DAY LENGTH IN *PTEROSTICHUS NIGRITA* PAYKULL (COLEOPTERA, CARABIDAE)*

HANS-ULRICH THIELE

Zoologisches Institut der Universität zu Köln, Lehrstuhl für Physiologische Ökologie,
Weyertal 119, D-5000 Köln 41, Federal Republic of Germany

ABSTRACT

Ground beetles of the species *Pterostichus nigrita* from different populations in Central and Northern Europe differ with regard to photoperiodism, measurement of day length, and karyotype. Beetles from Cologne (51 °N) and Rees on the Lower Rhine (51 ° 45′N) show a similar photoperiodism. In both stocks a hibernation dormancy of gonadal maturation takes place which is under the control of photoperiod. Males mature under short day; females need a sequence of short day followed by long day for completion of oogenesis. The discrimination of day length in these stocks is based on a system of circadian photophile and scotophile phases. This could be demonstrated especially by experiments with photoperiods deviating from 24 hrs. The short day dependent steps of maturation were nearly only possible in photoperiods representing multiples of 24 hrs in whole numbers. Short light interruptions during the scotophile phases of an LD 8:40 had a damaging effect on gonad maturation.

These light breaks, on the other hand, had no detrimental influence on a population from Northern Sweden (Lapland, 65 °N). Short day dependent maturation in this population was possible in all photoperiods differing from 24 hrs. From these and other experiments it could be concluded that measurement of day length under short day conditions in this Lapland stock is by no means based on circadian processes, but on some kind of an hourglass mechanism.

Selection experiments starting with the few beetles within the Cologne stock which were able to mature with an LD 8:28 regime showed – even if performed twice with succeeding generations – that the circadian mechanism of day length measurement persisted in those beetles reacting aberrantly, regardless of the fact that a considerable degree of variability can be seen in the Cologne population with respect to time measurement. There seems to be a fundamental difference between the photoperiodism and time measurement of both the Central European populations on the one hand and the Lapland stock on the other.

Whereas the two Central European stocks are equal with respect to photoperiodism, they differ in karyotype. The population from Cologne has 46 chromosomes. The population from Rees has only 40 and does not interbreed with the Cologne beetles. The Lapland beetles also have 46 chromosomes and produce fully fertile offspring with the *P. nigrita* from Cologne, regardless of their physiological differences concerning photoperiodism.

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INTRODUCTION

If one compares many carabids with regard to their morphological shape and their behaviour, one can conclude that closely related species often show greater variations in behaviour than in their body structure.

I have recently reviewed this thesis in my book 'Carabid Beetles in Their Environments' (THIELE, 1977). One can conclude from these observations that the genetic fundamentals of behaviour are more variable than those of body structure and change more quickly during evolution than the external characteristics.

If this assumption is valid, one has to expect that there must often be differences in the behaviour and the physiological properties between different populations of *one* species which show no significant differences in the shape of their bodies. As early as 1932, KRUMBIEGEL was able to demonstrate such differences in European populations of *Carabus nemoralis*, but more recent investigations of this kind concerning carabids are lacking.

We tried to investigate possible variations between populations of *Pterostichus nigrita* Payk. This is a European and western Palaearctic species with an extremely wide geographic range. In the north it nearly reaches the North Cape, southward it populates the whole Mediterranean region of Europe and is also found in Morocco. The westernmost point of distribution is Iceland and, eastward, it reaches as far as Siberia, the Caucasus and Turkey (TURIN et al. 1977, CZIKI 1932–33). Moreover, it is one of the most eurytopic species. This species requires a lot of moisture and is very sensitive to dryness (GERSDORF 1937; THIELE 1967). It can be found in very different habitats, provided that they are humid enough. It was with this far-ranging distribution of *Pterostichus nigrita* in mind that we selected it for the following investigations.

Until now, no serious attempt has been made to describe different subspecies of *P. nigrita* in its wide range of geographic distribution, apart from the discrimination between so-called α and β forms in Italy by BUCCIARELLI & SOPRACORDEVOLE (1958) and the description of the form 'rhaetica' from the Alps of Switzerland, Piemont and Tyrol by HEER in 1837 (cf. HORION 1941).

MATERIALS AND METHODS

P. nigrita has been reared in my laboratory for many years (concerning the methods of rearing, refer to THIELE 1968, and FERENZ 1975a, 1977). We now have several different stocks, including the following:

Cologne, from a water meadow forest in the lowlands (51 °N).

Rees, from a willow shrub located near our field station Grietherbusch on an old branch of the Rhine near Rees on the Lower Rhine (51° 45′ N).

Swedish Lapland, about 65 °N, from several locations in open country.

Istrien (Yugoslavia), from the river banks in the foothills (45° N). I should like to thank Dr. P. Brandmayr, University of Trieste, for providing me with this stock. No experiments have as yet been performed with this population.

The building up of the stocks from Cologne and Lapland is described in greater detail in preceeding papers (THIELE 1977b, c) where all of the methods which were applied are described.

RESULTS AND THEIR DISCUSSION

One of the first indications of differences between the Central European and the Subarctic populations was found by FERENZ (1975b), who demonstrated that the northern Swedish *P. nigrita* develop faster in all temperatures between 10°C and 30°C than the beetles from Cologne. Whereas the difference in developmental time is rather small for the majority of this range (2–6 days faster compared with a total duration of about 4–6 weeks for postmetabolic development from the hatching of the larva until the eclosion of the beetle from the pupa), the difference is most striking at 10°C. Here FERENZ found that the Scandinavian beetles develop in about three months compared with the nearly four and a half months for the Central European beetles. This phenomenon can be interpreted as an adaptation to development in the shorter and cooler northern summers. *P. nigrita* is an adult hibernator with summer larvae.

Differences between the populations with respect to their diel locomotory rhythms of activity are discussed by G. LEYK in another paper from this symposium. She demonstrated that beetles from Central Europe are better synchronized by light-dark changes and show a circadian rhythm in a greater percentage of individuals than do the Subarctic beetles. This again can be explained as an adaptation to the light conditions in the Subarctic midsummer when the sun does not sink below the horizon.

Annual Rhythm and Photoperiodism

In the following, I shall start to discuss some differences in the populations which are connected with their annual periodicity. The annual rhythm of *P. nigrita* from Cologne is determined by a hibernation dormancy of the gonads in the adults. In the females, this is controlled by photoperiod. The ovaries remain undeveloped in constant long day; they mature if the beetles are treated with a sequence of short days (resulting in previtellogenesis = PVG) and then long day (resulting in vitellogenesis, i.e., yolk formation in the eggs = VG). Females therefore are short day-long day animals and become mature in the spring following hibernation (THIELE 1966, 1971). The males only need short day in order to mature (in other words, the formation of spermiozeugmata can take place under short day conditions; THIELE 1971, FERENZ 1975a).

For beetles from Cologne 'short day' means that darkness must prevail for at least 8 hrs during a 24 hr period (THIELE 1977a). We can now understand the annual cycle of *P. nigrita*. During autumn and winter under short day conditions, the first step of ovarian maturation and the maturation of the males take place. The lengthening of the day in spring allows the females to accomplish egg development and full maturation. Thus, photoperiodic signals determine the breeding period of this univoltine species in spring. This is a very important adaptation, since larvae need the warmth of the summer for development (FERENZ 1975b). The species would die out if it would breed in late summer or autumn.

Under those conditions which in Central Europe mean short day for the beetles and allow the maturation steps associated with such a photoperiod (that is, in autumn and spring), it is too cold in Lapland to allow any developmental steps at all. Temperatures round freezing prevail in Lapland until the middle of May and thus neither previtellogenesis nor the maturation of the males could take place if the beetles would react in the same way as those of the Cologne stock, because a short time later the light phases are already 18–20 hrs per day.

It became clear that the photoperiodism of the Subarctic beetles must have properties other than those of the Central European ones. FERENZ (1975b) found that the critical photoperiod below which 'short day' processes are possible in the Lapland stock is shifted about 4–5 hrs into the long day range as compared to the Cologne stock. 19.5 hrs are required for PVG in the females (15.5 hrs in the Cologne stock) and about 22 hrs for the males (17 hrs in the Cologne stock). In other words, a night duration of 2–4 hrs is already enough to enable the maturation processes in this stock that is otherwise dependent on short day. This means that the maturation development which is dependent on considerably shorter day lengths in Central Europe is possible for the Subarctic beetles with the extreme long days of midsummer. I also demonstrated that under continuous light in experiments of prolonged duration, the Lapland beetles could reach 'short day' development, which is quite impossible for the beetles from more southern regions (THIELE 1977c).

Measurement of Day Length

Arriving at this point in our investigations, one might ask how the beetles from the different populations are able to determine the length of day.

Experiments with light interruptions of two hrs duration during the night following a short day gave the following results (THIELE 1977b). VG is possible if light falls into a probably circadian light sensitive phase during the second half of the 24 hr cycle. These

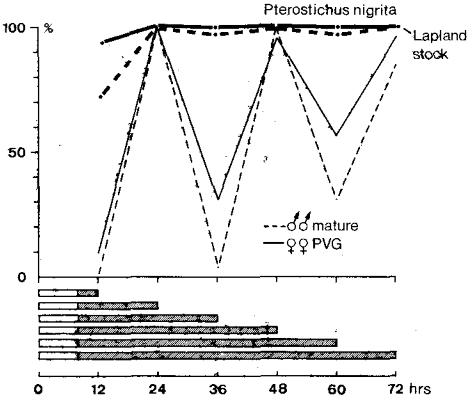

Fig. 1. Maturation of males and females in LD cycles deviating from 24 h. Heavy lines: Lapland stock. Each curve point from experiments with 21–30 specimens (n = 172 females and 163 males). Thin lines: Central European stock from Cologne for comparison. From THIELE 1977c.

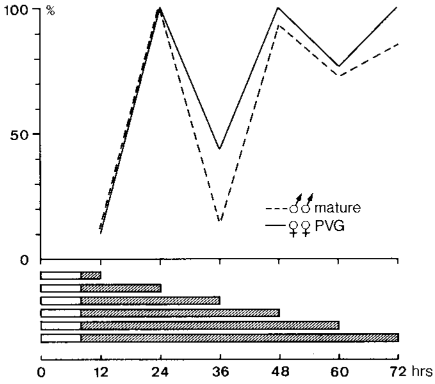

Fig. 2. Maturation of males and females of the population from Rees in LD cycles deviating from 24 hrs. Each curve point from experiments with 25–31 specimens (n = 151 females and n = 136 males). Data for LD 8:16 taken from other experiments.

light breaks are optimal when given about 15 hrs after 'light on'. This applies to both the Central European and the Subarctic populations. In both cases, the critical photoperiod is about 13 hrs per 24 hrs; i.e., VG is only possible after the spring equinox.

On the other hand, there are great differences when we ask how beetles from different regions measure the length of day under short day conditions. From a wide variety of experiments with the Cologne stock, I have concluded that there are scotophile phases in the second half of the day into which no light may fall if PVG or maturation of the males is to be made possible (Thiele 1977b). That these scotophile phases return in a circadian rhythm can be deduced especially from experiments with LD cycles deviating from 24 hrs (Fig. 1). In these experiments, the light phase was invariably 8 hrs combined with dark phases of different lengths. In all cycles which represent multiples of 24 hrs in whole numbers, about 100 % of the beetles showed the 'short day' maturation effects, but none or only a small percentage of the beetles showed maturation when the cycles were uneven multiples of 12 hrs. In the first case there was always darkness during the scotophile phases, in the second case alternating light or darkness. The same experiment with beetles from the 'Rees' stock (150 km or 45′ north of Cologne) produced a similar result (Fig. 2).

Thus, we can interpret the mode of measurement of day length. During late summer, light falls into the scotophile phases and the beetles remain immature. In autumn, winter, and early spring, darkness prevails during the scotophile phases, resulting in PVG in the females and maturation of the males. During the following spring, the photophile phase comes during the light phase of the long day and the females reach VG and breeding can start when day length exceeds 13 hrs per day.

If the Lapland beetles are treated in the same way with 'anomalous' photoperiods, only in LD 8:4 did a small percentage of the beetles fail to mature. In all other cycles, nearly all the *P. nigrita* reached maturity (Fig. 1). This means that the maturation processes dependent on short day in the Central European animals require only 2–4 hrs of darkness per 24 hrs in the Lapland stock. The measurement of day length does not depend on rhythmic processes but on something similar to an hourglass (Thiele

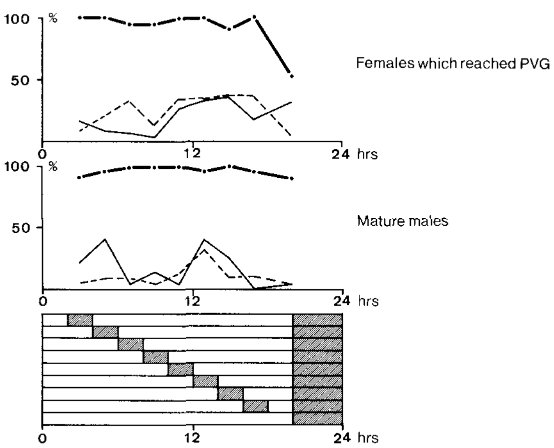

Fig. 3. Maturation of males and females in extreme long-day (LD 20:4) with 2 hr dark interruptions. Heavy lines: Lapland stock (each curve point from experiments with 19–25 specimens: n = 204 females and 212 males). Thin lines: Cologne stock (each curve point from experiments with 19–25 specimens: n = 205 females and 210 males). Thin broken lines: Once-selected Cologne stock S_1 (each curve point from experiments with 21–25 specimens: n = 217 females and 208 males). Partially derived from THIELE 1977c.

1977c), which demands only a minimal number of dark hours per 24 hr cycle.

This hypothesis is strongly supported by further experiments in which dark interruptions were given during the light phase of an extremely long day. In this case the 'short day' processes are only possible in the Central European beetles if the dark breaks are located in certain positions, resulting in peaks of maturation only at certain phases of the cycle. Quite in contrast to that we find that regardless of the position of the dark interruptions, nearly 100 % of the Lapland beetles matured in all experiments. So here, too, we come to the conclusion that there are no circadian processes underlying day length measurement in the Lapland stock (Fig. 3).

Selection Experiments Concerning Time Measurement

The following experiments were carried out to elucidate the question of how such a different mode of measurement of day length as that found in the Lapland stock could develop. We see from the experiment with LD 8:28 that not all of the beetles from the Cologne stock remained immature under these conditions. 4 % of the males matured and 31 % of the females reached PVG. One possible hypothesis is that these beetles could mature because they are 'non-rhythmical' and thus similar to the Lapland beetles.

To prove this hypothesis, beetles from the Cologne stock were treated first with LD 8:28 and then with LL (continuous light). LL was needed to allow VG in the females which had reached PVG under LD 8:28. All offspring from these beetles must descend from animals which were able to undergo gonadal development under LD 8:28. Those beetles were thus selected from the original population.

Once more I performed the experimental series of 'abnormal' photoperiods with the F_1 and F_2 generations reared from the original population treated in the above mentioned manner. The result was strikingly different from that of the original stock (Fig. 4). It is intermediate between the reaction of the Cologne stock and that from Lapland. It is not, however, possible to conclude from this experiment that the selected beetles

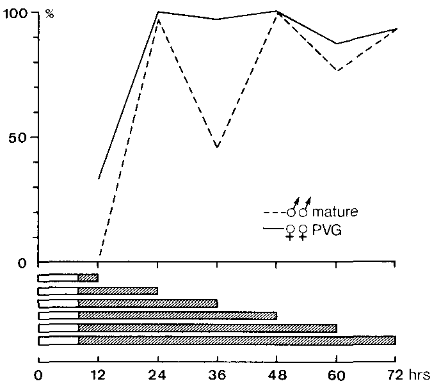

Fig. 4. Maturation of males and females of the once-selected Cologne stock S_1 in LD cycles deviating from 24 hrs. Each curve point from experiments with 24–30 specimens (n = 172 females and 178 males).

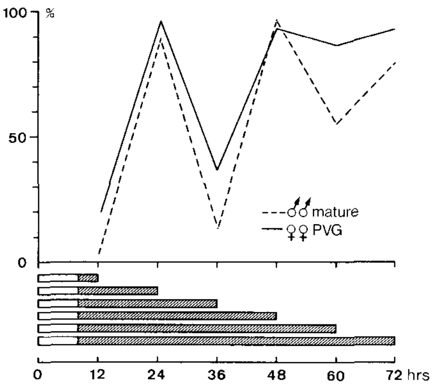

Fig. 5. Maturation of males and females of the twice-selected Cologne stock S_2 in LD cycles deviating from 24 hrs. Each curve point from experiments with 27–30 specimens (n = 179 females and 174 males).

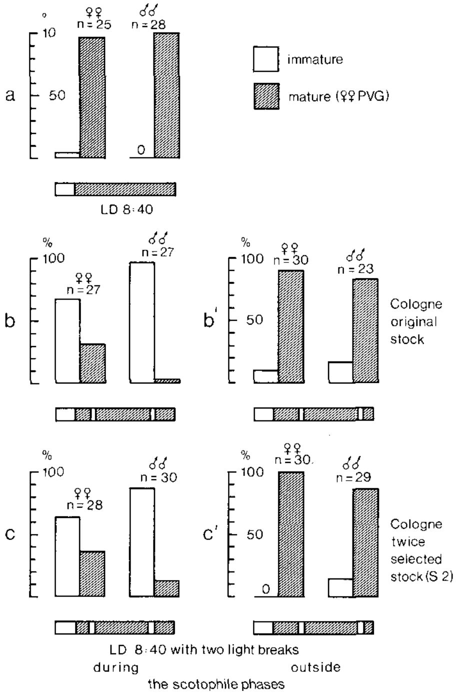

Fig. 6. Maturation of males and females under a 48 hr light regime (LD 8:40) with and without 2 hr light interruptions in the dark phase.

a: LD 8:40, original population from Cologne

b and b′: Original population from Cologne, LD 8:40 with two light interruptions of two hrs duration each within the scotophile phases (b) or 4 hrs thereafter (b′)

c and c′: Twice-selected population from Cologne, LD 8:40 with two light interruptions of 2.5 hrs duration each within the scotophile phases (c) or 4 hrs thereafter (c′).

(we called them stock S_1) were 'non-rhythmical'. This can be deduced from the following experiments.

The selection experiment was repeated with beetles from the S_1 stock, with first LD 8:28 and then LL. If the offspring from these beetles (we called them the S_2 stock) were treated with abnormal photoperiods, the result was again very similar to that of the original population (Fig. 5). That these beetles indeed are still rhythmically organized with regard to photoperiodism is convincingly demonstrated by the following experiments. If, with the original stock from Cologne, two light interruptions of 2 hrs each are given during a 48 hr day (LD 8:40) at the supposed scotophile phases (i.e., about 15 hrs after 'light on' and again 24 hrs later), the short day maturation is suppressed in most of the beetles, whereas the same light interruptions shifted to a location only four hours later in the cycle had no detrimental effect on maturation. Quite the same holds true for the beetles of the S_2 stock (Fig. 6). It can be demonstrated that a circadian rhythm is still always underlying time measurement in these beetles.*

Thus, we can also understand that the experiment done with dark interruptions in extreme long day in the S_1 stock reared from the Cologne beetles showed no similarity with the reactions of the Lapland beetles. Regardless of some differences from the original Cologne stock, it had remained similar to it (Fig. 3).

It is not yet understood what the reason was for the different reaction of the S_1 stock under 'abnormal' photoperiods. On the whole, circadian organization as a basis of day length measurement in the Central European beetles seems rather stable. We cannot conclude from the experiments that there are a few individuals within those populations whose circadian organization is rather loose and which thus could be 'preadapted' to day length measurement by means of an hourglass and thus to a shift into the climate of Subarctic midsummer.

On the other hand, the selection experiments show that there is a considerable degree of variability concerning the mode of time measurement within one population (Cologne). The divergently reacting beetles of the S_1 stock could belong to a type where the 'normal' position of the scotophile phase is shifted in an extreme manner to another temporal location, but no concise conclusions can be deduced from the experiments so far performed.

It is only recently that NETTMANN (1976) found out that *P. nigrita* is the only carabid species, as far as we know up until now, with a polymorphism of the karyotype. There are populations with 2n = 40 and others with 46 chromosomes. Our Lapland stock

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*When those experiments were carried out with beetles of the Lapland stock, the absence of an oscillatory element in time measurement was again clearly demonstrated. The same two light regimes as in the Cologne S_2 stock were applied: LD 8:40 with two light interruptions of 2.5 hrs each at the supposed scotophile phases or 4 hrs thereafter. In contrast to the Cologne stock and the beetles selected from the Cologne stock, maturation took place in the majority of the Lapland beetles in these experiments. Regardless of the location of the light interruptions in the cycle, at least 93 % of the males became fully mature and at least 89 % of the females reached PVG (n = 113).

seems to have 46 chromosomes, the beetles from Rees show 40; but to our surprise the beetles from Cologne also have 46 chromosomes. My co-worker Doris Koch tried to interbreed the different populations and found out that this was not possible between the *P. nigrita* from Rees and those from Cologne and Lapland. It was, however, possible between the Lapland and Cologne stocks, resulting in a normal number of offspring which are normally fertile.

Until now it was not possible to establish a simple correlation between karyotype and the many differences which could be demonstrated in requirements and behaviour between the Central European and the Subarctic *P. nigrita*. We see a great variety in the reactions between these stocks which can all be interpreted as adaptations to the very different climates of the regions to which *P. nigrita* could spread.

ACKNOWLEDGMENTS

I am very much indebted to Mrs. E. P. Fiedler, B.S., for her help in breeding the beetles and performing the experiments, as well as for correcting the English text of the manuscript. I must also thank my co-worker Doris Koch, Dipl. Biol., for her permission to quote from her unpublished results and Mr. J. Jacobi, who assisted with drawing the graphs. Mr. H. K. Nettmann, Dipl. Biol., University of Bremen, was so kind as to make the first analyses of the karyotypes from our stocks of beetles. The Deutsche Forschungsgemeinschaft has supported this work with several grants.

REFERENCES

BUCCIARELLI, I.: SOPRACORDEVOLE, C.: I *Platysma* della laguna Veneta del subg. *Melanius* con riferimento alle altre specie Italiane del sottogenere. Contributo alla conoscenza dei Pterostichini (Col. Carabidae). Boll. Mus. Civ. Venezia **9**: 187–206 (1958).

CSIKI, E.: Harpalinae II. In: Junk, W., Schenkling, S. (Edts.): Coleopterorum Catalogus. Berlin: Junk, 1932–1933.

FERENZ, H. J.: Photoperiodic and hormonal control of reproduction in male beetles, *Pterostichus nigrita*. J. Insect. Physiol. **21**: 331–341 (1975a).

FERENZ, H. J.: Anpassungen von *Pterostichus nigrita* F. (Coleoptera, Carabidae) an subarktische Bedingungen. Oecologia (Berl.) **19**: 49–57 (1975b).

FERENZ, H. J.: Two-step photoperiodic and hormonal control of reproduction in the female beetle, *Pterostichus nigrita*. J. Insect. Physiol. **23**: 671–676 (1977).

GERSDORF, E.: Ökologisch-faunistische Untersuchungen über die Carabiden der mecklenburgischen Landschaft. Zool. Jb. Syst. **70**: 17–86 (1937).

HEER, O.: Die Käfer der Schweiz. 1837.

HORION, A.: Faunistik der deutschen Käfer. 1: Adephaga – Caraboidea. Krefeld: Goecke und Evers, 1941.

KRUMBIEGEL, I.: Untersuchungen über physiologische Rassenbildung (Ein Beitrag zum Problem der Artbildung und der geographischen Variation). Zool. Jb. Syst. **63**: 183–280 (1932).

NETTMANN, H. K.: Karyotyp-Analysen bei Carabiden (Coleoptera). Mitt.dtsch. ent. Ges. **35**: 113–117 (1976).

THIELE, H. U.: Einflüsse der Photoperiode auf die Diapause von Carabiden. Z. angew. Entomol. **58**: 143–149 (1966).

THIELE, H. U.: Ein Beitrag zur experimentellen Analyse von Euryökie und Stenökie bei Carabiden. Z. Morphol. Ökol. Tiere **58**: 355–372 (1967).

THIELE, H. U.: Zur Methode der Laboratoriumszucht von Carabiden. Decheniana **120**: 335–341 (1968).

THIELE, H. U.: Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren. Zool. Jb. Syst. **98**: 341–371 (1971).

THIELE, H. U.: Carabid beetles in their environments (A study on habitat selection by adaptations in physiology and behaviour). Berlin, Heidelberg, New York: Springer, 1977a.

THIELE, H. U.: Measurement of day-length as a basis for photoperiodism and annual periodicity in the carabid beetle *Pterostichus nigrita* F. Oecologia (Berl.) **30**: 331–348 (1977b).

THIELE, H. U.: Differences in measurement of day-length and photoperiodism in two stocks from subarctic and temperate climates in the carabid beetle *Pterostichus nigrita* F. Oecologia (Berl.) **30**: 349–365 (1977c).

TURIN, H., HAECK, J., HENGEVELD, R.: Atlas of the carabid beetles of The Netherlands. Amsterdam: North-Holland Publ. Comp. 1977.

INTRASPECIFIC DIFFERENCES IN THE ACTIVITY RHYTHMS OF THE CARABID BEETLE *PTEROSTICHUS NIGRITA* PAYKULL (COLEOPTERA, CARABIDAE)*

GISELA LEYK

Zoologisches Institut der Universität zu Köln, Lehrstuhl für Physiologische Ökologie, Weyertal 119, D-5000 Köln 41, Federal Republic of Germany

ABSTRACT

The locomotor activity of a Subarctic and a Central European stock of *Pterostichus nigrita* was measured during different short- and long-days and constant conditions. Definite differences between the two populations were observed.

1. In general, the Central European beetles behaved rather uniformly. They showed a 'typical' continually reoccurring activity pattern with the main activity during the first hours after the onset of darkness in all of the long-day experiments (also in the short-day LD 8:16).

2. Concerning the Subarctic stock, merely a portion of the beetles showed the activity pattern typical for the Central European animals. One can observe the following differences: weaker entrainment to the 'Zeitgeber', less rhythmic behaviour in LD and constant conditions, more individual variation in the same experiment and less precision of the rhythm.

INTRODUCTION

This research work is concentrated on the comparison of the activity rhythms of two populations of *Pterostichus nigrita* coming from regions with different photoperiodic conditions. THIELE's studies on the photoperiodic control of gonad maturation in a Central European and a Subarctic stock of *Pterostichus nigrita* (THIELE 1977a, b) gave motivation to further comparative investigations. He discovered definite differences between the two populations. Therefore, it appeared to be of interest to investigate the circadian behaviour of the different stocks as well. Hence, the locomotor activity of the Central European and the Subarctic beetles was measured first during different short- and long-days (LD 8:16, LD 4:20, LD 2:22, LD 1:23, LD 16:8, LD 20:4, LD 22:2, LD 23:1, LD 23.5:0.5).

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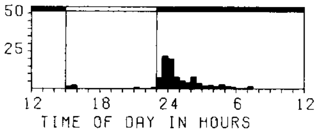

Fig. 1. Activity of an 'average' Central European beetle from Cologne in LD 8:16 (mean of ten animals).

The figures 2–3 show the average activity of single animals for about ten days. During this time, the sum of all impulses produced by the beetles while crossing the light barriers was set at 100%. Referring to this value, means in per cent for the single half hours were calculated. Ordinate: activity in per cent, abscissa: time of day in hours. The black parts of the bars above the figure indicate darkness.

METHODS

During the experiments, the beetles were kept at a temperature of 20 ± 1 °C in temperature controlled rooms illuminated with fluorescent tubes of the type 'white'. The

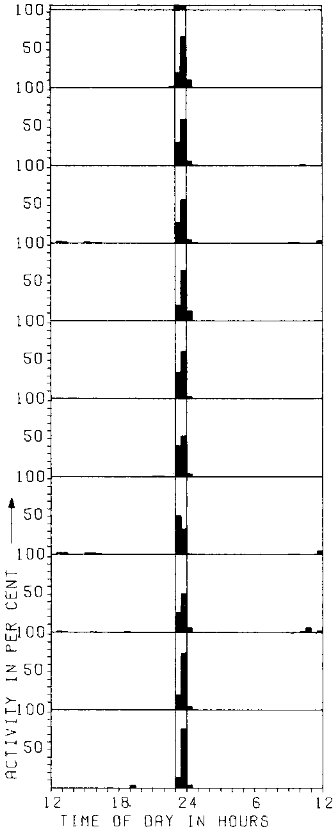

Fig. 2a. Activity of ten different Central European beetles from Rees in LD 23:1.

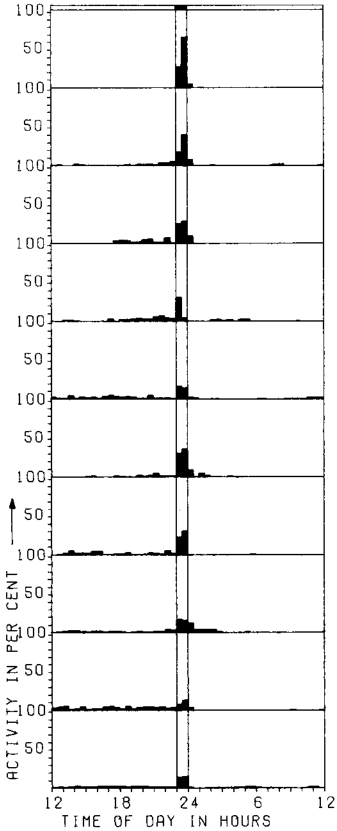

Fig. 2b. Activity of ten different Subarctic beetles in LD 23:1.

activity of the animals (kept singly in round containers, twenty per experiment) was measured by IR-light barriers (maximum intensity at 978 nm). A pulse-counting printer recorded the impulses produced by the animals, printing them out every half hour. All animals used for experiments originated from laboratory stocks. The Subarctic ones were derived from *Pterostichus nigrita* caught in Swedish Lapland (64–66 °N). Two Central European populations were used, offspring of beetles coming from the eastern border of Cologne (51 °N) and offspring of *Pterostichus nigrita* caught at Rees-Grietherbusch (Lower Rhine region, 51° 45′N).

RESULTS AND THEIR DISCUSSION

In general, the Central European animals behaved rather uniformly. The 'typical' activity pattern continually appearing is shown in Fig. 1: main activity during the first hours after the onset of darkness.

Concerning the beetles from Rees-Grietherbusch, K. SCHLINGER was able to confirm this activity behaviour by the results obtained by catching them in time-sorting pitfall traps in the field (SCHLINGER 1978). The strong restriction of activity to the night, preserves this carabid beetle, which is very sensitive to desiccation, from intensive solar irradiation. The short-day experiments in the laboratory exhibited a decreasing force of the 'Zeitgeber' with increasing night-length: scattering of the regular activity pattern in more and more animals and appearing of free-running rhythms with $\tau < 24$ h. In all the long-day experiments (also in the short-day LD 8:16), the Central European *P. nigrita* displayed the 'typical' activity pattern very uniformly. It is surprising that they do not change their behaviour even in experiments with extremely short nights. The activity hardly extends into the light phase (Fig. 2a). Whereas in short-days the synchronising effect is already diminishing with a light phase lasting only four hours, in long-days the force of the 'Zeitgeber' is not reduced with only half an hour of darkness.

In general, merely a portion of the Subarctic beetles show the activity pattern typical for the Central European animals. The greater individual variation in behaviour is striking (Fig. 2b). Often one can see the activity scattering to a longer period of the 24-hr day (Fig. 2b). In addition, other phase relations to the 'Zeitgeber' can be observed (Fig. 3). In general, there are also greater variations in the activity pattern from day to day (Fig. 4). With increasing night length, the Subarctic animals tend to scatter their activity to a longer period of the day rather than to turn to the free-running behaviour as observed in the Central European beetles. Again, the behaviour of the Subarctic *Pterostichus nigrita* varies individually. In constant conditions (LL and DD) there is a greater proportion of beetles in the Central European stock with distinct free-running rhythms.

For the present, one can in general observe the following differences respecting the behaviour of the Subarctic stock in contrast to the Central European one: weaker entrainment to the 'Zeitgeber', other phase relations to the 'Zeitgeber' to some extent,

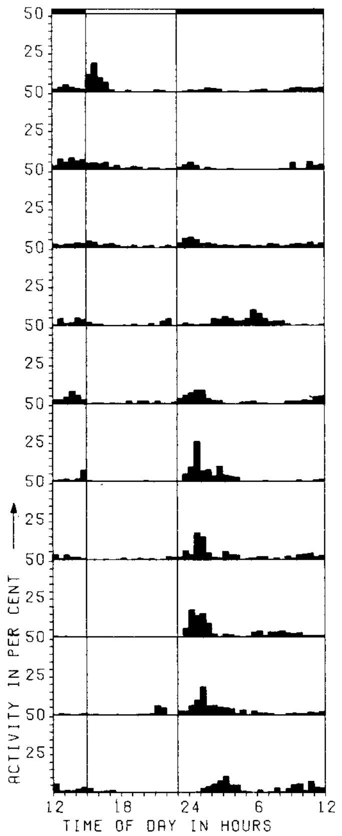

Fig. 3. Activity of ten different Subarctic beetles in LD 8:16.

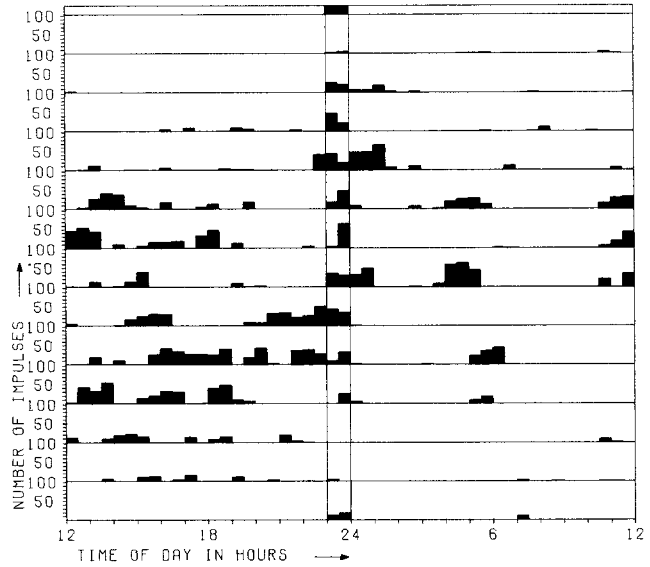

Fig. 4. Activity of a Subarctic beetle in LD 23:1 for thirteen days. Each horizontal line represents a 24-hour day.

less rhythmic behaviour in LD and constant conditions, more individual variation in the same experiment, and less precision of the rhythm (more variation in behaviour from day to day, more scattering of activity instead of a strong pattern). These tendencies were confirmed by experiments under natural light conditions performed in Cologne in the summer of 1978.

The differences in the rhythms can be analysed quantitatively with various methods of time series analysis. The computer program system 'Timesdia' (Martin and Brinkmann, 1976a, b) proved to be valid for these purposes. Among other things periodogram analysis, spectral analysis, signal averaging techniques, and complex demodulation are applied to the data by means of this program. With the help of complex demodulation, one can decide whether a significant peak in the periodogram indicates an unstable periodicity or a stable one which has a time-independent amplitude and frequency.

Additionally, according to Lamprecht and Weber's periodogram analysis (Lamprecht and Weber, 1970 and 1977), 'precision numbers' giving a criterion for the precision of the rhythm can be calculated. As for the experiments already estimated in this way, these numbers differ on an average in the Subarctic and Central European populations. So far, it is possible to conclude that the populations not only differ with respect to the control of gonad maturation, but also as far as activity behaviour is concerned. In accordance with a less distinct periodicity of environmental conditions in the Subarctic, the animals from this region displayed a less rhythmic behaviour.

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REFERENCES

LAMPRECHT, G. and WEBER, F.: Eine neue Methode zur Bestimmung von Periodenlängen rhythmisch ablaufender physiologischer Prozesse. Pflügers Arch. **315**: 262–272 (1970).

LAMPRECHT, G. and WEBER, F.: Die Lichtempfindlichkeit der circadianen Rhythmik dreier Höhlenkäferarten der Gattung *Laemostenus*. J. Insect Physiol. **23**: 445–452 (1977).

MARTIN, W. and BRINKMANN, K.: A computer program system for the analysis of equispaced time series. J. Interdiscipl. Cycle Res. **7**: 251–258 (1976a).

MARTIN, W. and BRINKMANN, K.: Detection and measurement of periodicities in time series. Int. J. Chronobiol. **4**: 185–195 (1976b).

SCHLINGER, K.: Die Tages- und Jahresrhythmik der Aktivität und die Gonadenreifung von *Pterostichus nigrita* F. (Coleoptera, Carabidae) mit Vergleichsuntersuchungen über die Rhythmik weiterer Carabidenarten in einem Auwaldgebiet am Niederrhein (Rees-Grietherbusch). Diplomarbeit, Köln, 1978.

THIELE, H. U.: Measurement of day-length as a basis for photoperiodism and annual periodicity in the Carabid beetle *Pterostichus nigrita* F. Oecologia (Berl.) **30**: 331–348 (1977a).

THIELE, H. U.: Differences in measurement of day-length and photoperiodism in two stocks from subarctic and temperate climates in the Carabid beetle *Pterostichus nigrita* F. Oecologia (Berl.) **30**: 349–365 (1977b).

THE REGRESSIVE EVOLUTION OF THE CIRCADIAN SYSTEM CONTROLLING LOCOMOTION IN CAVERNICOLOUS ANIMALS*

GÜNTHER LAMPRECHT
Universität Bremen, Rechenzentrum D-2800 Bremen, Federal Republic of Germany

FRIEDRICH WEBER
Universität Münster, Zoologisches Institut, D-4400 Münster, Federal Republic of Germany

ABSTRACT

The cavernicolous animals, which have up to now been examined, can be grouped according to a preliminary model with six stages describing the regressive evolution of the chronometrical system. In this model the proportion of periodical components in the patterns of activity decreases successively whereas the proportion of stochastical components increases. Four stages are represented by carabid species, one stage by a cavernicolous form of the fish *Astyanax mexicanus* and one more stage by amphipods of the genus *Niphargus*. – From a detailed knowledge of the various stages of degeneration conclusions may be drawn regarding the biological significance, the physiology and genetics of the intact circadian clock. – In species, in which periodical components in the patterns of activity are missing, special types of stochastical control of activity enable a simple form of time-measuring. Constant mean durations of bursts of activity and pauses of rest can be guaranteed by stochastical control if the probabilities for the transition from activity to rest and from rest to activity do not change during a larger time-span.

1. INTRODUCTION

Recent cavernicolous animals adapted in varying degree to the conditions of subterranean life reflect the course of evolution, which beginning with epigeous forms has led to troglophile troglodytes and eventually to extremely specialized and adapted troglobites. By analysing sequences of adaptation as a representation of lines of evolution one can study the influence of varying selection pressures on the extent and rate of evolutionary changes. Previous studies have chiefly dealt with sequences of morphological adaptation, whereas there have been only few investigations of the gradual changes of behavioural patterns during phylogenetic adaptation to a life under constant conditions (e.g. PARZEFALL, 1974).

This study presents experimental results concerning the regressive evolution of the capability of time-measuring. The fact that extreme troglobites have lost the capability of estimating the time of day has been shown by several studies (GINET, 1960; DELEURANCE-GLACON, 1963; GÜNZLER, 1964). – But as the circadian system is con-

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trolled polygenetically (compare studies of fungi, FELDMAN and WASER, 1971), one may suppose that during evolutionary adaptation to life under constant conditions the circadian physiological clock does not disappear abruptly but degenerates gradually as complex organs do. From a deeper insight into such stages of degeneration, however, conclusions might be drawn regarding the biological significance and the physiology and genetics of the intact circadian clock.

There are two main reasons why our team decided to study cavernicolous carabids. On the one hand, the circadian system of the epigeous carabids is well known (WEBER, 1968; LAMPRECHT & WEBER, 1971, 1973), on the other hand, many cavernicolous forms of carabids with a different evolutionary status exist in Europe, both in the systematic group of the Sphodrini and of the Trechini. Moreover, we study cavernicolous pisces of the species *Astyanax mexicanus*.

The physiological clock can control numerous functions, for example, in man several dozens are known (RENSING, 1973). But in epigeous carabid beetles only one periodical circadian function has up to now been measured: the daily change between rest and locomotion. If, under certain environmental conditions the pattern of activity should prove to be structured aperiodically, one must not directly conclude that the controlling circadian oscillator itself is extinct. Possibly the function has only been separated from the oscillator. Therefore, a valid description about the state of the oscillator is not possible until the behaviour of locomotion has been studied under different environmental conditions. Among these, especially light has an important influence on the expression of the circadian rhythm of locomotion in carabid beetles (LAMPRECHT & WEBER, 1977).

2. MATERIAL AND METHOD

2.1. Actographs and method of recording

The actographs, in which the animals are tested individually, consist of two identical plastic dishes (for the larger Sphodrini 14 cm ∅, for the smaller Trechini 8.5 cm ∅). The lower dish is filled with gypsum, the upper one covers it conversely. The gypsum bottom is kept wet by the opening of a little bottle filled with water. In this actograph, the animal is offered a darkened hiding-place. In order to avoid disturbances the animals were not fed during the experiments, which mostly lasted for three weeks. Unless mentioned otherwise, the animals were tested under constant temperature (in a cryothermostat), the temperature being adjusted to that of their natural habitats.

Running activity was recorded by an IR-ray barrier (800 nm). The frequency with which the animals pass through the measuring ray is counted and transferred every ten minutes to a tape recorder as well as to a teletype. Thus, every experiment with one animal provides a continuous series of approximately 3000 10 min-data.

*2.2. Evaluation**

The testing program for analysing the recorded series of time data with regard to their periodical and stochastical components comprises

- a test for periodical components (periodogram analysis, LAMPRECHT & WEBER, 1970, see fig. 1) and
- a test for stochastical distribution of activity and rest, whenever the periodogram analysis does not indicate any periodicities (for details see LEHMANN et al., 1974; KAISER & LEHMANN, 1975; LAMPRECHT & WEBER, in press).

  In this part of the test
- the coefficients of linear correlations between the duration of bursts of activity (A) and pauses of rest (R) and the reverse are calculated $(r_{A_i - R_{i+1}}; r_{R_{i+1} - A_{i+2}})$;
- if relevant correlations are missing, the constancy of behaviour during the experiment is checked. This is done by drawing and comparing the frequency histograms of the duration of bursts of activity as well as of pauses of rest for separate parts of the experiment;
- in cases of aperiodicity, of missing correlations and of constancy of behaviour the probabilities of transition from activity to rest and from rest to activity can be computed, either by approximating the observed frequency histograms to theoretical functions (exponential, Poisson, or standard function, see fig. 4), or by computing the probabilities of transition directly from the observed frequencies of the classes.

2.3. The carabid species tested

Laemostenus (*Pristonychus*) *terricola* was collected in cellars in the Hümmling (Northwestern Germany), *Laemostenus* (*Ceutosphodrus*) *oblongus* in caves of the region around St. Girons (Pyrenees), *Laemostenus* (*Ceutosphodrus*) *navarricus* in caves of the region around Tardets (Pyrenees), *Laemostenus* (*Antisphodrus*) *schreibersi* in caves of southern Carinthia (Austria). *Aphaenops cerberus* and *pluto* and *Geotrechus orpheus* were taken from caves near St. Girons, *Duvalius balazuci* and *delphinensis* from caves near Valence (Rhône). The animals of the *Duvalius doriai* group were collected in caves north of Lucca (Tuscany) and *Duvalius exaratus* in wood gorges in southern Carinthia. – Morphologically and ecologically speaking, *Aphaenops cerberus* and *pluto* are so similar that the data measured for these two species could be combined. The same was done for the very closely related species *Duvalius balazuci* and *delphinensis*. – It has not up to now been possible to identify the individuals of the *Duvalius doriai* group correctly. At any rate, the several species of this group do not differ from each other in their state of phylogenetic adaptation (JEANNEL, 1928).

3. RESULTS

3.1. Periodical components in the actograms of cavernicolous animals

All these cavernicolous animals which have up to now been carefully examined, can be grouped according to a preliminary model with six stages describing the regressive evolution of the chronometrical system. In this model the proportion of periodical components in the patterns of activity decreases successively, whereas the proportion of stochastical components increases.

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*Carried out with the help of the computer centres of the University of Münster and the University of Bremen.

Stage 1. This stage comprises carabid beetles with an intact temperature-compensated circadian clock which controls their activity in constant darkness (DD) as well as under lighting conditions (in light-dark cycles = LD, or constant light = LL). The troglophile species *Laemostenus terricola* and *oblongus* were already described as examples of this evolutionary stage (LAMPRECHT & WEBER, 1975, 1977). Probably the troglobite *Laemostenus schreibersi* also belongs here. The activity of this species is predominantly circadian-periodical under cave conditions (DD, constant temperature; 12 of 14 animals tested). The period of its activity is temperature-compensated, too ($\overline{Q}_{10} = 1.08$).

Stage 2. This stage includes all those species whose circadian clock controls their activity only under conditions of illumination (LD or LL), whereas aperiodical patterns of activity prevail in DD. The troglobite *Laemostenus navarricus* has been described as an example for this stage (LAMPRECHT & WEBER, 1975, 1977). Continuous measurements of the O_2-consumption confirmed the recordings of activity (unpublished). – Possibly, the epigeous *Duvalius exaratus* living mostly in DD conditions under stones and in thick leaf layers can also be assigned to this stage. Nine of eleven animals tested under DD conditions were active aperiodically, whereas twenty four of thirty

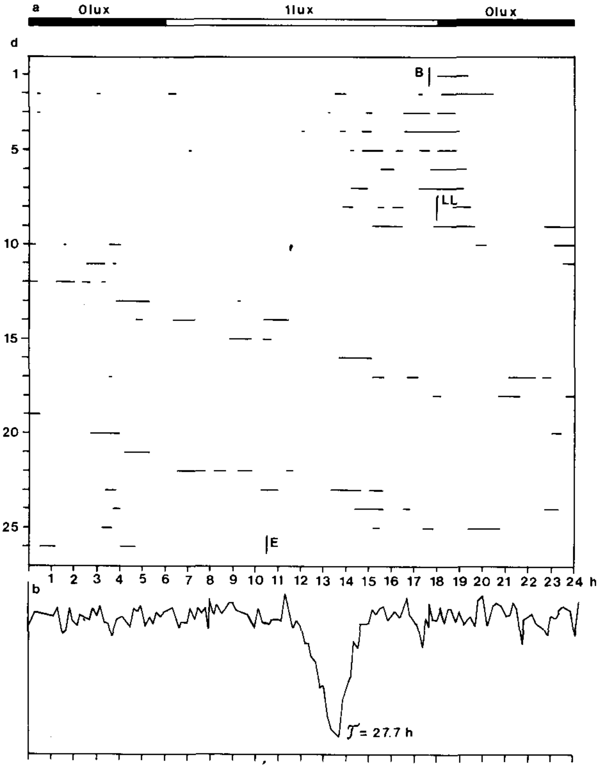

Fig. 1. a. Distribution of activity in a specimen of *Duvalius exaratus* in LD (day 1–8) and LL (day 9–26, 1 lux). In LD the animal is running preferably at the end of the light phase and at the beginning of the dark phase. In LL its period of activity is longer than 24 hours.

b. The periodogram of the LL actogram. The minimum indicates a period of τ = 27.7 hours.

two animals were circadian-periodical in LL of 1 lux (fig. 1). In LD (0/1 lux) 13 of 15 animals tested in autumn showed an increasing activity at the end of the light phase. This phenomenon, too, demonstrates the control by an endogenous chronometrical mechanism (fig. 2). The period of the spontaneous LL activity is temperature-compensated ($\bar{Q}_{10} = 0.96$). – A final assignment of *Duvalius exaratus* and *Laemostenus schreibersi* to any stage of the model will not be possible before a greater number of animals have been tested.

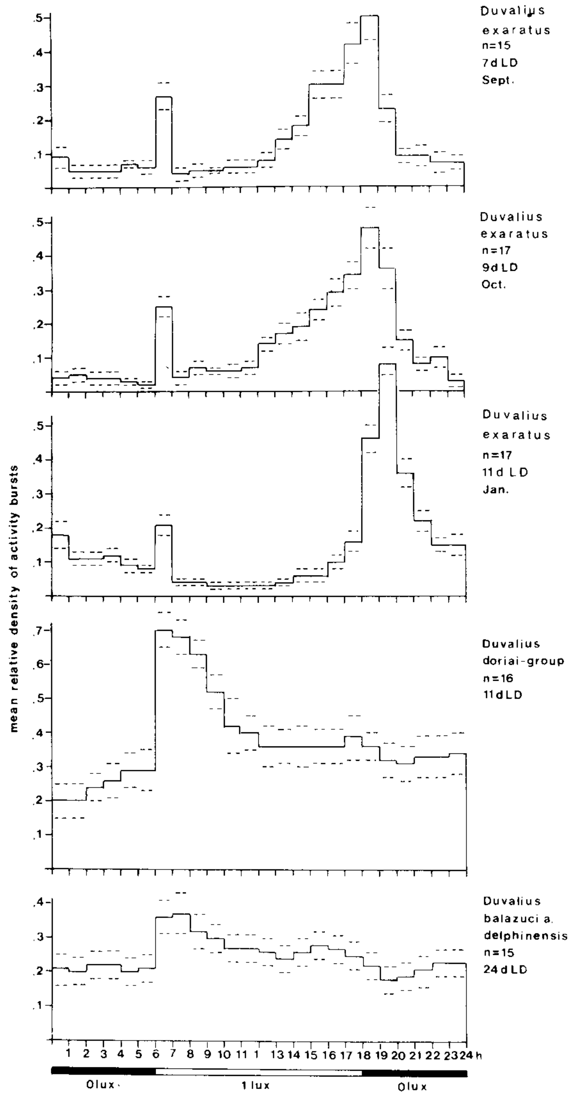

Fig. 2. LD-behaviour of the macrophthalmic *Duvalius exaratus* and of anophthalmic species of *Duvalius*. Ordinate: the 'relative density of the bursts of activity' is 1 for a distinct hour, if the animal is active at all 10 min-intervals of this hour. The 'mean relative density' is the average of the relative density of corresponding hours. – Interrupted lines: standard deviations of mean values ($\sigma/\sqrt{n}$).

Stage 3. This stage is characteristic of cavernicolous animals lacking self-sustained circadian rhythms. LD induces periodicity of locomotion. After the transition from LD to constant conditions the animals show post-oscillations. Example: the blind cavernicolous form of *Astyanax mexicanus* (ERCKENS & WEBER, 1976).

Stage 4. This stage is represented by blind species lacking self-sustained circadian rhythms as well as post-oscillations after a transition from LD to constant conditions. LD cycles induce a periodical distribution of activity, the animals being active mostly in the dark phases. Example: cavernicolous amphipodes of the genus *Niphargus* (GINET, 1960; GÜNZLER, 1964).

Stage 5. This newly described stage comprises species without self-sustained circadian rhythms of locomotion and without recognizable post-oscillations. LD cycles induce periodical distributions of activity, but the animals are more active in the light than in the dark phases. Thus, the animals are no longer able to adapt their activity behaviour to LD cycles in an ecologically significant manner. Examples are anophthalmic species of the genus *Duvalius*. The LD reaction is intense in the specimen of the *doriai* group but weak in *D. balazuci* and *delphinensis* (fig. 2, 3). The LD reaction probably arises from the fact that the animals try to escape from light, but are unable to look directly for a hiding-place.

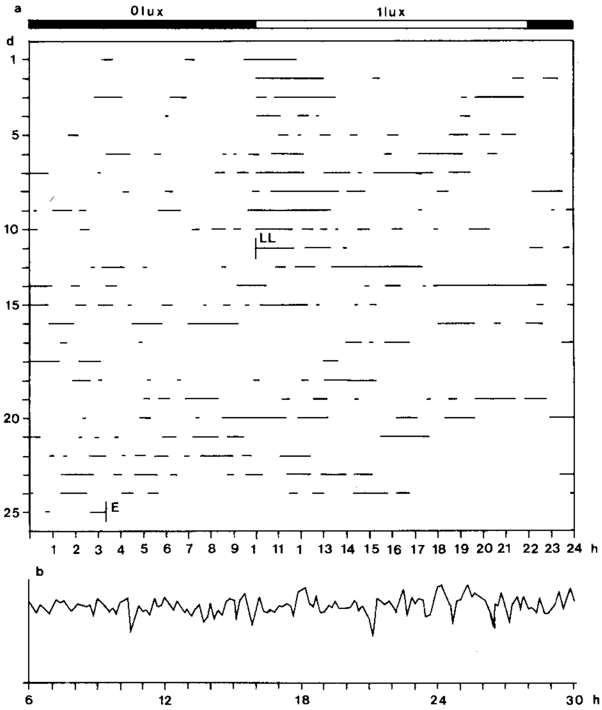

Fig. 3. a. Distribution of activity in a specimen of the group of *Duvalius doriai* in LD (day 1–11) and LL (day 11–25, 1 lux). In LD the animal is frequently active after 'light on'. In LL it is aperiodically active. – Coefficients of linear correlations in the LL pattern: $r_{A_i - R_{i+1}} = +0.21$ (significant at the 5% level), $r_{R_{i+1} - A_{i+2}} = -0.03$ (not significant).

b. The periodogram of the LL actogramm. No deviations from the 'background noise'.

Stage 6. This stage is typical of aperiodic species which do not any longer react to LD cycles of small amplitude (LAMPRECHT & WEBER, in press). It is only by cycles of temperature that a periodical distribution of rest and activity is induced. Examples: species of the genus *Aphaenops* and *Geotrechus*. – The assignment of *Speonomus diecki* (Catopidae, Bathysciinae) to either stage 4, 5 or 6 is not yet possible because this species was only tested in DD and LL, but not in LD (LAMPRECHT & WEBER, in press).

3.2. Stochastical components in the actograms of cavernicolous carabids

The aperiodical carabid actograms fulfil the conditions of constancy of activity (with only a few exceptions). In *Aphaenops*, *Geotrechus* and *Speonomus*, in only one fifth of the cases there are significant correlations between the duration of succeeding bursts of activity and pauses of rest on the 5 % or 1 % level (see fig. 3). But the coefficients of correlation are positive as well as negative and rarely exceed $r = /0.3/$. Except for one case they are smaller than $r = /0.4/$, i.e., the parameter $B = r^2 \cdot 100$ is usually so small that the variation of the one variable (e.g. the duration of the pauses of rest) is caused by the variation of the other one (e.g. the duration of the bursts of activity) to a negligible extent only. In the aperiodical actograms of the mentioned carabids, therefore, the sequence of rest and activity can be approximatively described as stochastical: the duration of a pause of rest does not influence the duration of the succeeding burst of activity or vice versa.

The exception mentioned above is an actogram of a specimen of *Geotrechus orpheus* (DD, $r_{R_{i+1} - A_{i+2}} = +0.64$, $\alpha = 0.1\,\%$) (see LAMPRECHT & WEBER, in press). This animal is excluded from tab. 1. In *Laemostenus navarricus*, every third actogram, in the anophthalmic *Duvalius* species every second actogram exhibits significant (mostly positive) correlations. But in these cases, B is always smaller than 16. Only in *Duvalius exaratus*, there are more relevant correlations: 7 of 11 animals exhibit positive correlations; in 4 cases B is greater than 16.

Rare (and weak) correlations, however, do not as such point to the existence of (heavily disturbed) periodicities in the actograms which were evaluated as aperiodical in the periodogram analysis. Nothing but a negative correlation with a regression of approximately –1 would be an indication for periodicity. On the other hand, the fact that such correlation parameters are missing is no proof for the non-existence of periodicities. The required parameter would occur only if the 'phase of activity α' were not interrupted by short pauses of rest and if the 'phase of rest ρ' were not interrupted by short bursts of activity ($\alpha + \rho = \tau$). The actograms are evaluated as 'periodical' or 'aperiodical' in our test program by a mathematical method. In the periodograms of the 'aperiodical' actograms there are no conspicuous deviations (minima) from the 'background noise' either in the circadian or ultradian or infradian range. Occasional very slight minima can be caused accidentally, as simulation experiments have shown (LAMPRECHT & WEBER, 1977). But in this field, too, the final evidence for the complete aperiodicity of the actogram is missing. The evaluation of an actogram as aperiodical is only an approximation that to a great extent squares with reality.

GÜNZLER (1964), JEGLA & POULSON (1968), MEAD & GILHODES (1974), LAMPRECHT & WEBER (1974) have looked for (heavily disturbed) periodical residues especially for

Table 1. Description of the frequency histograms of the durations of bursts of activity and pauses of rest by exponential (e), Poisson (P) or standard functions (s). ?: a theoretical function cannot be approximated. n: number of analysed distributions.

species	conditions	bursts of activity					pauses of rest				
		n	e	P	s	?	n	e	P	s	?
Laemostenus navarricus	DD	21	10	–	3	8	21	15	–	1	5
Duvalius exaratus	DD	11	7	1	–	3	11	1	–	–	10
Duvalius doriai group	1 lux LL	15	9	–	–	6	15	4	–	–	11
Duvalius balazuci a. *delphinensis*	DD a. 1 lux LL	33	17	–	–	16	33	4	–	–	29
Aphaenops cerberus a. *pluto*	DD, 10^{-2}lux LL, LD (0/0.5 a. 0/5 lux)	37	26	1	–	10	40	23	–	–	17
Geotrechus orpheus	DD, 10^{-2}lux LL, LD (0/0.5 lux)	21	7	8	1	5	23	7	–	7	9
Speonomus diecki	DD, 10^{-2}lux LL	18	8	5	–	5	19	8	–	2	9

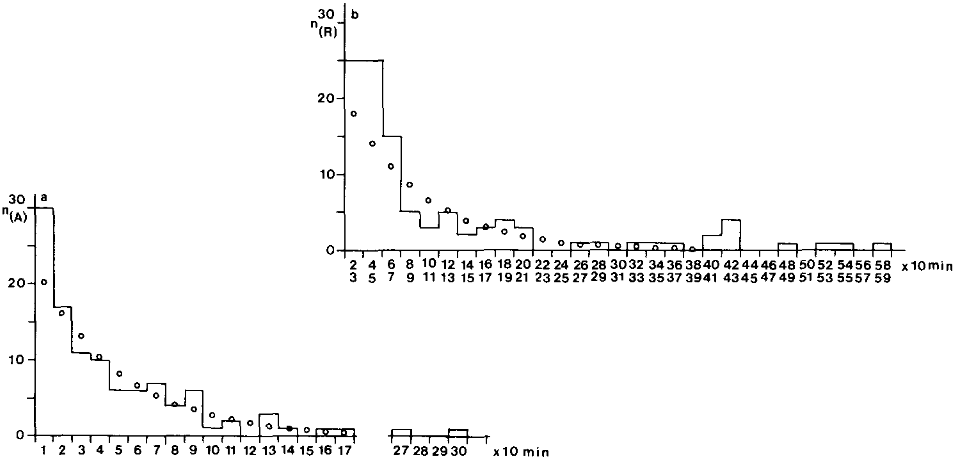

Fig. 4. Frequency distributions of the duration of the bursts of activity (A) and pauses of rest (R) of the LL actogram in fig. 3. – The distribution of the A frequencies can be described by an exponential function (points; $\chi^2 = 9.05$; $\alpha = 0.55$). The distribution of the R frequencies does not agree with an exponential function ($\chi^2 = 18.29$; $0.025 < \alpha < 0.05$). – Because the R histogram includes many classes, the frequencies of classes are lower in the R than in the A histogram. Therefore, in the R histogram the frequencies of neighbouring classes must be summarized, before the χ^2 test can be applied. – The smallest pauses of rest have a duration of 20 min (isolated 10 min intervals without recording do not reliably indicate rest; they are very frequently caused by the fact, that accidentally the active animal has not crossed the IR barrier during an interval of measuring; therefore isolated 10 min intervals without recording are added to the bursts of activity).

such of ultradian and infradian period. We believe that in none of these studies the existence of such residues could be proved beyond doubt. In the numerous actograms of cavernicolous animals analysed by us (see tab. 1), it is only once that we found an ultradian period in the actogram as well as in the periodogram (in *L. navarricus*, DD, $\tau = 10$ hours).

It seems to be more promising to look for stochastical regularities which determine the sequence of rest and activity in the actograms. In this case one can try to relate the frequency histograms of the duration of bursts of activity and pauses of rest to a theoretical function. If a histogram can be described by an exponential function of the form $y = a \cdot e^{-f \cdot x}$, the probability for a transition from rest to activity, or from activity to rest respectively, is constant, i.e., the probability for a transition is independent of the duration of activity or rest (time-invariance, see LEHMANN et al., 1974) (fig. 4). If an observed distribution can be approximated to a Poisson or standard function, the probability for a transition to the alternative state increases continuously (see LAMPRECHT & WEBER, in press).

50% or more of the distributions of the duration of bursts of activity can be described by one or the other of the mentioned theoretical functions (tab. 1, fig. 4). Among these, the exponential functions (i.e. the time-invariant probabilities for a transition from activity to rest) prevail. It is only in *Geotrechus orpheus* that a greater number of Poisson distributions occur, i.e., the probability of a transition increases continuously with the duration of activity.

In *L. navarricus*, in the *Aphaenops* species and *Geotrechus orpheus*, too, the histograms of the duration of pauses of rest can be frequently described by theoretical functions (especially by exponential functions). But only seldom is this possible in *D. exaratus* and the blind *Duvalius* species (tab. 1, fig. 4). The reason for this remarkable difference is probably the fact that in these species the pauses of rest are on average very long so that their variance is very large. – In all the distributions that could not be described by a theoretical function, the probabilities for a transition were computed directly from the frequencies of the classes. In such cases constancy or continuous increase of the probability for a transition are often found for longer ranges of the histograms (compare LAMPRECHT & WEBER, in press).

4. DISCUSSION

4.1. The regressive evolution

The characteristics of the intact circadian system are so uniform in all eukaryont organisms that the basic molecular mechanisms which control chronometry can be assumed to be identical (BÜNNING, 1978). For this reason similar stages of degeneration are to be expected in different lines of evolution. Thus, the preliminary grouping of such different organisms as carabids, amphipods, and pisces according to one model of regression is justified. But it is still doubtful, whether the six various stages distinguished in chapter 3.1. are actually passed through in every case in the course of regressive evolution. In order to define more exactly how the physiological clock degenerates one ought mainly to compare closely related forms with each other. Therefore, our investigations will be extended to cavernicolous carabids which by their morphological characteristics can be expected to belong to stages which lie between stage 2 and 5 of the model.

The usefulness of carabids as the main subjects of our investigations has been confirmed. Both Sphodrini and Trechini fulfil an important requirement of the test program: the recent epigeous or troglophile forms possess an intact circadian clock. The same may be assumed for the epigeous ancestors of the troglobite species. We expect interesting intermediate stages of regression, especially in microphthalmic species of the genus *Duvalius*.

4.2. The biological significance of the circadian control of activity in carabid beetles

In other organisms numerous functions are controlled by the endogenous clock (see chapter 1). In carabids we have investigated only one function, viz. locomotion (the rhythm of O_2-consumption can be considered as an immediate consequence of locomotion). Therefore, we cannot answer the overall question concerning the biological significance of the clock itself. We can only try to clarify the significance of the circadian patterns of locomotion.

The evolutionary stage 2 is important for our reflections. Since the forms belonging to this stage are mainly aperiodical in DD, we may conclude that periodical activity is disadvantageous under cave conditions. On the other hand, these animals possess an intact circadian oscillator which can only be kept genetically fit by natural selection.

Under cave conditions however, selection could be effective only if some other function were performed periodically in the form of a circadian periodicity. This is improbable. It is true that in the inside of caves conditions of selection are hypothetically imaginable which prevent a rhythmic system from degenerating completely. Sometimes the hypothesis is formulated that a rhythmic organization is advantageous just because a temporal segregation of incompatible metabolic reactions can be achieved in this way (compare JEGLA & POULSON, 1968; BÜNNING, 1978). But there is no inherent reason why such a system should be advantageous only within a circadian period. In *L. navarricus* (and in *L. schreibersi*, too) we have, however, observed periods, which are without doubt circadian. Therefore, the clock of these species must be genetically controlled under diurnal conditions of selection. Surely, both the species are obligatory cave inhabitants, but they live in cave entrances, too. The weak diurnal amplitudes of environmental factors in cave entrances are evidently strong enough to generate a pressure of selection which suffices to compensate the pressure of mutation. This means that the physiological clock must be of paramount ecological importance in Sphodrini in as much as it guarantees an optimal synchronization of activity and rest with the time of day. An experimental result conforms to these reflections: LD cycles can synchronize periodical activity even if their amplitude is very small ($0/10^{-4}$lux)

(LAMPRECHT & WEBER, 1977). Possibly it is not the LD, but a different diurnally varying factor or complex of factors that is ecologically relevant (selective). In this case the LD would only act as 'zeitgeber' (ASCHOFF, 1954). Selection preserves the fitness of the circadian system by controlling the phase angle difference between the periodicity of environment and activity. This difference essentially depends on the duration of the spontaneous period (LAMPRECHT & WEBER, 1973).

4.3. Physiology and genetics of the circadian clock

Do the results of our investigations concerning regressive evolution allow us to draw conclusions about the physiology and genetics of the intact circadian clock? We have already explained in an earlier study that the results of the activity control in DD and LL in *L. navarricus* are consistent with PAVLIDIS's hypothesis (1969) about the nature of the circadian oscillator (as a population of suboscillators of high frequency). This hypothesis excludes the generation of infradian periods in a degenerating circadian system. On the other hand, it admits the generation of ultradian periods. In the periodograms of DD actograms of *L. navarricus* the slight minima in the ultradian range ($\tau < 20$ hours) are about three times more frequent than in the periodograms of the LL actograms. The slight minima in the infradian part ($\tau > 30$ hours) are equally frequent. If these minima should indicate at least partly genuine (but heavily disturbed) periodicities, their different frequencies would not conflict with PAVLIDIS' hypothesis.

It has not up to now been possible to confirm the expectation that a phenetical system of the physiological clock might be established by examining the regressive evolution of the clock, i.e., that the clock might be described by independently combineable basic characteristics as shown in fungi (compare FELDMAN & WASER, 1971).* But we found a new phenetical element in the system which controls the activity in carabids: a sensibility to light, which outlasts the regression of eyes and clock in the course of evolution under cave conditions (see the LD experiments with the blind *Duvalius* species, page 74). – Whether the phenomenon of post-oscillations observed in the cavernicolous form of *Astyanax mexicanus* (page 74 is a new phenetical element of the chronometrical system, must be examined in further investigations. More detailed insights into the phenetics of the circadian clock are to be expected in cavernicolous carabids which, according to their morphological evolutionary state can be grouped between *L. navarricus* and the blind *Duvalius* species (stages 2 and 5).

Genetic investigations concerning the physiological clock may not be possible in carabids because forms of a different evolutionary stage probably can not be crossed. We expect more success with cross-breedings in *Astyanax mexicanus* whose cavernicolous forms breed well with the epigeous form.

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*'Als Phän werden solche elementaren Variationen von Merkmalen oder Eigenschaften bezeichnet, welche in einem der Untersuchung zugänglichen, ausreichend großen Material nicht weiter unterteilt werden können.' (TIMOFEEFF-RESSOSKY et al., 1977 p. 129).

4.4. Stochastic control

In the aperiodic actograms of the tested animals the sequence of rest and activity, in a first approximation is controlled stochastically. Frequently the accidental events determining the transition from one state to the other can be described by simple mathematical regularities. Stochastical control of locomotion was demonstrated for the first time in *Uca* species which live under tidal conditions (LEHMAN et al., 1974). Cockroaches of the species *Blaberus fuscus* which as a rule are periodically active, often show stochastical sequences of rest and activity after removal of their optic lobes (the centres of the circadian 'master clock' in Blattoidea) (LUKAT & WEBER, 1979). We assume that stochastical control of activity is a wide-spread phenomenon, but that it is usually superimposed by the clock in epigeous animals, and is therefore often overlooked. If this hypothesis could be verified, one might conclude that in the course of regressive evolution cavernicolous animals did not need to develop a new nervous mechanism controlling spontaneous activity but that they could activate the mechanism of stochastical control which was already present in their epigeous ancestors.

Stochastic control seems to be very unbiological, especially with time-invariant probabilities of transition. But in fact constant *mean* durations of bursts of activity and pauses of rest can be guaranteed by stochastical control if the probabilities of transition do not change during a larger time-span. In so far stochastical control by an endogenous mechanism is a simple form of time-measuring. Such a mechanism would become biologically significant if it could react adaptively to environmental changes (e.g., if it reacted to scarcity of food by reducing the probability for the transition from activity to rest and/or by increasing the probability for the transition from rest to activity). Indeed, the stochastical mechanism shows adaptive characteristics in *Aphaenops*. The probabilities for the transition from rest to activity and from activity to rest do not change independently from each other, but they are in a weak degree correlated negatively with each other (LAMPRECHT & WEBER, in press). Thus a reaction increasing activity includes both the reduction of the probability for the transition from activity to rest and the increase of the probability for the transition from rest to activity.

But it is not yet known in detail which factors induce changes in the probabilities of the transition. Only temperature-dependence has been more exactly investigated. The probability for the transition from activity to rest is less temperature-dependent than the probability for the transition from rest to activity.

Periodical-temporal control of the functions of cavernicolous organisms is often considered as advantageous because it allows for a temporal segregation of metabolic reactions that prevent each other (see page 78). But in principle, time-control by stochastical mechanisms can also achieve such a segregation. Therefore we believe that it is more fruitful to look for other functions in troglobite animals, which fit into a stochastical time-structure, than to search for hidden and heavily disturbed periodicities.

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REFERENCES

ASCHOF, J.: Zeitgeber der tierischen Tagesperiodik. Naturwiss. **41**: 49–56 (1954).

BÜNNING, E.: Evolution der zirkadianen Organisation. Arzneimittelforsch. **28** (II): 1811–1813 (1978).

DELEURANCE-GLACON, S: Recherches zur les Coléoptères troglobies de la sous-famille des Bathysciinae. Ann. Sc. Nat. Zool. **5**: 1–172 (1963).

ERCKENS, W. and F. WEBER: Rudiments of an ability for time measurement in the cavernicolous fish *Anoptichthys jordani* HUBBS and INNES (Pisces Characidae). Experientia **32**: 1297–1299 (1976).

FELDMAN, J. F. and N. M. WASER: New mutations affecting circadian rhythmicity in *Neurospora*. In: Biochronometry (ed. M. MENAKER), Nat. Acad. Sc. Washington 1971, pp. 652–656 (1971).

GINET, R.: Ecologie, ethologie et biologie de *Niphargus* (Amphipodes Gammarides hypogés). Ann. Spéléol. **15**: 1–254 (1960).

GÜNZLER, E.: Über den Verlust der endogenen Tagesrhythmik bei dem Höhlenkrebs *Niphargus puteanus puteanus* (KOCH). Biol. Zentralbl. **83**: 677–694 (1964).

JEANNEL, R.: Monographie des Trechinae. L'Abeille, J. Entomol. **35**: 1–808 (1928).

JEGLA, F. G. and T. L. POULSON: Evidence of circadian rhythms in a cave crayfish. J. exper. Zool. **168**: 273–282 (1968).

KAISER, H. and U. LEHMANN: Tidal and spontaneous activity patterns in fiddler crabs. II. Stochastic models and simulations. J. comp. Physiol. **96**: 1–26 (1975).

LAMPRECHT, G. and F. WEBER: Eine neue Methode zur Bestimmung von Periodenlängen rhythmisch ablaufender Prozesse. Pfügers Arch. **315**: 262–272 (1970).

LAMPRECHT, G. and F. WEBER: Die Synchronisation der Laufperiodik von *Carabus*-Arten (Ins. Coleoptera) durch Zeitgeber unterschiedlicher Frequenz. Z. vergl. Physiol. **72**: 226–259 (1971).

LAMPRECHT, G. and F. WEBER: Mitnahme, Frequenzdemultiplikation und Maskierung der Laufaktivität von *Carabus*-Arten (Coleoptera) durch Lichtzyklen. J. Insect Physiol. **19**: 1579–1590 (1973).

LAMPRECHT, G. and F. WEBER: Die Circadian-Rhythmik von drei unterschiedlich weit an ein Leben unter Höhlenbedingungen adaptierten *Laemostenus*-Arten. (Col. Carabidae). Ann. Speleol. **30**: 471–482 (1975).

LAMPRECHT, G. and F. WEBER: Die Lichtempfindlichkeit der circadianen Rhythmik dreier Höhlenkäfer-Arten der Gattung *Laemostenus*. J. Insect Physiol. **23**: 445–452 (1977).

LAMPRECHT, G. and F. WEBER: Spontane und induzierte Aktivitätsmuster bei troglobionten Käfern (Genera *Aphaenops*, *Geotrechus*, *Speonomus*). Intern. J. Speleol., in press.

LEHMANN, U., D. NEUMANN and H. KAISER: Gezeitenrhythmische und spontane Aktivitätsmuster von Winkerkrabben. I. Ein neuer Ansatz zur quantitativen Analyse von Lokomotionsrhythmen. J. comp. Physiol. **91**: 181–221 (1974).

LUKAT, R. and F. WEBER: The structure of locomotor activity in bilobectomized cockroaches (*Blaberus fuscus*). Experientia **35**: 38–39 (1979).

MEAD, M. and J. C. GILHODES: Organisation temporelle de l'activité locomotrize chez un animal cavernicole *Blaniulus lichtensteini* BRÖL. (Diplopoda). J. comp. Physiol. **90**: 47–52 (1974).

PARZEFALL, J.: Rückbildung aggressiver Verhaltensweisen bei einer Höhlenform von *Poecilia sphenops* (Pisces, Poeciliidae). Z. Tierpsychol. **35**: 66–84 (1974).

PAVLIDIS, T.: Populations of interacting oscillators and circadian rhythms. J. theor. Biol. **22**: 418–436 (1969).

RENSING, L.: Biologische Rhythmen und Regulation. Fischer, Stuttgart 1973.

TIMOFEEFF-RESSOVSKY, N. W., A. N. JABLOKOV and N. V. GLOTOV: Grundriß der Populationslehre. Fischer, Jena 1977.

VANDEL, A.: Biospeleology. Pergamon-Press, Oxford 1965.

WEBER, F.: Circadian-Regel und Laufaktivität der Caraben (Ins. Coleoptera). Oecologia (Berl.) **1**: 155–170 (1968).

L'ÉVOLUTION DES COLÉOPTÈRES TRECHINAE SOUTERRAINS (COLEOPTERA, CARABIDAE)

C. JUBERTHIE

Laboratoire souterrain du C.N.R.S. Équipe de Biologie souterraine
Moulis, 09200 Saint-Girons, France

ABSTRACT

The possible evolution of the sensory apparatus in the Trechinae cave beetles is described and related to the characteristics of the subterranean life- and ecosystem. Endogeous, troglobite, and specialized troglobite species are compared.

The Trechinae cave beetles are carnivorous and occupy the upper part of the underground foodweb. The food factor will have exerted the strongest selective pressure, because food is sparse, with little diversification, and showing quantitative seasonal variations; the food factor will have been closely connected with the evolution of the antennary chemoreceptors.

In the caves many species of *Aphaenops* are living in the stalagmited area which is moistened by infiltrating rainwater which carries organic matters; they also live in the limestone cracks. The *Aphaenops*, for instance *A. cerberus*, occur between 6 and 11,5 °C.

In the caves, they undergo seasonal temperature variations, and also irregular and fast temperature fluctuations with only a small amplitude. The *Aphaenops* react to these microclimatic variations; they disappear into the cracks in winter when the variations in these caves are relatively great and return to the caves in spring, when microclimatic variations are only slight.

It was observed, that the troglobitic species possess special long trichobothria on the elytra to record microclimatic air-flow variations close to the substrate. The observation of the sensory equipment of various Trechinae species suggests that the most specialized species show an increased olfactory sensitiveness, and an increased mechanic sensitiveness with regard to the air-flow.

The evolution of antennary chemoreceptors can be characterized in the following ways:

- increase in the number of chemoreceptors (Sensilla ampullacea, S. basiconica, S. basiconica sub-inflata, S. basiconica inflata);
- increase of the receptive area of the external part of Sensilla basiconica giving S. b. inflata, a type of olfactive sensilla characteristic of *Aphaenops*, *Hydraphaenops*, *Geotrechus*, *Geotrechidius;*
- increase of the diameter of S. ampullacea and increase of the lenght of the sensory peg.

Regarding the different species, the main feature is either the increase of receptive area *(Cerbaphaenops)*, or the increase in the number of receptors *(Allegretia)*, or an intermediate solution observed in those troglobite species having still relationships with endogeous life *(Aphaenops ludovici, Geotrechus, Geotrechidius)*.

On the other hand, all these species exhibit a regressive evolution consisting of a complete regression of eyes, cuticular and epidermal black pigment, loss of the activity controlling

mechanism and of the circadian rhythm of spontaneous activity, and a reduction of the ability to regulate the rate of transpiration through the cuticle.

Conclusions on the importance of the adaptive sensory evolution in the Trechinae cave-beetles are generally supported. Hence *Aphaenops* and other specialized troglobite species do not represent ancestral morphological types or 'living fossiles' conserved in caves, but are species with a specialized adaptation to the underground ecosystem with both progressive and regressive morphological and physiological characters.

Les Coléoptères Trechinae troglobies vivent dans les cavités des massifs calcaires et participent au fonctionnement de l'écosystème karstique. Quelques espèces ne se limitent pas à cet écosystème, ce sont: les *Aphaenops* du groupe *A. rhadamantus*, *A. linderi*, *A. ludovici* et *A. gaudini*, qui ont été plus souvent récoltés sous les pierres enfoncées des Pyrénées occidentales que dans les grottes, et des *Duvalius* dont certaines populations mènent une vie endogée en altitude.

I – Écosystème souterrain karstique et place des Trechinae

L'écosystème souterrain karstique tire son énergie du soleil; sa production primaire est localisée au niveau de la végétation de surface (sol, forêts, pelouses) et dans les rivières; son fonctionnement énergétique se caractérise par un transfert de cette production primaire vers les consommateurs secondaires et tertiaires qui vivent sous terre. Le véhicule majeur de ce transfert est l'eau, l'eau de pluie qui s'infiltre après avoir lessivé les sols, l'eau des rivières qui se perdent sous terre. L'apport de nourriture est saisonnier. Les matières organiques dégradées dominent; les chaînes alimentaires souterraines sont donc à base de détritivores. Les Coléoptères Bathysciinae troglobies se situent à la base de la pyramide alimentaire, ce sont des saprophages. Les Coléoptères Trechinae, se situent au-dessus d'eux, car ils sont carnassiers.

II – Peuplement souterrain et populations

Le milieu de vie souterrain karstique est constitué des grottes, parties accessibles à l'homme des réseaux souterrains, et de parties accessibles seulement aux Invertébrés de petite taille, fentes, diaclases, cavités reliées entre elles par des fentes etc..

La méthode de marquage et recapture appliquée aux populations de Bathysciinae, a montré que la population en relation avec une grotte peut atteindre plusieurs dizaines de milliers d'individus, mais qu'un faible pourcentage de ces Coléoptères, de 3 à 15 % en général, seulement, vit dans la grotte; elle a montré également l'existence d'un turnover continuel d'animaux entre la grotte et les autres portions du réseau souterrain.

Appliquée aux Trechinae, cette méthode donne des résultats moins précis, du fait que le nombre des Coléoptères susceptibles d'être marqués est le plus souvent réduit, mais les résultats obtenus vont dans le même sens.

La population d'*Aphaenops loubensi* de la station des schistes dans la salle de la Verna du réseau de la Pierre Saint-Martin a été estimée à 400 individus environ (CABIDOCHE, 1966), celle de *Rhadine araizai howdeni* dans la Fern Cave au Texas a été estimée à 5311 individus ± 2615 (MITCHELL, 1970), celle de *Pseudoanophthalmus tenuis* dans la Murray Spring Cave (Indiana) à 3298 ± 952 (KEITH, 1975), celle de *Neaphaenops tellkamfii* dans une station de 400 m^2 et une autre de 300 m^2 dans la Mamoth Cave respectivement à 2761 et 800 individus (BARR et KUEHNE, 1971).

Une petite portion du réseau souterrain étant accessible, la population réelle de l'ensemble est plus élevée, mais son estimation ne peut être qu'une extrapolation. Ainsi la population de *Neaphaenops tellkamfii* dans les 250 km du réseau de la Mamoth Cave est estimée à 800000 individus par BARR et KUEHNE.

Le nombre des individus capturés dans la grotte représente selon les cas de 5 à 30 % de la population totale estimée.

De façon générale et bien que mal connues, les populations des Trechinae souterrains sont de beaucoup plus petites que celles des Bathysciinae; ceci tient en grande partie à leur position dans la pyramide alimentaire souterraine, ce sont en effet des carnassiers, tandis que ces derniers sont saprophages.

Le nombre des Trechinae varie saisonnièrement dans les grottes. Ainsi les *Aphaenops cerberus* du système souterrain de la grotte de Sainte-Catherine (Ariège) apparaissent en avril-mai dans les galeries de la grotte lorsque le régime estival de ventilation calme, s'installe; leur nombre croît jusqu'en août-septembre, puis diminue progressivement à l'automne; les imagos disparaissent de la grotte et se réfugient dans les fentes lorsque le régime hivernal, ventilé et froid s'installe (fig. 1). Ce phénomène a été observé chez tous les Trechinae et Bathysciinae étudiés, aussi bien dans les karsts froids d'altitude (Pierre Saint-Martin dans les Pyrénées, Getharul de la Scarisoara en Roumanie) que dans ceux de moyenne altitude (grotte de Sainte-Catherine, grotte du Pigailh), que la grotte présente plusieurs ouvertures et un régime fortement ventilé s'inversant saisonnièrement, ou une seule ouverture et un régime de type convection, plus calme.

III – MILIEU DE VIE ET PRESSIONS DE SÉLECTION

Le milieu souterrain, dans ses zones habitées par les Coléoptères notamment, a été longtemps considéré comme constant, et comme un milieu refuge conservateur de types morphologiques ancestraux auxquels le nom de 'fossiles vivants' a été donné. Pour JEANNEL (1943), l'évolution souterraine serait une évolution orthogénique indépendante du milieu souterrain, et les espèces ainsi évoluées auraient peuplé le milieu souterrain lorsque les conditions climatiques externes leur seraient devenues défavorables. A cause de leur 'sténygrobiose', les Trechinae les plus évolués ne pouraient pas vivre sous le climat actuel même dans les habitats les plus humides des forêts, et ils auraient disparu par extinction s'ils n'avaient pas pu coloniser le sous-sol.

Or, cette interprétation, essentiellement basée sur les caractères régressifs des troglo-

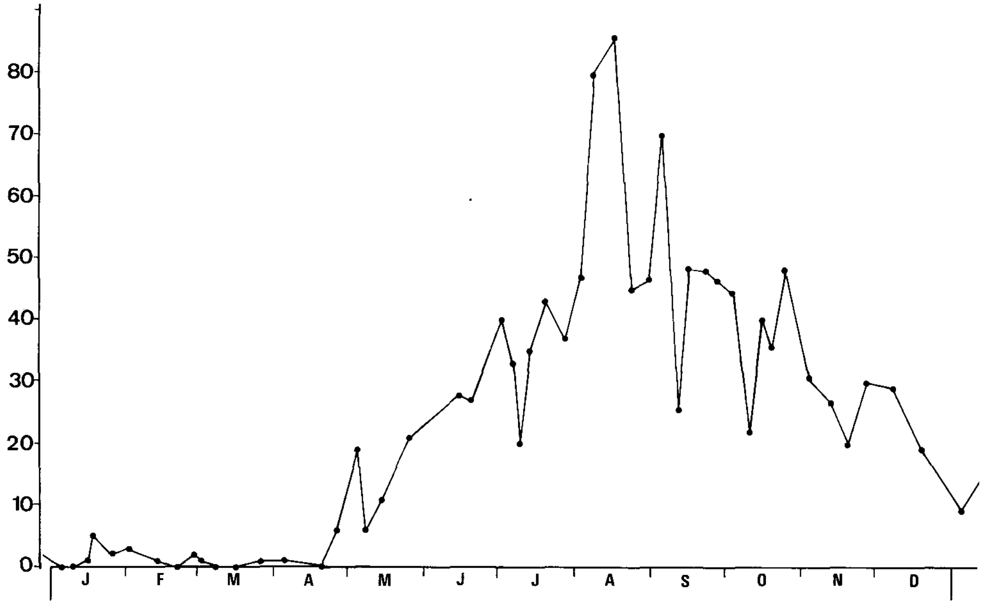

Fig. 1. Courbe montrant les variations du nombre des *Aphaenops cerberus* au cours d'une année dans la grotte de Sainte-Catherine. Les variations numériques observées ne sont pas dues à un rythme saisonnier dans l'émergence des imagos, mais à des migrations des fentes vers la grotte et réciproquement. Ce phénomène découle du fait que le climat souterrain n'est pas constant tout au long de l'année dans la grotte considérée.

bies, postule l'absence de pression de sélection dans l'écosystème souterrain, ou l'absence de réponse de ces 'fossiles vivants' à des pressions de sélection relativement faibles.

Les études écologiques menées ces dix dernières années sur le fonctionnement de l'écosystème souterrain ne sont pas en faveur d'un milieu constant jouant le rôle de refuge; elles ont en effet montré l'existence de variations saisonnières dans les paramètres climatiques et nutritionnels; l'amplitude de leurs variations est plus faible que dans les écosystèmes de la surface, mais les Coléoptères souterrains répondent à de très faibles variations, par exemple de température, pour des raisons qui tiennent aux caractéristiques biologiques de leur développement; la lenteur de ce dernier, entraînant une constante de développement élevée, leur permet à chacune des phases du cycle vital d'intégrer les lentes et faibles variations de température. Ces recherches ont dégagé l'existence de pressions de sélection exercée par une nourriture relativement peu abondante et peu variée et la compétition qui en résulte.

Dans l'interprétation de JEANNEL et des auteurs qui l'ont suivi, les espèces, au moment où elles ont commencé leur évolution vers la vie souterraine, ne peuplaient pas conjointement le milieu endogé et le milieu souterrain ou les fronts de glaciers et les réseaux karstiques dans le cas de la lignée des *Aphaenops*.

Or, au moins pour les Trechinae du genre *Duvalius* moins évolués que les *Aphaenops*, une espèce *D. scarisoarae* peuple selon l'altitude et les conditions climatiques correspondantes la surface du sol vers 1500 m, le compartiment sol de l'écosystème forestier vers 900 m, les grottes vers 500 m d'altitude. Nous pensons que ce double peuplement représente une situation originelle fréquente pour les lignées souterraines et que l'évolution s'est ensuite poursuivie dans le milieu souterrain, lorsque les populations ont été coupées du flux génique provenant de la population mère endogée.

IV – FACTEURS DU MILIEU SOUTERRAIN ET REPONSE DES COLÉOPTÈRES

1. Humidité du substrat et humidité relative de l'air

Les Trechinae troglobies ne sont pas uniformément répartis dans le système de cavités souterraines; ceci est connu depuis bien longtemps et tient au fait que le milieu de vie n'est pas homogène.

Les imagos d'*Aphaenops cerberus* (fig. 2), par exemple, s'observent dans les grottes sur les plaques argileuses très humides et sur les parois concrétionnées humidifiées soit par l'écoulement d'un film d'eau provenant d'infiltration de la zone supérieure des karsts, soit par l'eau qui coule entre la roche et la concrétion et traverse la croûte concrétionnée. Les imagos se déplacent le long de ces coulées humides, ainsi que dans

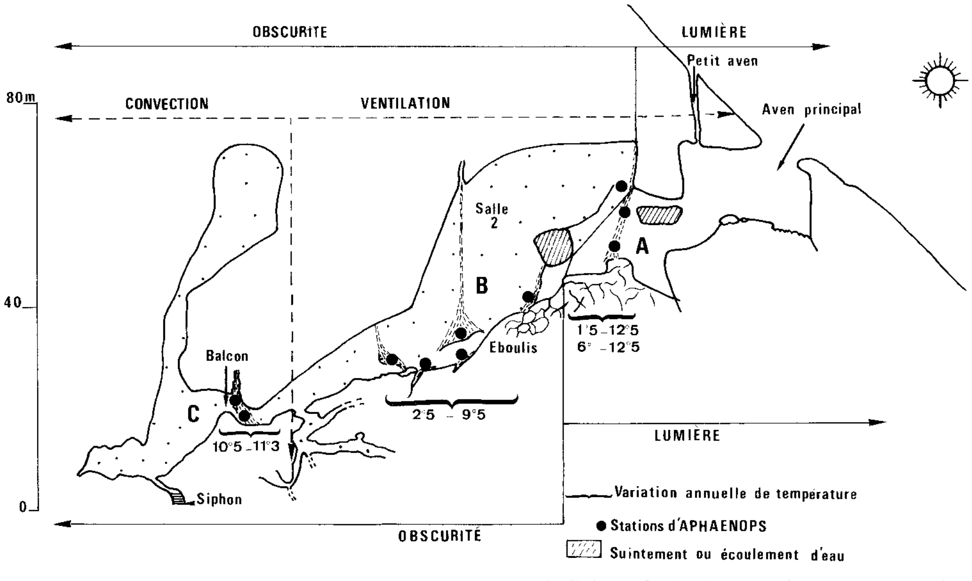

Fig. 2. Coupe schématique longitudinale de la grotte de Sainte-Catherine (Ariège), montrant la limite entre la zone éclairée et la zone obscure, et l'emplacement des zones suintantes d'eau. Les *Aphaenops cerberus* peuplent dans les zones A, B, et C les coulées suintantes, et en A ne sont pas à l'obscurité totale.

les fentes qui les prolongent et qu'empruntent de faibles circulations d'eau. Dans la grotte de Sainte-Catherine prise en exemple, des cellules de convexion s'établissent en juillet et août; elles provoquent des condensations en plages étendues sur les parois qui relient certaines des coulées humides précédentes, de sorte que les *Aphaenops cerberus* peuvent transiter d'une coulée à l'autre, ce qui contribue au brassage de certains des ensembles qui constituent la population de la grotte et des fentes qui lui correspondent. Ce type de localisation se retrouve dans les autres systèmes souterrains que peuple cette espèce (grottes de Liqué, de l'Estelas, etc.), et semble général pour le groupe comprenant les espèces *A. pluto*, *tiresias*, *crypticola*. La première conclusion est que l'habitat souterrain est, pour ces *Aphaenops*, hétérogène dans l'espace, en ce qui concerne l'humidité du substrat et l'H. R. de l'air à son contact, la seconde est que les *Aphaenops* sont sensibles à ces différences, et qu'ils ont probablement un équipement sensoriel spécialisé permettant de les détecter.

2. *Facteur nourriture*

Les Trechinae sont carnassiers mais leur régime alimentaire reste mal connu. J'ai observé des *Aphaenops cerberus* transportant dans leurs mandibules des larves de Diptères; les Collemboles, les Bathysciinae et les autres Microarthropodes qui se développent sur les débris organiques déposés par les eaux souterraines peuvent, également, leur servir de proies.

La nourriture de base des proies des *Aphaenops* est peu variée; celle qui provient, par les eaux qui s'infiltrent dans la zone supérieure des karsts, du lessivage des sols superficiels, est en majeure partie composée de matières organiques figurées ou dissoutes à divers degrés de dégradation; celle apportée par les pertes de rivière (flood factor de HAWES) est plus variée, mais ce sont encore les matières organiques déposées le long des berges argileuses après les crues, assez loin à l'intérieur des massifs, qui interviennent dans l'alimentation des proies des *Aphaenops*. La teneur en matière organique des sédiments émergés ou des limons immergés varie de 0,5 à 9 %; cette quantité varie saisonnièrement en relation avec les rythmes d'activité du couvert végétal et les périodes de pluviosité ce qui peut introduire des maximums saisonniers dans la reproduction. La densité des proies des *Aphaenops* est le plus souvent faible. Il en résulte que le facteur nourriture a exercé une forte pression de sélection, et l'évolution des organes chémorécepteurs lui est en partie liée.

3. *Obscurité*

Le principal facteur synchroniseur des rythmes circadiens en milieu épigé, la photopériode n'existe pas et l'obscurité est totale. La disparition des yeux lui a été associée; cet aspect régressif de l'évolution souterraine a attiré en premier les zoologistes et reste encore le trait le plus évident et, pour certains, majeur de leur évolution.

Les faibles luminosités n'ont cependant pas un effet létal sur les Coléoptères ou n'entraînent pas un réflexe comportemental de fuite. Ainsi, au fond de l'aven de Sainte-Catherine vit de mai à octobre une petite population d'*Aphaenops cerberus*; elle y est soumise à un éclairement de 1 à 15 lux selon une périodicité journalière. En hiver les individus se réfugient dans les fentes et les éboulis et se trouvent de ce fait à l'obscurité totale.

4. *Température*

Dans les Pyrénées, les Trechinae troglobies vivent dans une échelle de températures comprises entre 5 et 12°C selon l'altitude de la grotte.

Dans les grottes, sur le substrat où ils se déplacent (parois concrétionnées, argile) les *Aphaenops* enregistrent deux types de variations de température.

1. Des variations de longues périodes, saisonnières, liées au passage d'ondes thermiques engendrées par les variations climatiques externes; elles peuvent jouer sur la reproduction et le développement. L'amplitude de ces variations atteint par exemple 6°C dans la salle 2 de Ste-Catherine.
2. Des variations de très courtes périodes, de l'ordre de quelques minutes et de quelques dixièmes de degré d'intensité, provoquées par l'écoulement turbulent de masses d'air le long des parois humides et rugueuses; elles s'accompagnent d'échanges thermiques et hydriques entre les deux phases. Elles jouent sur les déplacements et l'activité locomotrice des *Aphaenops.*

De plus les conditions thermiques peuvent différer dans l'espace en fonction de la profondeur de la station et du régime de ventilation auquel elle est soumise. Ainsi, dans la galerie ventilée de la grotte de Sainte-Catherine, les *A. cerberus* y subissent des températures qui varient de 6 à 7°C, tandis que ceux qui vivent au fond vivent entre 10,5°C et 11,3°C. Cette différence de 4°C est suffisante pour influer sur la vitesse de la vitellogenèse et sur la fécondité.

La température létale supérieure du développement embryonnaire joue un rôle important dans la répartition des Bathysciinae en altitude dans les Pyrénées; elle est basse, comprise entre 9 et 16°C selon les espèces, et joue le rôle de facteur limite. Un polymorphisme physiologique vis-à-vis de la température a été mis en évidence dans des populations vivant dans des grottes situées à différentes altitudes; les changements climatiques au cours des glaciations du quaternaire ont donc pu favoriser les individus, les populations, ou les espèces psychrophiles en compétition lors d'un refroidissement, et l'inverse lors d'un réchauffement (DELAY, 1978). Les Trechinae présentent peut être le même phénomène, mais les difficultés d'élevage font qu'aucune donnée n'existe.

5. *Agitation de l'air, ventilation*

Les fentes ont un régime de ventilation pratiquement nul, tandis que les grottes qui possèdent plusieurs ouvertures situées à des altitudes différentes, telle Sainte-Catherine, présentent un régime ventilé descendant d'air froid et sec en saison froide, et un régime remontant beaucoup plus calme, d'air chaud et humide, en saison estivale.

Cette ventilation se traduit à Sainte-Catherine, à 3–4 mm de la paroi sur laquelle se déplacent les *Aphaenops cerberus*, par un écoulement en régime turbulent, qui peut atteindre 20 cm/s. Les Trechinae vivent dans ces conditions microclimatiques, sans modifications apparentes du comportement, aussi longtemps qu'un certain seuil de perturbation n'est pas atteint; au delà ils fuient.

Ce seuil est atteint saisonnièrement à l'entrée de l'hiver; ces modifications du microclimat pariétal des galeries ouvertes à l'extérieur sont responsables des migrations des *Aphaenops cerberus* des galeries perturbées vers les fentes plus calmes, et inversement au printemps. Les *A. cerberus* de la grotte de Sainte-Catherine disparaissent lorsque les variations rapides de la température, à 3–4 mm de la paroi, s'élèvent à 1/10–6/10° toutes les 2 à 3 minutes, ou que leur fréquence augmente, les variations se succédant toutes les 10 à 15 secondes; ils disparaissent donc lorsque la vitesse d'écoulement de l'air et sa turbulence augmentent.

Ces migrations traduisent, à notre avis, une extension du domaine de chasse des imagos lorsque les conditions microclimatiques deviennent favorables dans la grotte, et inversement. Il reste à déterminer si cette extension est passive, et résulte de la levée de la barrière microclimatique, ou s'il s'y adjoint une attraction positive par d'autres facteurs.

IV – ASPECTS POSITIFS DE L'ADAPTATION DES COLÉOPTÈRES TRECHINAE AU MILIEU SOUTERRAIN

1. 1. *Évolution de l'équipement sensoriel des antennes en fonction du degré d'adaptation à la vie souterraine.*

Cet équipement sensoriel a été étudié chez des espèces endogées troglophiles et troglobies appartement à plusieurs lignées évolutives de Trechinae (tableau).

a. L'équipement sensoriel type d'un article antennaire distal de Trechinae est le suivant:

- 1 sensille campaniforme dans le tiers basal,
- 1 couronne sub-apicale de macrochètes (sensilla chaetica de grande taille),
- des sensilla chaetica de taille moyenne implantées sans régularité sur l'article,
- 1 sensilla styloconica en position ventrale et sub-apicale,
- 1 plage ventrale de sensilla basiconica entourée de sensilla trichoïdea,
- des sensilla trichoïdea face dorsale,
- des sensilles basiconiques modifiées, plus ou moins élargies (S. basiconica subinflata et S. basiconica inflata) au sein de la plage ventrale.

Cet équipement type s'établit progressivement à partir du 3e, 4e, 5e et 8e article selon le récepteur sensoriel considéré et selon l'espèce. Un bilan complet a été établi chez *Aphaenops crypticola* prise comme espèce de référence (JUBERTHIE et MASSOUD, 1977); la nature chémoréceptrice ou mécanoréceptrice de certaines sensilles a été contrôlée en microscopie électronique à transmission.

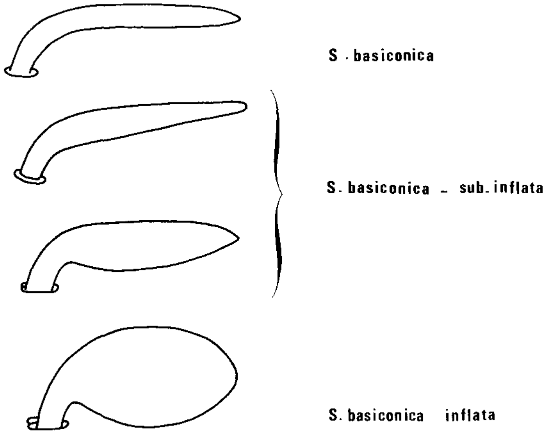

Fig. 3. Sensilla basiconica. Modification de la forme et augmentation de la surface réceptrice de la partie externe de ce type de chémorécepteur, en fonction du degré d'adaptation à la vie souterraine.

b. Les espèces strictement endogées, tels les *Trechus* étudiés, ont l'équipement sensoriel le plus simple, que l'on semble en droit de considérer comme l'équipement primitif car il représente le fond commun à tous les Trechinae étudiés, tel qu'il vient d'être décrit. Les sensilles basiconiques modifiées sont représentées par des récepteurs externes légèrement élargis au niveau du coude qu'ils font, ou sur toute leur longueur, et les sensilla basiconica inflata font défaut. Le nombre des chémorécepteurs est peu élevé, de 374 à 479 chez les 3 espèces étudiées, et en corollaire les sensilla ampullacea sont peu nombreuses et n'apparaissent qu'au 5e ou au 6e article, de même que les S. basiconica sub-inflata qui n'apparaissent qu'au 5e. Les S. ampullacea ont une très petite ouverture tégumentaire et l'ampoule et la tigelle sensorielle sont courtes.

Le même type d'équipement est porté par les espèces endogées de la lignée des *Duvalius*, à la différence près que le nombre des organes sensoriels est plus élevé.

c. Les espèces souterraines, particulièrement les plus évoluées, ont un équipement sensoriel qui semble dériver de l'équipement de base des endogés, selon différentes modalités qui représentent autant de radiations évolutives, caractéristiques d'un groupe d'espèces, ou d'un genre.

Ainsi, dans la lignée des *Aphaenops*, l'évolution vers la vie souterraine se caractérise:

- par la transformation de toutes les sensilles basiconiques en S. b. inflata à partir du 8e article, chez les espèces du sous-genre *Cerbaphaenops* et du genre *Hydraphaenops* ce qui correspond à une forte augmentation de leur surface réceptrice; ce phénomène s'accompagne chez les *Cerbaphaenops* de l'apparition des S. basiconica et des S. ampullacea dès le 4ème article et d'une augmentation du nombre des S. ampullacea, chez les *Hydraphaenops* les S. ampullacea n'apparaissent qu'au 5e article comme chez presque tous les Trechinae troglobies étudiés et leur nombre est moins élevé (le triple de celui des *Trechus* au lieu du quintuple). Les S. ampullacea sont profonds et ont une très large ouverture.

- par une modalité différente, particulièrement nette dans le genre *Allegrettia* et caractérisée par une augmentation considérable du nombre des sensilles chémoréceptrices, sans changement de leur forme, S. ampullacea excepté, ni formation de S. b. inflata. Cette modalité se retrouve, en moins accentué chez les *Speotrechus* et les *Paraphaenops* si on les compare aux *Geotrechus* et *Geotrechidius* de la même lignée qui bien que troglobies ont conservé sous terre un mode de vie endogé.
- une solution intermédiaire est réalisée chez les espèces troglobies qui ont gardé des attaches avec le milieu et le mode de vie endogé *(Aphaenops ludovici* du sous-genre *Geaphaenops)*, *Geotrechus* et *Geotrechidius;* elle est caractérisée par une augmentation du nombre des S.b. sub-inflata, la transformation conjointe d'un certain nombre de sensilles en S. b. inflata et une nette augmentation du nombre des S. ampullacea. Ces derniers n'ont qu'une ouverture de taille moyenne chez les *Geotrechus* et les *Geotrechidius* et sont de type intermédiaire entre ceux des *Trechus* et des *Aphaenops*.

Dans la lignée des *Duvalius* l'on observe une certaine augmentation du nombre des chémorécepteurs, spécialement des S.b. sub-inflata, sans transformation en S.b. inflata; leur évolution sensorielle est du même type que celle des *Paraphaenops* et *Speotrechus* de l'autre lignée.

L'évolution des *Neaphaenops* de la lignée des *Trechoblemus* se caractérise par une augmentation du nombre des chémorécepteurs particulièrement des S. ampullacea et l'absence de S. b. inflata.

En conclusion, sous l'action de pressions de sélection dans l'écosystème souterrain, l'équipement sensoriel antennaire chémorécepteur originel caractéristique des Trechinae endogés a évolué, et cette évolution s'est faite selon plusieurs modalités comportant ou non, ou à des degrés divers:

- l'augmentation des nombres des chémorécepteurs, (Sensilla ampullacea, S. basiconica sub-inflata, S. basiconica).
- la transformation d'un certain nombre de Sensilla basiconica type répandu chez tous les Insectes en S. b. inflata, type qui n'est connu que chez certains Trechinae troglobies et qui traduit une augmentation de la surface réceptrice de la partie externe du récepteur.
- l'augmentation du diamètre de l'ouverture, de la profondeur et de la longueur de la tigelle réceptrice des S. ampullacea.

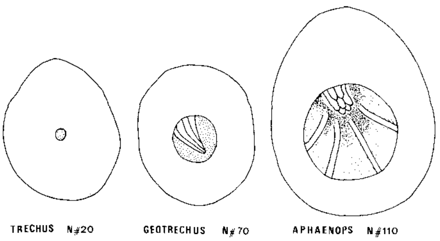

Fig. 4. Sensilla ampullacea. Augmentation du diamètre et du volume de la cavité tégumentaire en fonction du degré d'adaptation à la vie souterraine. Les chiffres indiquent le nombre moyen de ce type de sensilles dans les genres étudiés.

Les termes les plus élaborés de cette évolution sont réalisés, d'une part chez les *Aphaenops* du groupe *Cerbaphaenops*, d'autre part chez *Allegrettia.*

L'évolution sensorielle chez les Trechinae troglobies se traduit donc par une augmentation de la sensibilité olfactive, soit par augmentation des surfaces réceptrices, soit par augmentation du nombre des chémorécepteurs, soit par combinaison de ces deux modalités.

2. *Évolution de l'équipement sensoriel des élytres.*

Les Trechinae troglobies en particulier les *Aphaenops*, *Hydraphaenops Neaphaenops*, etc., portent sur la face dorsale de chacune de leurs élytres, une série de 10 longues trichobothries dénommées 'fouets' par JEANNEL, dont 3 dépassent la moitié de la longueur de l'élytre. Chaque trichobothrie possède un neurone mécanorécepteur typique avec son corps tubulaire; de ce fait, l'animal peut enregistrer, par les déplacements de ces soies, la microventilation pariétale.

La position dorso-latérale des trichobothries les fait se mouvoir dans la couche d'air la plus éloignée du substrat (2 à 4 mm) et qui est plus pertubée que les couches les plus proches.

Ces soies ne sont pas des néoformations, elles existent en effet, chez les espèces épigées mais elles y sont très courtes. L'allongement des trichobothries est donc un phénomène propre aux espèces troglobies; cet allongement apparaît comme une évolution spéciale aux Trechinae, qui ne se retrouve pas dans les autres groupes. Elle peut être mise en relation avec leur sensibilité très élevée à l'agitation de l'air. Ces trichobothries interviennent très probablement en fournissant les informations nécessaires à la réponse nette et précises des *Aphaenops* aux variations du microclimat pariétal.

De plus, les 3 trichobothries les plus longues possèdent un second neurone sans corps tubulaire; les autres présentent de 4 à 5 neurones bipolaires supplémentaires sans corps tubulaire, à segment distal court dont la fonction reste inconnue; il n'y a aucun pore ni dans la paroi ni à l'extrémité de la soie.

V – ASPECTS RÉGRESSIFS DE L'ADAPTATION DES TRECHINAE AU MILIEU SOUTERRAIN

1. Le plus anciennement connu, (LESPES, 1868; BERNARD, 1937) est la disparition totale des yeux et des centres optiques chez les Trechinae troglobies tels que les *Aphaenops* et les *Duvalius*. BERNARD constate ainsi chez *Aphaenops cerberus* et *Duvalius delphinensis* l'absence de ganglions optiques et d'appareil visuel externe. Cette régression totale représente le terme d'une évolution dont certaines étapes intermédiaires ont été décrites dans la lignée des *Laemostenus*, qui renferme des espèces endogées, troglophiles guanobies, et troglobies peu spécialisées.

2. Le second trait régressif est la disparition des pigments noirs granulaires mélaniques. La dépigmentation de la cuticule n'est cependant que partielle, les imagos conservant une couleur fauve plus ou moins foncée; celle-ci a été mise en relation chez

Trechinae	Sensilla basiconica et trichodea 	S. basiconica sub-inflata 	S basiconica inflata 	S ampullacea 	Total des Chemorecepteurs
Lignée des Aphaenops		Troglobies			
Aphaenops inaequalis	318	6	157	119	600
Aphaenops crypticola ♀	219	0	188	107	514
Aphaenops crypticola ♂	219	0	158	107	484
Hydraphaenops sollaudi	495	0	117	61	673
Aphaenops ludovici	458	157	192	106	913
Allegrettia boldorii	1395	758	0	180	2333
Speotrechus mayeti	328	352	0	54	734
Paraphaenops breuilianus	425	191	0	96	712
Geotrechidius gallicus	163	111	69	77	420
Geotrechus vulcanus	248	33	124	68	473
Lignée des Trechoblemus					
Neaphaenops tellkampfi	641	95	0	248	984
Lignée des Duvalius					
Sardaphaenops supramontanus	1052	197	0	171	1420
Trichaphaenops gounellei	521	359	0	62	942
Arctaphaenops gaudini	442	316	0	80	838
Duvalius delphinensis	660	253	0	78	991
Duvalius simoni	600	186	0	55	841
Duvalius baldensis tombeanus	557	Endoges 184	0	46	787
Duvalius breiti	707	129	 92	74	1002 (T.E)
Lignée des Trechus					
Trechus custos	375	81	0	23	479
Trechus quadristriatus	422	10	0	18	450
Trechus latericola	288	67	0	19	374

Fig. 5. Variation du nombre et des types de sensilles chémoréceptrices chez les Trechinae, en fonction de la lignée, de l'espèce et du mode de vie. T.E. = espèce endogée-troglobie.

le Bathysciinae *Antrocharis querilhaci* avec la sclérification de la cuticule et l'élaboration de mélanines jaunes correspondant à des pigments monobenzoquinoïques, et de mélanines brunes correspondant à des pigments di- ou polybenzoïquinoniques en partie liés à des protéines cuticulaires (Bernasconi, 1965). Il semble que chez les Coléoptères troglobies le métabolisme de la thyrosine soit dirigé sélectivement vers la formation de mélanines jaunes et brunes et que leur synthèse ne soit partiellement régressée que chez les genres les plus dépigmentés, tels les *Aphaenops*.

3. Le troisième est la disparition de tout rythme circadien dans l'activité locomotrice spontanée des Trechinae troglobies, *Aphaenops pluto*, *A. cerberus*, *Geotrechus orpheus*, en obscurité constante ou en lumière constante faible de 10^{-2} lux, et l'impossibilité de resynchroniser l'activité de ces Insectes troglobies en les soumettant à une photopériode. L'horloge biologique interne, qui est le mécanisme de contrôle du temp, est donc régressée (LAMPRECHT et WEBER, 1977).

4. Le quatrième est la disparition chez les *Aphaenops* de la plus grande partie des capacités d'autoréguler la perte en eau par transpiration; ce n'est qu'aux humidités relatives proches de la saturation que ce pouvoir se manifeste partiellement (VANNIER et JUBERTHIE, 1978).

En revanche, dans des conditions optimales de température, le flux d'évaporation d'*Aphaenops cerberus* reste faible (2 mg 10^{-4}/mm^2/minute); de ce fait, contrairement à ce qui était postulé, ces Insectes présentent une résistance à la dessiccation assez élevée, la limite létale de déshydratation n'étant atteinte qu'au bout de 31 h à 76,5 % HR. Ceci implique que les téguments n'ont pas entièrement perdu leurs couches protectrices, lipidiques, épicuticulaires ou intralamellaires.

CONCLUSION

1. Les Trechinae troglobies présentent un mélange de caractères archaïques et de caractères adaptatifs très évolués.

– Les caractères morphologiques archaïques représentent les restes d'une évolution indépendante du mode de vie souterrain qui permet de reconnaître les affinités entre les lignées. Ainsi les espèces de la lignée phylétique des *Aphaenops* ont conservé une pièce copulatrice en position latérale, des tibias antérieurs pubescents et présentent deux articles dilatés aux tarses antérieurs des mâles.

– Les caractères adaptatifs aboutissent à la formation d'un type morphologique et physiologique original; ces caractères sont de deux types:

● les uns sont régressifs, ce sont la disparition des yeux et des lobes optiques, la dépigmentation des téguments, la disparition des rythmes nycthéméraux d'activité locomotrice, la diminution du pouvoir d'autorégulation de la perte en eau au travers des téguments.

● les autres traduisent des adaptations écologiques aux conditions et pressions de sélection au milieu souterrain. Certains de ceux-ci, morphologiques et connus depuis longtemps, tel que l'allongement des appendices et l'apparente physogastrie de l'abdomen, sont contestés par certains auteurs comme représentatifs de l'évolution souterraine. D'autres, décrits dans ce travail, consistent en une augmentation du nombre et en un changement de forme des organes chémorécepteurs antennaires et en un allongement des trichobothries des élytres; ils traduisent une augmentation de la sensibilité olfactive et de la sensibilité mécanique à l'agitation de l'air. Dans la lignée des *Aphaenops*, cette évolution se traduit, aux deux extrêmes, chez certaines espèces par une augmentation du nombre des sensilles olfactives antennaires avec une faible modification de leur forme (type *Allegrettia*), et chez d'autres (type *Cerbaphaenops*) par une transformation des sensilles basiconiques en sensilles à plus large surface réceptrice (sensilla basiconica inflata) avec une petite augmentation de leur nombre.

– D'autres modifications adaptatives sont biologiques et communes à l'ensemble des espèces troglobies spécialisées; ce sont le ralentissement du développement, la diminution de la fécondité et l'augmentation de la taille des oeufs. Elles traduisent l'adoption d'une stratégie de type 'K' qui privilégie la survie de l'individu, et qui se retrouve dans les milieux qui ont, comme le milieu souterrain, une nourriture peu variée et peu abondante, et une faible variabilité des paramètres physiques.

2. Dans les ouvrages sur l'évolution souterraine, où sont formulées des hypotheses sur ses étapes et sur les biotopes où elle s'est effectuée (humus des forêts, sol, grottes) ne sont presque exclusivement pris en compte que les aspects régressifs. Or ceux-ci, comme nous l'avons vu, ne sont pas seuls représentatifs de l'évolution souterraine. De plus, certains ne sont pas importants pour la survie de l'espèce; la disparition des yeux, par exemple, est un caractère neutre pour la survie d'une espèce qui vit en permanence dans un milieu obscur. D'autres, mis en évidence récemment et de nature biologique, n'ont pas encore été pris en compte dans ces théories évolutives. Or certains ont une composante positive; ainsi, la disparition des rythmes circadiens dans l'activité locomotrice, caractère biologiquement régressif, présente une composante de ce type, en permettant aux *Aphaenops* d'utiliser tout le nyctémère pour chasser les proies, ce qui augmente leur compétitivité.

– Les adaptations sensorielles, essentiellement chémoréceptrices, représentent, donc, l'autre volet de cette évolution; dans le cas des Trechinae, les pressions de sélection ont tendu continuellement à sélectionner le plus apte pour la capture des proies. Un peu plus marquée chez la femelle que chez le mâle des *Aphaenops*, cette évolution semble bien en relation avec l'aptitude à reconnaître les proies, et non le partenaire sexuel comme chez les Insectes en général où ce sont les antennes des mâles qui présentent un hyperdéveloppement sensoriel.

3. La théorie actuellement admise sur l'origine des Coléoptères cavernicoles, veut que les Trechinae soient des néotroglobies, les uns, en particulier les *Aphaenops*, relictes d'une faune nivicole d'altitude, d'autres relictes d'une faune de l'humus des forêts froides et humides d'altitude. Les réchauffements et dessèchements post-glaciaires, par exemple après le Wurm, en détruisant leurs biotopes superficiels ou en rendant défavorables les conditions de leur vie à la surface, auraient entraîné leur migration dans les grottes, où ils auraient subsisté grâce aux conditions climatiques considérées comme constantes qui y règnent (JEANNEL, 1942; 1943; VANDEL, 1964; GUEORGUIEV, 1977). Il y a de plus consensus pour admettre que les premiers stades de l'évolution

souterraine se seraient déroulés dans l'humus des forêts, le sol, le bord des névés. Pour certains auteurs même, (LANEYRIE, 1974) le facies morphologique des Coléoptères cavernicoles, caractérisé par l'aptérisme, la dépigmentation, la micro ou l'anophthalmie, signes de sénéscence, a été entièrement acquis en dehors du milieu souterrain, où toute évolution serait stoppée pour les espèces qui y ont migré.

– Des remarques s'imposent:

● La première est liée à la présence aussi bien chez les Trechinae *(Duvalius)* que chez les Bathysciinae de peuplements conjoints, en altitude dans l'humus et le sol de l'écosystème forestier montagnard et à basse altitude dans les cavités souterraines karstiques; elle ne plaide pas en faveur de la généralité du phénomène de migration du sol des forêts vers les grottes, lorsque les conditions climatiques deviennent défavorables à l'extérieur, au cours des périodes géologiques. Une situation fréquente semble avoir été au contraire, celle d'un peuplement conjoint et contemporain du compartiment sol de l'écosystème forestier montagnard et des milieux similaires et de l'écosystème souterrain*.

● La seconde est que l'opposition entre les conditions climatiques offertes par l'écosystème souterrain karstique et celle des sols forestiers n'est pas aussi tranchée que le postulent les auteurs. Les données récentes montrent, en effet, que les facteurs abiotiques et biotiques varient dans l'écosystème souterrain du fait qu'il tire son énergie de la surface, qu'il en reçoit les ondes thermiques et les eaux météoriques, sujettes à des multiples variations*.

● La troisième est que le milieu souterrain ne peut être considéré comme un milieu exclusivement 'refuge', neutre pour les espèces qui y vivent. Du fait de ses caractéristiques, de son hétérogénéité, de la faible quantité et diversité de la nourriture disponible, l'écosystème souterrain exerce des pressions de sélection sur les animaux qui y vivent.

Tous ces faits suggèrent que l'évolution souterraine s'est poursuivie dans le milieu souterrain; elle a pu aboutir aux formes les plus spécialisées lorsque les populations souterraines ont été coupées du flux génique des populations endogées ou similaires, que ces dernières soient remontées en altitude avec les forêts ou détruites par la karstification ou la compétition interspécifique lors des réchauffements post-glaciaires, ou qu'elles aient été détruites par les glaciers lors de leurs avancées.

Les *Aphaenops* et leurs congénères représentent des Insectes qui se sont parfaitement adaptés par une série de spécialisations régressives et positives à l'écosystème souterrain et à ses conditions de vie. Ils ne représentent pas un type morphologique ancestral qui se serait conservé dans le milieu souterrain, en raison des caractères de constance au cours des temps géologiques qui lui ont été attribués; en ce sens ils ne sont pas des 'fossiles vivants'.

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* Depuis la présentation de cette communication, la découverte d'un nouveau milieu souterrain, localisé sous le dernier horizon du sol des Forêts et des pelouses montagnardes des Pyrénées, sur roche non-calcaire, renforce l'idée d'un peuplement conjoint du sol et du milieu souterrain, et réduit encore l'amplitude des différences climatiques entre le milieu endogé et le milieu souterrain (JUBERTHIE, DELAY et BOUILLON, sous-presse)

BIBLIOGRAPHIE

BARR, T. C. et KUEHNE, R. A.: Ecological studies in the Mamoth Cave system of Kentucky. II. The ecosystem. Ann. Spéléol., **26**: p. 47–96 (1971).

BERNARD, F.: Recherches sur la morphogenèse des yeux composés d'Arthropodes. Développement, croissance, réduction. Bull. biol. Fr. Belg., Suppl. **23**: p. 1–162 (1937).

BERNASCONI, R.: Recherches biochimiques sur les pigments des cavernicoles. 3e communication: pigmentation mélanoïque et sclérification cuticulaire d'*Antrocharis querilhaci*. Caractérisation des mélanines jaunes et brunes. Ann. Spéléol., **20**: 1, p. 141–149 (1965).

CABIDOCHE, M.: Contribution à la connaissance de l'Ecologie des Trechinae cavernicoles pyrénéens. Thèse Univ. Toulouse, p. 1–175, 1966.

DELAY, B.: Milieu souterrain et écophysiologie de la reproduction et du développement des Coléoptères Bathysciinae hypogés. Mém. biospéol., **5**: p. 1–349 (1978).

DECU, V. et NEGREA, St.: Aperçu zoogéographique sur la faune cavernicole terrestre de Roumanie. Act. zoo. cracov., **14**: 20, p. 471–545 (1969).

GUEORGUIEV, V. B.: La faune troglobie terrestre de la péninsule balkanique. Origine, formation et zoogéographie. Ed. Acad. Bulgare Sci., p. 1–182 (1977).

JEANNEL, R.: Sur l'évolution des Coléoptères aveugles et le peuplement des grottes dans les monts du Bihar en Transylvanie. C. R. Acad. Sci. Paris, **186**: p. 1670–1673 (1923).

JEANNEL, R.: Monographie des Trechinae. L'Abeille, **35**: p. 1 (1928).

JEANNEL, R.: La genèse des faunes terrestres. P. U. F. Paris, 514 pp., 1942.

JEANNEL, R.: Les Fossiles vivants des cavernes. Gallimard Paris, 321 p., 1943.

JEANNEL, R. et LELEUP, N.: L'évolution souterraine dans la région méditerranéenne et sur les montagnes du Kivu. Notes biospeol., **7**: p. (1952).

JUBERTHIE, C.: Relation entre le climat, le microclimat et les *Aphaenops cerberus* dans la grotte de Sainte-Catherine (Ariège). Ann. Spéléol., **24**: 1, p. 75–104 (1969).

JUBERTHIE, C. et DELAY, B.: Influence des facteurs abiotiques, température et nature du substrat, sur le développement embryonnaire du Coléoptère Bathysciinae troglobie *Speonomus longicornis*. Ann. Spéléol., **28**: 4, p. 689–696 (1973).

JUBERTHIE, C. et MASSOUD, Z.: L'équipement sensoriel de l'antenne d'un Coléoptère troglobie *Aphaenops crypticola* Lender (Coleoptera, Trechinae). Int. J. Insect. Morphol. Embryol., **6**: 3–4, p. 147–160 (1977).

JUBERTHIE, C., PIQUEMAL, F. et MASSOUD, Z.: Equipement sensoriel des Coléoptères souterrains Trechinae. I. Étude au microscope à balayage de l'élytre d'*Aphaenops* et de *Geotrechus*. Ann. Spéléol., **30**: 3, p. 483–494 (1977).

JUBERTHIE, C. et PIQUEMAL, F.: Equipement sensoriel des Trechinae souterrains (Coléoptères). II – Ultrastructure des trichobothries de l'élytre. Int. J. Spéléol., **9**: p. 137–152 (1977).

KEITH, J. H.: Seasonal changes in a population of *Pseudoanophthalmus tenuis* (Coleoptera Carabidae) in Murray Spring Cave, Indiana: A preliminary report. Int. J. Speleol., **7**: p. 33–44 (1975).

LANEYRIE, R.: Coléoptères cryptiques, évolution régressive et biogéographie. Ann. Spéléol., **29**: 2, p. 213–228 (1974).

LELEUP, N.: Origine et évolution des faunes troglobies terrestres holarctiques et intertropicales. 4e Congr. Suisse Spéléol. Neuchatel. p. 199–204 (1971).

LESPES, Ch.: Recherches anatomiques sur quelques Coléoptères aveugles. Ann. Sci. nat. zool., ser. 5, **9**: p. 63–71 (1868).

MITCHELL, R. W.: Total number and density estimates of some species of cavernicolous beetles inhabiting Fern Cave in Texas. Ann. Spéléol., **25**: 1, p. 73–90 (1970).

RACOVITZA, G.: Quelques aspects de la dynamique des populations de Coléoptères cavernicoles. L. Cinquant. Inst. Spéléol. E. Racovitza. Ed. Acad. RSR Bucarest, p. 409–419 (1973).

VANDEL, A.: Biospéologie. La biologie des animaux cavernicoles. Gauthier-Villars Ed. Paris, 1964.

VANNIER, G. et JUBERTHIE, C.: Étude dynamique de la transpiration chez *Aphaenops cerberus*, Coléoptère Trechinae troglobie. C. R. Acad. Sci. Fr., **285**: p. 805–808 (1977).

WEBER, F. et LAMPRECHT, G.: Spontane und induzierte Aktivitätsmuster bei troglobionten Käfern (Genera *Aphaenops*, *Geotrechus*, *Speonomus*). Int. J. Spéléol., sous-presse.

3. Behaviour and life-history phenomena

EVOLUTION OF HABITAT PREFERENCE ILLUSTRATED BY THE PHYLOGENY OF *CHRYSOCARABUS* SPECIES (COLEOPTERA, CARABIDAE)

DIETRICH MOSSAKOWSKI

Universität Bremen, Postfach 330440, D-2800 Bremen 33, Federal Republic of Germany

ABSTRACT

It is the aim of the introductory discussion to point the attention to the fact that evolution of habitat preference is a historical process which may be reconstructed by composing a phylogenetic tree. Incorporating information about the ecological demands of the species makes it possible to develop additional ideas about the evolution of habitat relations.

A specific example is given by a discussion of the possible phylogeny of the *Chrysocarabus*-species, a subgenus of *Carabus* including the european species *hispanus*, *rutilans*, *olympiae*, *solieri*, *lateralis*, *lineatus*, *splendens*, *punctatoauratus* and *auronitens*.

There are several closely related species with very similar or even equal ecological demands. From the suggested phylogenetic tree one can derive two possible ways of differentiation of habitat preference.

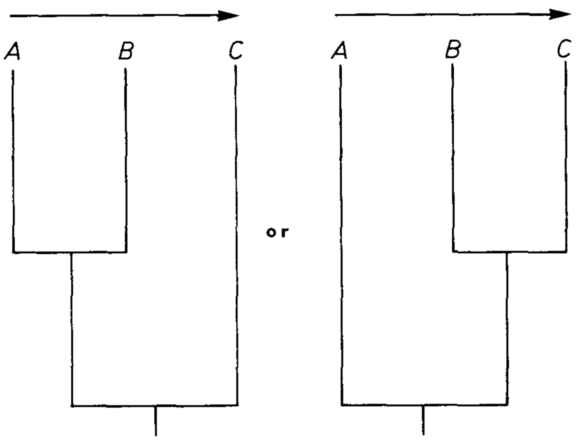
INTRODUCTION

The term evolution covers two different fields of investigation:

1. the historical process of the development of organisms, the phylogenetic aspect including alteration of the organisms and speciation, and
2. the problem of factors promoting this process, the genetical and selectional-ecological aspect.

In regard to phylogenetics it is important to distinguish two applications. Very often people speak about the evolution of a single or a few characters (clines, trends, 'Merkmalsreihen'). That is a very helpful concept which allows a better understanding of adaptations like that of the cave inhabiting Carabidae. Apart from this an evolutionary biologist is not only interested in a model concerning single characters but also in the real development which can only be reconstructed with respect to all available characters because selection is directed against the whole organism.

Let us consider for example three carabid species, a black pigmented one living outside caves, (A), a moderately pigmented one living near the entrance of the caves, (B), and one with a weak light brown pigmentation living inside the cave, (C). It is obvious, that this order is correct in regard to direction of evolution, carabid beetles originally lived outside caves; but the phylogenetical relationships are not at all clear. For example:



To decide between these alternatives one has to look at more characteristics and to evaluate these according to HENNIG's (1950) scheme of arguments.

Our knowledge of the phylogenetic relationships of carabid beetles (see THIELE, 1977) is such, that it appears bold to try to say something about evolution of habitat preference. On the other hand, this subject is so very attractive that I want to give some of its aspects and indications suggested by the knowledge available, with the aim of combining ecological and evolutionary points of view.

I shall intentionally avoid 'habitat selection', this term clearly means an active process which might be the only way many species can find their habitat. In other cases the selection of the habitat is not made by the animal, but by the environment. DEN BOER (1970) pointed out that *Carabus problematicus* as far as it occurs in heathery sites in Drenthe, puts its eggs in the ground where the larvae grow up, but the pupae do not hatch. The beetles living in this area are immigrants from the nearby woods.

REMMERT (1961) described another kind of example of flies of the genus *Coelopa* living on the seaweed at the seashore: the females lay their eggs on several substrates but only those eggs hatch which are laid on a substrate with a certain content of salt, thus strongly limiting the organism to a specific habitat. I therefore prefer the term habitat preference for this phenomenon, from which follows that the concept of the ecological niche must also be discussed.

SOME REMARKS ABOUT THE ECOLOGICAL NICHE

The use of the term ecological niche is diverse, misleading as well as unnecessary. Nevertheless the discussion of the ecological niche – whatever it may be – has hit the headlines, but before speaking about ecological niches one has to define it. The term as it was used by ELTON (1927) means the role of a species in a community, refering primarily to the food aspect.

The first modern and comprehensive concept of the ecological niche was described by GÜNTHER (1950) in his enthusiastic article, overlooked, both by anglo-american (see VANDERMEER, 1972) and european authors (REJMANEK and JENIK, 1975). According to GÜNTHER, the ecological niche is the interaction between the organism (autozoic dimension) and the environment (ecological dimensions); this concept corresponds fully with the n-dimensional hypervolume of HUTCHINSON's (1957) fundamental niche and, taking into account competition and predation, the realized niche.

Ecological niche covers a wide field of diverse uses which can be described as different modifications of the multidimensional niche. Some ecologists draw attention to the resource exploitation, others to reproduction (MACARTHUR and CONNELL, 1966; PIANKA, 1974; MAY, 1976; EMLEN, 1973). Evolutionary biologists like MAYR (1967) use niche in the sense of habitat or place. However, compare MAYR (1979, p. 243) where he used niche as an external projection of the genetic potential of the species. OSCHE (1973) however, follows GÜNTHER's definition. Only very few authors suggest the elimination of this term, e.g. EMLEN (1973) and REMMERT (1978). The latter called it a quantitative description of the ecological demands of a species.

The confusing usage was clarified by WHITTAKER et al. (1973). Using GÜNTHER's (1950) concept I believe that it is not necessary to have a new term indicating an interaction. Regarding the organismic part I cannot see why the term phenotype should not be used in an ecological sense, interacting with those particular resources of the environment which are relevant to the organism (compare PEUS, 1954). It is necessary, however, to criticize GÜNTHER (1950), because he restricted his own meaning, discussing LUDWIG (1948), who introduced annidation as a new evolutionary factor additional to selection. GÜNTHER considered that selection might be the same as this new ecological factor in evolution.

There are two consequences of GÜNTHER's suggestions which are unacceptable: (1) Speciation is the process of constitution of niches, and (2) sympatric speciation is thus possible in a wide range. The first point is selfexplanatory. Entomologists often tend to believe the second point because of the great number of insect species.

As a result of the confused usage, measuring the dimensions of a niche – niche width and breadth – is done by diverse methods which range from simple counts of the presence of a species, through fully detailed studies, to mathematical reductions which leave only hatchings on a graph. I would like to emphasize one of the problems in measuring habitat dimensions. Counting host plants makes it difficult to measure niche breadth in phytophagous insects. The Lepidoptera family Pieridae for instance prefer Crucifera as host plants because of their mustard oil content. They also feed on the non-cruciferous *Tropaeolum* which also contains mustard oil. Have these Pieridae a narrow or a broad niche? If one does not know the particular situation one might say a broad one. The concept stenotopic- eurytopic describes this situation exactly: these Pieridae are relatively eurytopic; regarding the diverse plants they are generalists, but regarding the chemical agent they are specialists. In particular, the correlation between genetic variability and niche breadth has been discussed in respect to specialists vs. generalists (VAN VALEN, 1965).

There are papers concerning evolution of habitat preference (ROSENZWEIG, 1974; ROUGHGARDEN, 1972) which derive mathematical models at the population level. Another question is: what has really happened in evolution? One could say that speciation has to be specialisation in general, therefore, niche breadth should be decreasing. And if this is correct then the REMANE's (1952) morphological 'Nullwert-Ahne' (a monster without characters) assumes an ecological dimension: the earliest ancestor must have been omnivorous and enjoyed cosmopolitan ubiquity. It is obvious that, if this hypothesis was correct we now would only find specialists.

However, considering the fossil record, e.g. of horses, one can easily demonstrate that there were radiations with perhaps particular divisions of the ecological demands of the species but also changes in the food preference. KOVALEVSKI's hypothesis from 1876, that the ancestral horses lived in woods and fed on leaves, was proved by the finding of the fossil horse in the Messel quarry near Darmstadt in western Germany (FRANZEN, 1979).

The evolutionary process which occurred, started at the species level with a change in food preference, and built up a new ecological zone for horses. The evolutionary significance of the ecological zone has been appreciated by SIMPSON (1944). In contrast to the idea that a niche is established by each particular species, the ecological zone is not bound to a particular taxonomic category.

General statements about the evolution of habitat preference concerning specialists vs. generalists cannot be accepted because in evolution there is only the strategy of non-strategic: many different ways are possible. In respect to specialists the evolutionary consequences include, among others, (1) a restrained morphological variability in comparison to that type of generalist where the individuals are specialists or (2) narrow gene flow between the populations of those species whose preferred habitats are insularly distributed (MOSSAKOWSKI, 1971).

TESTING EVOLUTION OF HABITAT PREFERENCE IN CARABIDAE

Considering Carabidae in respect to evolution of habitat preference it is obvious that the fossil record gives little information, and this is not surprising. Looking at the evolution of horses, one of the best investigated examples of a phylogenetic tree, there is little knowledge of the particular development of habitat preference. A reconstruction of the evolutionary pathway on the basis of living species can be done at different systematic levels. EVANS (1977) has postulated different types of running behaviour in the two subfamilies Carabinae and Harpalinae. In respect to running speed there are so many exceptions, however, that a greater number of differentiations is required (STIER, 1978).

At the species level many carabid genera are of great interest in relation to this question. Our detailed knowledge of the phylogenetics of many Carabidae, however, is either poor (see: THIELE, 1977; for exceptions see e.g. BRANDMAYR, 1977), or detailed information on ecological demands are restricted to a few related species of these beetles. I shall take a subgenus of *Carabus* as an example because of personal knowledge of these animals and their habitats (MOSSAKOWSKI and WEBER, 1976), and because it is possible to give some character valuations which differ from those in literature.

In discussing the evolution of habitat preference it is necessary to combine the phylogenetic reconstruction in a specific example with the ecological factors. A very helpful form to demonstrate the results of such a reconstruction is a phylogenetic tree composed of structural characters. Incorporating information about the ecological demands of the species makes it possible to develop additional conceptions of the evolution of habitat relations.

In order to obtain a phylogenetic tree the first step is to find homologous characters. In respect to higher categories this might often be a real problem; e. g. to discover the identical genetic origin of the primary jaw articulation of reptiles and the auditory ossicles of mammals. There is no doubt that the latter is the derived form (synapomorph character of HENNIG, 1950). At the species level, however, it is very difficult to distinguish synapomorph from parallel evolving characters particularly in a group of closely related species such as in *Chrysocarabus*.

SPECIATION IN CHRYSOCARABUS

I have followed JEANNEL (1941) and PUISSEGUR (1964) who placed *Carabus rutilans* and *C. hispanus* together with the species which form *Chrysocarabus* in the sense of BREUNING (1932–1936).

PUISSEGUR (1964) proved that *C. auronitens* and *punctatoauratus* are distinct species. The hybrids are not fully fertile, the F1 males are sterile.

The situation in the *C. lineatus*-complex is not yet clear enough. JEANNEL (1941, p. 150) says 'Le *lineatus* Dej. est une espèce bien distincte du *lateralis* Chevr...'. PUISSEGUR (1975) – besides his older, numerous, and successful hybridisations between *Chrysocarabus*-species – produced cross-breedings of *lateralis* × *lineatus* in both directions with a fertile F1, the results however depended on the country of origin. In respect to the extraordinary variability of *C. lineatus* (X-chromosome, apex of penis etc.), and the stability of characters in *lateralis*, I believe that the status of *lateralis* must be cleared up by further investigations.

In order to describe the situation in a differentiated manner I will consider *lateralis* as a separate species. If one puts them together the synapomorph characters become autapomorph.

1. Sculpture of elytra:

The plesiomorph form of elytral sculpture is without doubt represented, e.g. by *Carabus olympiae* whose primary carinae show interrupted, less pronounced ridges. From this form one has to derive the strongly elevated elytral carinae of *C. solieri* and other *Chrysocarabus*-species. In several groups there is a secondary reduction of these elevated carinae to a more or less smooth elytral surface. In *Chrysocarabus* one can demonstrate this in different phylogenetical lines: in the group of *C. solieri* to *C. auronitens*, in *splendens* and partly in *lineatus*, *punctatoauratus* and *auronitens*. In all these smooth forms one can see a remainder of the carinae. Independently in another line this development also occurred: it is obvious that the smooth elytral structure of *rutilans* is derived from that of *hispanus*, since in the former there is no sign of a reduced carina.

2. Male antennal segments:

This character is determined polyfactorially (PUISSEGUR, 1964), and at first sight looks like a synapomorphy. However, the nodulations on the seventh and eighth segments were only found in one of two closely related species, e.g. *punctatoauratus* has it, but *auronitens* does not, whereas in *C. lateralis* both forms are present in the same population.

3. X-chromosome:

Following WEBER (1966; MOSSAKOWSKI and WEBER, 1976) only in *C. lineatus* is a deviation of a mediokinetic X-chromosome known, these are clearly submediokinetic except in one population known of the Picos de Europa, which is therefore not significantly different from *C. lateralis* in this respect.

4. Male protarsal segments:

The males of many *Carabus*-species have 4 strongly dilated protarsal segments.

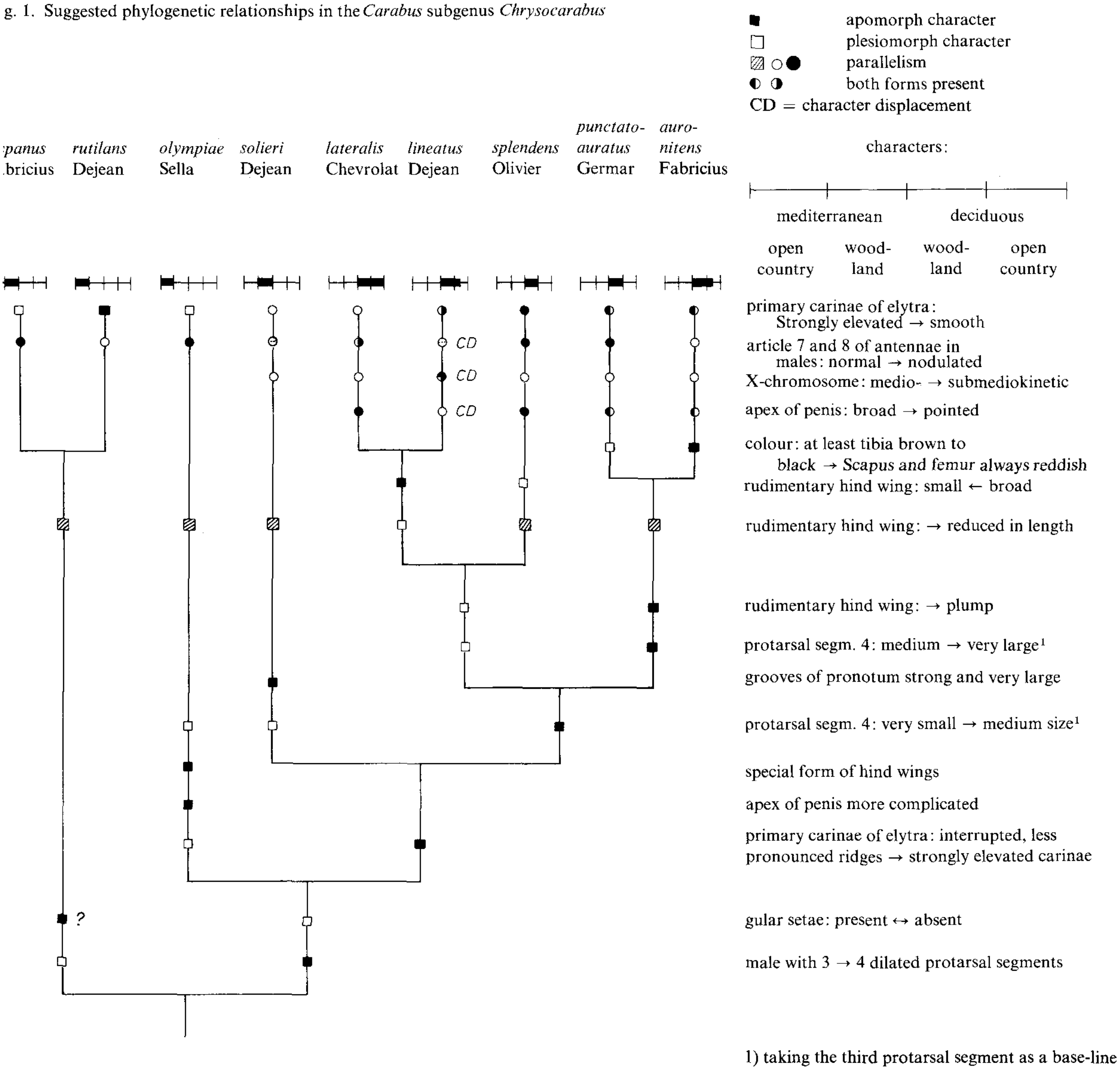
In *Chrysocarabus* there is a line which shows increasing size of the fourth, in relation to the third segment. In *C. rutilans* and *C. hispanus* three dilated segments occur; in some specimens of *hispanus* a small area of adhesive hairs at the lower side of the fourth is present (BREUNING, 1932–1936, p. 1052).

I measured the area of the hairpatch in all species of *Chrysocarabus* and found, that *C. solieri* has a dilated fourth segment, a fact which has been overlooked in the literature. The fourth segment of *C. solieri* has practically the same size as that of *C. olympiae* (in relation to the size of the third segment taken as a base-line in each species).

5. Rudimentary hind wings:

It is obvious, that the fully developed hind wings are primary, and that there are

g. 1. Suggested phylogenetic relationships in the *Carabus* subgenus *Chrysocarabus*



1) taking the third protarsal segment as a base-line

parallel reductions of this state. In general the classification of reductions is not easy. In this case it is the simplest hypothesis that this polyfactorially determined character (PUISSEGUR, 1964) is primary in *C. lineatus* and *C. lateralis* as far as wing length is concerned.

Following this idea and assuming that the phylogenetic tree of fig. 1 is right, the consequence must be that the still more reduced wings are the result of a parallel development. The opposite hypothesis necessitates a more complicated process: at first a reduction to a form like that of *C. splendens* or *C. solieri* which must be followed again by an extension of the narrow part of the leading edge of the wing. The special forms of the hind wings in several species are of high specifity. They are aut-or synapomorph characters.

PHYLOGENETIC TREE AND HABITAT PREFERENCE OF CHRYSOCARABUS

PUISSEGUR (1964) summed up the conceptions of DE LAPOUGE, FRADOIS, JEANNEL and his own, but they gave no valuations of the characters in the sense of phylogenetic systematics. For example PUISSEGUR (1964, p. 269) combines *C. solieri* and *C. auronitens* because of 'un fonds commun d'aptitudes factorielles originelles qui autorisent à rapprocher *solieri* d' *auronitens* plus que de toutes les autres espèces de *Chrysocarabus* s.l.' The phylogenetic relationship of *Chrysocarabus*-species as shown in fig. 1 has some weak points since there is a low number of aut- and synapomorphies, which are even absent in some lines. In particular, one might attach *C. splendens* to *C. auronitens-punctatoauratus*, but that is not more likely. Here also there is no synapomorph character; the very problems of derivation remain and the two species, which perhaps show a character displacement (MOSSAKOWSKI and WEBER, 1976) would become more separated.

If we take the suggested phylogenetic tree as valid it is clear that this tree can also be used as a scheme of arguments in relation to the evolution of habitat preference. In comparison with the mediterranean species, which have a restricted range of distribution (the extreme is *C. olympiae*, found only in an area of a few hundred square meters in the Italian Val Sessera), the 6 species from *C. solieri* to *C. auronitens* are more successful, particularly *C. auronitens*. The ancestor of this group of species probably accomplished the remarkable habitat change from mediterranean to decidous forest vegetation. Most of the *Chrysocarabus* species belong to the fauna of SW Europe which is the quarternary refuge (RENSCH, 1943).

The current information however about present habitats and ecology of *Chrysocarabus* is incomplete, therefore a discussion of their habitat preference is unsatisfactory and in addition no experimental study is available. Because of the phenomenon that particularly *C. lateralis* and to some extent *C. lineatus* and *C. auronitens* are found in open country at higher altitudes, it is possible that these species are really woodland species which also may find their ecological demands realized outside woodlands. The *C. lateralis* of the Serra del Estrela of Portugal lives at some distance from woods, but the high rainfall in this area perhaps provides the same living conditions as occur at lower altitudes only in woodlands.

The ecological differences in the *C. lineatus-splendens* group are small. They have a sympatric areal in the Basque territory and live together in the same forests. It has been reported that in higher regions only *C. lineatus* may be found (BREUNING 1932–1936), but PUISSEGUR (1964) states that *C. punctatoauratus* and *auronitens* have very similar or even equal ecological demands.

From the given phylogenetic tree one can derive two possible ways of differentiation of habitat preferences whilst the process of speciation in *Chrysocarabus* continued:

1. there was a change in the preferred habitat several times, because the ancestor had a small width of adaptation ('specialist'): or
2. there was a specialisation several times, because the ancestor had a broad width of adaptation ('generalist').

Only detailed further studies can give us the correct answer.

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REFERENCES

BOER, P. J. DEN: On the Significance of Dispersal Power for Populations of Carabid Beetles (Coleoptera, Carabidae). Oecologia (Berl.) **4**: 1–28 (1970).

BRANDMAYR, P.: Ricerche etologiche e morfofunzionale sulle cure parentali in Carabidi Pterostichini (Coleoptera: Carabidae, Pterostichinae). Redia **60**: 275–316 (1977).

BREUNING, S.: Monographie der Gattung *Carabus*. Best.-Tab. europ. Coleopt., Heft 104–110. Reitter, Troppau, 1932–1936.

ELTON, C.: Animal Ecology. London, Sidgewick and Jackson, 1927.

EMLEN, J. M.: Ecology: An Evolutionary Approach. Addison-Wesley, Reading, Massachusetts, 1973.

EVANS, M. E. G.: Locomotion in the Coleoptera Adephaga, especially Carabidae. J. Zool., London **181**: 189–226 (1977).

FRANZEN, J. L.: Die Bedeutung der Messeler Fossilien für das Verständnis der Erd- und Lebensgeschichte. Natur und Museum **109**: 112–119 (1979).

GÜNTHER, K.: Oekologische und funktionelle Anmerkungen zur Frage des Nahrungserwerbes bei Tiefseefischen mit einem Exkurs über die ökologischen Zonen und Nischen. Moderne Biologie (Ed. Grüneberg and Ulrich), Festschrift Nachtsheim. Peters, Berlin, 1950.

HENNIG, W.: Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin, 1950.

HUTCHINSON, G. E.: Concluding remarks. Cold Spring Harbour Symp. Quant. Biol. **22**: 415–427 (1957).

JEANNEL, R.: Coléoptères Carabiques 1. Faune de France **39**: 1–571 (1941).

LUDWIG, W.: Darwins Zuchtwahllehre in moderner Fassung. Kramer, Frankfurt a.M., 1948.

MACARTHUR, R. H. and J. H. CONNELL: The Biology of Populations. Wiley, New York, 1966.

MAY, R. M.: Theoretical Ecology. Principles and Applications. Blackwell, Oxford, 1976.

MAYR, E.: Artbegriff und Evolution. Parey, Hamburg, 1967.

MAYR, E.: Evolution und die Vielfalt des Lebens. Springer, Berlin, 1979.

MOSSAKOWSKI, D.: Zur Variabilität isolierter Populationen von *Carabus arcensis* Hbst. (Coleoptera). Z. zool. Syst. Evolut.-forsch. **9**: 81–106 (1971).

MOSSAKOWSKI, D. and F. WEBER: Chromosomale und morphometrische Divergenzen bei *Carabus lineatus* und *C. splendens* (Carabidae). I. Ein Vergleich sympatrischer und allopatrischer Populationen. Z. zool. Syst. Evolut.-forsch. **14**: 280–291 (1976).

OSCHE, G.: Evolution. Grundlagen – Erkenntnisse – Entwicklungen der Abstammungslehre. Herder, Freiburg, 1973.

PIANKA, E. R.: Evolutionary Ecology. Harper and Row, New York. 1974.

PEUS, F.: Auflösung der Begriffe 'Biotop' und 'Biozönose'. Dt. Ent. Z. N.F. **1**: 271–308 (1954).

PUISSEGUR, C.: Recherches sur la genétique des Carabes. Vie et Milieu, Suppl. **18**: 1–288 (1964).

PUISSEGUR, C.: Un hybride intersubgénérique de *Chrysocarabus* (s.l.) Thomsen (Coleopt. Carab.): *Chrysocarabus* (s.str.) *lineatus lateralis* Chevr. × *Chrysocarabus (Chrysotribax) hispanus* Fabr. Considerations sur la validité spécifique de *Cc. lateralis*. C. R. hebd. Séances Acad. Sci. Ser. D Sci. nat. **280**: 909–910 (1975).

REJMÁNEK, M. and J. JENÍK: Niche, Habitat, and related ecological Concepts. Acta Biotheor. **24**: 100–107 (1975).

REMANE, A.: Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Geest and Portig, Leipzig, 1952.

REMMERT, H.: Mitt. zool. Mus. Berlin **37**: 147 (1961).

REMMERT, H.: Ökologie. Springer, Berlin, 1978.

RENSCH, B.: Studien über Korrelation und klimatische Parallelität der Rassenmerkmale von *Carabus*-Formen. Zool. Jb. Abt. Syst. **76**: 103–170 (1943).

ROSENZWEIG, M. L.: On the Evolution of Habitat Selection. Proc. 1st. Int. Congr. Ecology, 401–404, 1974.

ROUGHGARDEN, J.: Evolution of niche width. Am. Nat. **106**: 683–718 (1972).

SIMPSON, G. G.: Tempo and Mode in Evolution. Columbia Univ. Press, New York, 1944.

STIER, J.: Die Laufgeschwindigkeit verschiedener Carabiden-Arten als Ausbreitungsfaktor. Unpublished Staatsex.-arbeit, Bremen, 1978.

THIELE, H. U.: Carabid Beetles in Their Environments. Springer, Berlin, 1977.

VALEN, L. VAN: Morphological Variation and the Width of Ecological Niche. Am. Nat. **99**: 377–389 (1965).

VANDERMEER, J. H.: Niche Theory. Ann. Rev. Ecol. Syst. **3**: 107–132 (1972).

WEBER, F.: Beitrag zur Karyotypanalyse der Laufkäfergattung Carabus L. (Coleoptera). Chromosoma (Berl.) **18**: 467–476 (1966).

WHITTAKER, R. H., S. A. LEVIN and R. B. ROOT: Niche, Habitat, and Ecotope. Am. Nat. **107**: 321–338 (1973).

A REDUCED NUMBER OF LARVAL INSTARS, AS AN ADAPTATION OF THE DESERT CARABID BEETLE *THERMOPHILUM (ANTHIA) SEXMACULATUM* F. (COLEOPTERA, CARABIDAE) TO ITS ARID ENVIRONMENT

W. Paarmann

Zoologisches Institut der Universität, D-8700 Würzburg, Röntgenring 10, Federal Republic of Germany

Abstract

Shortening of the period of larval activity by reducing the number of larval instars (prothetely?) seems to be the main adaptation of stages of development of the desert carabid *Thermophilum sexmaculatum* to its arid environment.

Carabid beetles, living in temporary dry habitats of the African tropics and subtropics, have a marked annual periodicity (Paarmann, 1970, 1975, 1976a, 1977). They pass the dry season in a state of gonad dormancy (Paarmann, 1974, 1976b, 1976c, 1977). Reproduction and development take place during the rainy season. Only the adults are able to survive under dry season conditions. Such an ability is not known for the other stages of development. The larvae are very sensitive to desiccation (Paarmann, 1973). Pupae and especially eggs are even more sensitive to desiccation (Paarmann, unpublished data). For a successful development they not only need 100 % r.h. but also contact water in the soil. The inability of the developmental stages to survive under dry season conditions in general, seems to be the main problem for carabid beetles to adapt to arid environments. However, there are some species of Carabidae that live in desert regions. The question thus arises: What special adaptation to the extremely arid environment has evolved in the stages of development of these desert carabid beetles?

During a journey through the Sahara desert in March and April 1977, I caught beetles of the species *Thermophilum sexmaculatum*, in Tunesia and Algeria specimens of the subspecies *T.s. sexmaculatum*, and in Mali specimens of the subspecies *T.s. marginatum*. Under laboratory conditions (LD 13:11; 7h 27°/17h 20°) the females of both subspecies laid eggs, to my surprise only in humid substrate (sand). For egg-laying the beetles were kept in a plastic container with a 5 cm layer of sand, devided into two parts of equal size. One part contained air-dried sand, the other part humid sand. So the females could choose between dry and humid sand. All 10 females, kept under the above conditions, laid their eggs into the humid sand. In a control experiment both parts contained humid sand, 5 of the females (n = 10) laid their eggs in each part. In *T.s.*

Fig. 1. Full-grown *Thermophilum*-larva of stage 1.

sexmaculatum one clutch consists of 4 (4.2) eggs on the average (1–9, n = 89), and in *T.s. marginatum* of 3 (3.3) eggs on the average (1–7, n = 61) in both cases in a chamber the size of the body of the female. These eggs are remarkably large: 8.2 mm long and 3.4 mm wide. By absorbing water they reach a length of 9.4 mm and a width of 4.7 mm (n = 11).

In 95% r.h. (25°) the eggs die from desiccation. But in 100% r.h. (25°) without contact water, some eggs are able to develop, an adaptation unknown until now in carabids. However the eggs in 100% r.h. without contact water do not increase in volume, therefore the larvae hatching from these eggs are much smaller than normal larvae. Their head-width is 3.08 mm only, that of normal larvae 3.44 mm ($p < 0.001$, t-test).

The L1 of *T.s. sexmaculatum* was already described by CHOPARD (1936). USCIDA (1974) described it for a second time. At a temperature of 25/28° this L1 feeds for about five days only, provided that enough food is available. After these 5 days of feeding the larva is full-grown (fig. 1). Under natural conditions this full-grown L1 presumably digs itself into deeper layers of the soil, where it finds sufficient humidity to complete its development. From the results of the laboratory culture we can conclude that the L1 will dig a chamber in the deep and humid soil layer. In this chamber it usually moults to an L2 (fig. 2). Contrary to the L1, the L2 is very pale in colour. This means that the L2 is only slightly sclerotized. The L2 never leaves the chamber, built by the L1; it also pupates there. In one case the pupation of an L1 could be observed.

Generally the Carabidae have three larval stages. More or fewer instars are exceptions. BOUSQUET (1977) gives a survey of this literature. There are cases known with respectively one, two, four, or five larval stages. These exceptions often seem to be the result of special adaptations. So carabids with a parasitoid mode of life have five instars in the genus *Brachinus* (ERWIN, 1967), four or two in the Lebiini (ERWIN, 1975; LINDROTH, 1954; SILVESTRI, 1904).

A cave dwelling carabid (genus *Aphaenops* – Trechini) is known with only one larval stage (DAJOZ, 1961). This L1 pupates without preceding food consumption (an adaptation to food shortage?). Two larval stages are also mentioned for a single *Carabus* species (STURANI, 1962), and for five species among the Harpalini (KIRK, 1974; BILY, 1975). In these cases there are no indications that there are any connections with special adaptations.

Fig. 2. *Thermophilum*-larva of stage 2.

In laboratory cultures of Carabidae (genus *Pterostichus*) I found shortened development as a disturbance of the normal one (PAARMANN, 1967). The pupation of the L2 was the most extreme case of this shortened development. Such pupae were very small because of the small size of the L2. Only in a few cases did beetles hatch from these small pupae. As a rule Carabidae chiefly grow during their third larval stage. Reduction of the number of larval instars will be a useful adaptation for an insect species only, if the growth of the body can be completed in an earlier larval stage. In *T. sexmaculatum* the complete growth takes place in the first larval stage. Hence, there is no need for more developmental instars. A third larval stage never occurred in the cultures of *T. sexmaculatum*. A degenerated second larval instar is usually observed, but there is an evolutionary trend towards a direct pupation of the first larval stage. It is known from literature (VAN EMDEN, 1942) that among related species of the tribe Anthiini three larval stages are the rule. I was able to prove this by breeding experiments, for two species of the genus *Thermophilum (T. venator, T. galla)*. The adult of *T. galla* is nearly the same size as the imago of *T. sexmaculatum*. I saw one L3 of this *Anthia* species. The head-width of this L3 was 3.5 mm nearly the same as that of the normal L1 (3.3–3.75 mm) of *T. sexmaculatum*.

Shortening of the period of larval activity by reducing the number of larval stages seems to be the main adaptative strategy of both subspecies of *T. sexmaculatum* in coping with arid conditions. In this way they are able to take advantage of the humidity in the upper soil layers which is only available for short periods.

The resistance of the larvae of *T. sexmaculatum* against desiccation – higher than is found in other North African carabids (PAARMANN, 1973) – and the ability of the eggs to develop in 100 % r.h. without contact water, are of minor importance only as an adaptation to desert or semidesert environments.

At 30° and 75 % r.h. the L1 of *T. sexmaculatum* lives for 5 days on average (range: 3.5–6 days, n = 9). This is higher than the data found for the larvae of North African 'winter breeders'. Under the above mentioned conditions the longest survival time was found for an L1 of *Broscus laevigatus:* 19.6 h. But in 75 % r.h. (30°) also the larvae of *T. sexmaculatum* are already irreversibly damaged one day before death.

The small larvae, hatched from eggs that developed in 100 % r.h. without contact water, never reach the size of normal full-grown larvae, even if enough food is available. Thus they produce only small beetles. In females of such a small size, as the first available data show, the rate of reproduction, too, is much lower than in females of normal size.

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REFERENCES

BILY, S.: Larvae of the genus *Amara* (subgenus *Celia* Zimm.) from Central Europe (Coleoptera, Carabidae). Stud. CSAV **13**: 1–74 (1975).

BOUSQUET, Y.: Remarques sur le nombre de stades larvaires chez les Carabidae (Coleoptera). Cordulia **3**: 159–162 (1977).

CHOPARD, L.: La larve de l'*Anthia sexmaculata* F. (Col. Carabidae). Bull. Soc. ent. France **1936**: 168–173 (1936).

DAJOZ, R.: Etude analytique et critique des travaux récents sur les Carabiques de la faune de France (Coleopterères). Cah. Natur. **17**: 1–48 (1961).

EMDEN, F. J. VAN: A key to the genera of larval Carabidae (Col.). Trans. R. Ent. Soc. Lond. **92**: 1–99 (1942).

ERWIN, T. L.: Bombardier beetles (Coleoptera, Carabidae) of North America: Part II. Biology and behavior of *Brachinus pallidus* Erwin in California. Coleopt. Bull. **21**: 41–55 (1967).

ERWIN, T. L.: Relationships of predaceous beetles to Tropical forest wood decay. Part I. Description of the immature stages of *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini). Coleopt. Bull. **29**: 297–300 (1975).

KIRK, V. M.: Biology of a ground beetle, *Harpalus erraticus*. Ann. Ent. Soc. Amer. **67**: 24–28 (1974).

LINDROTH, C. H.: Die Larve von *Lebia chlorocephala* Hoffm. (Coleoptera, Carabidae). Opusc. Entomol. **19**: 29–33 (1954).

PAARMANN, W.: Prothetelie bei Carabiden der Gattung *Pterostichus*. Zool. Beitr. **13**: 121–135 (1967).

PAARMANN, W.: Untersuchungen über die Jahresrhythmik von Laufkäfern (Coleoptera, Carabidae) in der Cyrenaika (Libyen, Nordafrika). Oecologia (Berl.) **5**: 325–333 (1970).

PAARMANN, W.: Bedeutung der Larvenstadien für die Fortpflanzungsrhythmik der Laufkäfer *Broscus laevigatus* Dej. und *Orthomus atlanticus* Fairm. (Coleopt., Carab.) aus Nordafrika. Oecologia (Berl.) **13**: 81–92 (1973).

PAARMANN, W.: Der Einfluss von Temperatur und Lichtwechsel auf die Gonadenreifung des Laufkäfers *Broscus laevigatus* Dej. (Coleoptera, Carabidae) aus Nordafrika. Oecologia (Berl.) **15**: 87–92 (1974).

PAARMANN, W.: Freilanduntersuchungen in Marokko (Nordafrika) zur Jahresrhythmik von Carabiden (Coleoptera, Carabidae) und zum Mikroklima im Lebensraum der Käfer. Zool. Jb. Syst. **102**: 72–88 (1975).

PAARMANN, W.: Jahreszeitliche Aktivität und Fortpflanzungsrhythmik von Laufkäfern (Coleoptera, Carabidae) im Kivugebiet (Ost-Zaire, Zentralafrika). Zool. Jb. Syst. **103**: 311–354 (1976a).

PAARMANN, W.: Die Trockenzeitdormanz der Carabiden des zentralafrikanischen Hochlands und ihre Steuerung durch Aussenfaktoren. Verh. Dtsch. Zool. Ges. **1976**: 209 (1976b).

PAARMANN, W.: Die Bedeutung exogener Faktoren für die Gonadenreifung von *Orthomus barbarus atlanticus* Fairm. (Col., Carab.) aus Nordafrika. Ent. exp. & appl. **19**: 23–36 (1976c).

PAARMANN, W.: Propagation rhythm of subtropical and tropical Carabidae (Coleoptera) and its control by exogenous factors. Advances in Invertebrate Reproduction **1**: 49–60 (1977).

SILVESTRI, F.: Contribuzione alla conoscenza della metamorfosi e dei costumi della *Lebia scapularis* Fourc. con descrizione dell'apparato sericiparo della larva. Redia **2**: 68–84 (1904).

STURANI, M.: Osservazioni e ricerche biologiche sul genere *Carabus* Linnaeus (sensu lato) (Coleoptera, Carabidae). Mem. Soc. Ent. Ital. **41**: 85–202 (1962).

USCIDA, C.: La larva di *Megacephala euphratica* Latr. e Dej. e *Thermophila sexmaculata* (Fabr.). Risultati delle missioni entomologiche dei Proff. G. Fiori ed E. Mellini nel Nord-Africa XXXI. Studi Sassaresi III, Ann. Fac. Agr. Univ. Sassari **22**: 1–15 (1974).

IDEAS ABOUT THE EVOLUTION OF THE VARIOUS ANNUAL REPRODUCTION RHYTHMS IN CARABID BEETLES OF THE DIFFERENT CLIMATIC ZONES

W. PAARMANN

Zoologisches Institut der Universität, D-8700 Würzburg, Röntgenring 10, Federal Republic of Germany

ABSTRACT

The possible evolution of types of annual reproduction rhythms of carabids is discussed in this paper. The discussion is based on two assumptions:

1. the tropics, especially of the Old World, are the main evolutionary centre of Carabidae. From this centre waves of migration started to other climatic zones.
2. all dormancies in Carabidae are based on a uniform hormonal system, so a manifold convergent evolution was possible.

Two 'lines of descent' among the types of annual reproduction rhythms of carabids from the different climatic zones are postulated. These two 'lines of descent' may also be seen as two ways of successive adaptation, which the carabids may follow during their migration from the tropics to higher latitudes. One way, beginning in habitats without any annual climatic periodicity goes through continuously humid habitats with periodical inundation in the tropics (first annual rhythms) to continuously humid habitats with and without periodical inundations in the subtropics (summer breeders). This way comes to an end in the temperate zones with the spring breeders type 2. The second way starts in the same habitat, passes periodically dry habitats in the tropics (summer breeders) and subtropics (winter breeders), and passes the temperate zones and subarctic areas, too. Here the ways have split and we find many related types of annual rhythms (autumn breeders types 3 and 4, spring breeders type 1, carabids with a development potentially free of dormancies – type 5, and species with a two-year development types 6 and 7). Possibly this second way ends in the arctic zone with the 'arctic Carabidae'.

INTRODUCTION

Carabidae are the only group of insects studied on a worldwide scale with regard to their annual rhythms and control by environmental factors. THIELE (1977) gives a summary of all research done in this field on carabid beetles of the temperate zones. Publications of FERENZ (1973a, 1975a), and KAUFMANN, (1971) give indications of the annual rhythms of Carabidae in subarctic and arctic regions. My own work (PAARMANN, 1970, 1973, 1974, 1975, 1076 a, b, c, d) is concerned with the annual reproduction rhythms of the Carabidae in the tropics and subtropics.

Tab. 1 gives a summary of all known types of annual rhythms in Carabidae of the temperate zone, the subtropics and tropics. The data in tab. 1 show the distinct ability of the Carabidae to adapt to the greatly varying seasonal differences in environmental factors. The question arises whether there is any relationship between the different types of annual rhythms in Carabidae, and whether it is possible to draw conclusions about the evolution of these types.

As a rule, Carabidae of different degrees of taxonomic affinity may belong to one type of annual reproduction rhythm. On the other hand, we often find a similar spectrum of reproduction rhythms in different lines of descent, independent of their systematic position. This indicates a repeated convergent evolution of types of annual reproduction rhythms. For example, from 31 species of the genus *Carabus* – known as primitive (see ALI, 1967) – that were examined, 19 belonged to the 'spring breeders' (probably type 1), 11 to the 'autumn breeders' (type 3: 5 species, type 4: 3 species, uncertain: 3 species), and 1 species to the 'Carabidae with unstable hibernating conditions' (type 5) (HŮRKA, 1973). In the more advanced Pterostichini, ALI (1967) also includes the Agonini, where we find species that develop without dormancies: *Abacetus* spec.; with rainy season propagation, for example: *Paramegalonychus tshibindensis;* with dry season propagation: *Paramegalonychus paludicola* (PAARMANN, 1976a); with winter propagation: *Orthomus barbarus* and *Pterostichus crenulatus* (PAARMANN, 1970, 1975, 1976c); with autumn propagation and no gonad dormancy (type 3): *Pterostichus vulgaris* (KREHAN, 1970); with spring propagation type 1: *Pterostichus oblongopunctatus* (THIELE, 1975), *Pterostichus coerulescens* and *Pterostichus cupreus* (KREHAN, 1970); with spring propagation type 2: *Agonum assimile* (NEUDECKER und THIELE, 1974), *Agonum dorsale* (KRECKWITZ, 1978); with unstable hibernating conditions (type 5): *Abax ater* (LÖSER, 1972); with a two-year development (type 6): *Abax ovalis* (LAMPE, 1975), and an 'arctic carabid': *Pterostichus brevicornis* (KAUFMANN, 1971). To the Lebiini – known as a more advanced group (ALI, 1967) – belong species with rainy season propagation, for example: *Lebia andreinii* (PAARMANN, 1976a); with winter propagation: *Cymindis setifensis* (PAARMANN, 1970, 1975), and with spring propagation (type unknown) *Lebia cyanocephala* (LARSSON, 1939). The annual reproduction rhythms in Carabidae result from the phenomenon that the cycle of development is interrupted by a dormancy. Carabidae show dormancies either in one of their larval stages or in their imaginal stage. It may be supposed that in carabid beetles the gonad development is based on a uniform hormonal system. There are data which support this supposition. A dominant role for gonad development in Carabidae must be attributed to the juvenile hormone (JH). The dormancies of both sexes of spring breeders, type 1 (FERENZ, 1973a, b, 1975b, 1977; FERENZ and HÖLTERS, 1975; HÖLTERS, 1978; KÖNEN, 1978), spring breeders, type 2, summer breeders, winter breeders and rainy season breeders (PAARMANN, unpublished data) can be terminated by application of JH. So a gonad dormancy is likely to arise by the influence of such a uniform hormonal system. Possibly there are only a few ways by which environmental factors can influence this hormonal system. This would explain the repeated evolution of

Table 1. Types of annual reproduction rhythms, known from the tropics, subtropics and temperate zones (SD = short day; LD = long day).

temperate zones	*spring breeders* (Larsson, 1939)	spring breeders type 1 gonad dormancy during hibernation – complete gonad maturation: ♂♂ in SD, ♀♀ after a change of day length from SD to LD.
		spring breeders type 2 gonad dormancy during hibernation – complete gonad maturation in LD, SD retards maturation.
	autumn breeders (Larsson, 1939)	autumn breeders type 3 no gonad dormancy (ability to produce a temperature controlled gonad dormancy during hibernation) – temperature controlled larval dormancy during winter.
		autumn breeders type 4 gonad dormancy during aestivation – complete maturation after changing of day length from LD to SD temperature controlled larval dormancy during winter
	species with unstable hibernating conditions (Lindroth, 1949)	species with a development potentially free of dormancies type 5 ability to produce temperature controlled gonad and larval dormancies during hibernation.
		species with a two-year development type 6 ♀♀: gonad dormancy during hibernation – they reach their gonad maturity after a change of day length from SD to LD. ♂♂: no gonad dormancy, but ability to produce a temperature controlled dormancy during hibernation. temperature controlled larval dormancy during winter.
		species with a two-year development type 7 temperature controlled larval and gonad dormancies during hibernation.
subtropics-North Africa	*1. summer breeders* temperature controlled gonad dormancy (continuously humid habitats with and without periodical inundations).	
	2. winter breeders gonad dormancy during aestivation, controlled by temperature and day length – complete gonad maturation under low temperatures and SD – first indication of a temperature controlled larval dormancy during winter (periodically dry habitats).	
tropics-Central Africa	*3. species without an annual reproduction rhythm* (continuously humid habitats without periodical inundations)	
	4. species with an annual reproduction rhythm from continuously humid habitats (with periodical inundations) temperature controlled gonad dormancy.	
	5. rainy season breeders temperature controlled gonad dormancy during dry season (periodically dry habitats).	

gonad dormancies, that are controlled in the same or very similar ways. Larval dormancies of insects investigated up to now (see ENGELMANN, 1970; SAUNDERS, 1976), are controlled by the hormonal system responsible for moulting and metamorphosis during postembryonic development. Presumably larval dormancies in Carabidae are controlled in the same manner. This would explain a convergent evolution of larval dormancies in a similar way as in gonad dormancies.

Manifold convergent evolution, based on such a uniform hormonal system, would explain the appearance of different types of annual reproduction rhythms as 'reacting types' among members of different lines of descent. Therefore, it should be possible also to draw conclusions about the evolution of types of reproduction rhythms from data of different lines of descent. On this basis in the following I will try to develop ideas about the relationship between the known types of annual rhythms in the Carabidae. The term 'relationship between types of annual rhythms' will be used, if I want to emphasize that a more advanced type of annual rhythm evolved in a convergent way from a more primitive type also when the species concerned probably belong to different lines of descent. For the terms used to characterize the types of annual rhythms see Tab. 1.

CONCERNING THE MIGRATIONS OF CARABIDAE FROM THE TROPICS TO LESS FAVOURABLE CLIMATIC REGIONS

DARLINGTON (1959) supposes that the tropics are a centre of evolution of new dominant groups of organisms. He believes that under favourable climatic conditions there is a continuous migration of species from their centre of evolution to areas with less favourable conditions. After a detailed study of the New Guinean Carabidae DARLINGTON (1971) came to the conclusion that this insect family, too, has its main centre of evolution in the tropics, especially in the tropics of the Old World. DARLINGTON's supposition is supported by ERWIN (1970). He studied the systematics of the carabid group Brachinini, and came to the conclusion that the main evolutionary centre of this group of Carabidae is probably the eastern and central part of Equatorial Africa. From this area 5 different waves of migration started both north- and southwards.

In the tropics there are habitats without any annual periodicity of climatic conditions. In Central Africa, in such habitats as the shores of lakes and swamps, I only found polyvoltine Carabid species with a development free of dormancies (PAARMANN, 1976a). Probably the Carabidae of rainy forests do not have any adaptation to an annual climatic periodicity either. Supposing that Carabidae migrate from habitats with these optimal climatic conditions to habitats with more extreme conditions, i.e. with an annual unfavourable period, they may end up in two different situations:

1. Along river banks, where there is a humid soil all the year, but they are confronted with periodical inundations.
2. They settle in habitats with periodical dryness.

THE CONTROL OF ANNUAL RHYTHMS IN RIVERBANK HABITATS AND IN REGIONS WITH ALTERNATING RAINY AND DRY SEASONS

In such habitats in the tropics there is only a small annual change in day length and air temperature. The main problems for the Carabidae in these habitats arise from the periodicity of rainfall. In habitat 1 this will bring about periodical inundations, and in habitat 2 periodical dryness. Inundation as well as dryness destroy the developmental stages of Carabidae. As an adaptation to the periodical rainfall in both habitats many carabid species evolved an annual reproduction rhythm. These annual rhythms result from a gonad dormancy during unfavourable climatic conditions by which reproduction is delayed till conditions are more favourable. In river bank habitats the dormancy of Carabidae is controlled by a slight change in mean temperature.

The gonad dormancy of rainy season breeders in periodically dry habitats is also controlled by temperature, but in a more complicated way (PAARMANN, 1976b). During dry seasons the daily amplitude of temperature in the upper layers of the soil is greater and mean temperature lower than during rainy seasons. This periodicity of the temperature is closely connected with the annual fluctuation of the water content of the soil. The gonad dormancy is initiated by the great daily temperature amplitude. Not yet conclusive experiments give the impression, that the high-temperature fractions of the day actually cause the dormancy. Under the smaller daily amplitude of temperature during the rainy season gonad development is free of dormancy. Hence, there is still a close connection between rainy season breeders and the Carabidae under optimal climatic conditions. At the beginning of the rainy season the gonad development of rainy season breeders is accelerated and synchronized by a sudden rise of the mean temperature. The gonad dormancies of tropical Carabidae are not influenced by photoperiods within a range from continuous darkness (DD) to European long days (LD 18:6).

The species that live in constantly humid habitats can migrate along river banks into other climatic zones. DARLINGTON (1971) believes that such riverbank dwelling (riparious) species are of special importance with regard to the migration of Carabidae, because they are generally very active fliers.

At present I am studying the annual rhythms of three *Abacetus* species (*A. archambaulti*, *A. dainellii*, *A. villiersianus*) from riverbank habitats of the Sahel zone (tropics with summer rain). *A. dainellii* develops free of dormancies within a relatively wide range of temperatures. *A. archambaulti* and *A. villiersianus* show gonad dormancies controlled by the changing of the mean temperature, but not influenced by photoperiods (DD to LD 18:6). Hence, there are no real differences between the riparious carabid beetles of Central Africa and the Sahel zone with regard to their annual rhythms and control.

Typical representatives of the riparious Carabidae in the subtropics with winter rain (North Africa) are the 'summer breeders' (PAARMANN, 1975). As shown in the species *Pogonus chalceus* (PAARMANN, 1976d) they also have a temperature controlled gonad dormancy not influenced by photoperiods within the above mentioned range. Only these beetles developed the ability to live under a much wider range of temperatures than the riparious beetles of the tropics.

Representatives of the summer breeders are also found in the temperate zone. For example, the above mentioned species *P. chalceus* is distributed from North Africa northward to the shores of the North Sea. In the northern part of its area *P. chalceus* shows the same annual rhythm as spring breeders. That's why LARSSON (1939) and HEYDEMANN (1962) classed this species among the spring breeders. The investigation done with specimens of the North African population indicates the possibility that the annual rhythm of *P. chalceus* in the northern temperate zone may only be controlled by temperature and not by photoperiods, either, as in typical spring breeders (PAARMANN, 1976d). Observations done by HEYDEMANN (1962) on *Bembidion* species and BAUER (1974) on two *Elaphrus* species show that among the riparious Carabidae of the temperate zone there may be a high percentage of true summer breeders.

Hence, only the evolution of a gonad dormancy controlled by temperature enabled the riparious Carabidae to migrate successfully from the tropics to the temperate zones.

Probably the dry season dormancy of the rainy season breeders with its characteristic control by the changing of the two components of soil temperature (daily amplitude and mean) is typical for all Carabidae living in periodically dry habitats of the tropics. A similar control mechanism of the gonad dormancy can be established in the North African winter breeders (PAARMANN, 1976c). It may thus be supposed that the winter breeders have evolved from rainy season breeders, but under natural conditions the gonad dormancy of winter breeders is mainly maintained by a constantly high temperature. The beetles aestivate in deeper soil layers, where they are exposed to high temperatures with a small daily amplitude. But as mentioned above, also in rainy season breeders the gonad dormancy seems to be maintained by the high-temperature fractions of the day. Also in rainy season breeders the influence of a continuous high temperature brings about a gonad dormancy (PAARMANN, 1977).

THE DEVELOPMENT OF PHOTOPERIODIC CONTROL OF ANNUAL RHYTHMS IN THE SUBTROPICS

Hence, in the tropical Carabidae from periodically dry habitats we find a preadaptation, that opens the possibility for a successful settlement in periodically dry habitats of the subtropics. But in the winter breeders we find further control mechanisms, that seem to have evolved under the different climatic conditions of the subtropics. The winter breeders represent the first type of annual rhythm in Carabidae of lower latitudes, which also show a photoperiodic influence on the gonad dormancy. A successful development of gonads is possible only under short day conditions down to DD (PAARMANN, 1974, 1976c). North African long day conditions (LD 14:10) completely inhibit gonad development even if the temperature is favourable. In the larvae of winter breeders we find the first signs of a temperature controlled dormancy (PAARMANN, 1973). Thus the subtropical winter breeders already show the basic characteristics for a further adaptation to the climatic conditions of the temperate zone.

THE CONTROL OF ANNUAL RHYTHMS IN TEMPERATE ZONES

The preadaptations of winter breeders are successfully used by the autumn breeders type 4 of the temperate zone. They show an obligatory hibernation parapause (for classification of types of dormancies see MÜLLER, 1970) in the larval stage (temperature controlled, like all larval dormancies in Carabidae) and an aestivation parapause in the imaginal stage (THIELE, 1969) controlled by photoperiods.

A clearly recognizable 'relationship' exists between winter breeders and autumn breeders on one side and the autumn breeders type 3 (no dormancy in the imaginal stage) on the other side. The latter also show a larval dormancy during the winter (THIELE and KREHAN, 1969). The postembryonic development in this type ends in late summer. So the young beetles hatch at the beginning of their favourable propagation time. Therefore this type doesn't need a gonad dormancy during summer unlike type 4. At the moment it is impossible to decide whether this type shows a relatively primitive kind of autumn- or winterpropagation or has developed by the loss of aestivation dormancy. Possibly there is a closer relationship between this type 3 and winter breeders with a long lasting larval development like *Broscus laevigatus* (PAARMANN, 1973). VAN DIJK (1972) and LUFF (1973) suppose that from the autumn breeder type 3 possibly Carabidae with a two-year development (type 7) evolved (see Tab. 1 and Fig. 1) in higher geographical latitudes. The higher the latitude the longer the winter and with that the larval hibernation dormancy. The postembryonic development thus becomes retarded and the young beetles hatch so late in the warmer season that there is no time to reproduce immediately. Before the beetles reproduce they have to hibernate. This type of annual reproduction rhythm is still hypothetical. Only one species with a two-year-development (type 6) was examined. Its females have a gonad dormancy controlled by a change of the photoperiod from short day to long day. Therefore it seems not very probable that the two-year-development of type 6 evolved in the way assumed by VAN DIJK and LUFF.

Cave dwelling carabids of the temperate zone live under rather constant but low temperatures. They, too, seem to have evolved from winter breeders. Larvae and adults of winter breeders develop best and without dormancies under low temperatures and short day conditions down to DD. In the closely related genera *Laemostenus* and *Pristonychus* we find winter breeders in North Africa: *Laemostenus complanatus*, *Pristonychus picicornis* (PAARMANN, 1970); an autumn breeder: *Laemostenus terricola* (LARSSON, 1939) in Central and Northern Europe and two species more or less adapted to cave dwelling: *Laemostenus oblongus*, *Laemostenus navarricus* (LAMP-

RECHT and WEBER, 1975). This seems to support the postulated origin of the cave dwelling carabids. In the temperate zones, that offer a manifold combination of different environmental factors during the annual climatic change, further types of annual rhythms developed in carabid types 1, 2, 5 and 6 (see Tab. 1 and Fig. 1). To associate these types with the proposed two 'lines of descent' is more difficult, however.

Species with spring propagation are rather characteristic for areas with continental climatic conditions in the temperate zones (see HEYDEMANN, 1962) and also for the subarctic areas (FERENZ, 1973, 1975a). Type 1 (spring breeder with an obligatory gonad dormancy) is probably related to the autumn-winter-breeder group. A first indication for this supposition is given by the fact that ♂♂ of both these spring breeders and the winter breeders reach their maturity under short day conditions. A second indication is the fact that in different genera we find closely related species that propagate either during spring (type 1) or during autumn (type 3 and 4) (HŮRKA, 1973). It is equally possible that within the same genus one type evolved from the other or that both types evolved from the same ancestors. These ancestors possibly were slightly specialized winter breeders. Thus in the genus *Pterostichus* we find species with spring propagation type 1 (THIELE, 1966, 1968a, 1971, 1975; KREHAN, 1970), autumn propagation type 3 (KREHAN, 1970), and winter propagation (PAARMANN, 1975).

♂♂ and ♀♀ of the spring breeders type 2 (with facultative gonad dormancy) are able to reach their full sexual maturity under continuous European long day conditions (NEUDECKER and THIELE, 1974; KRECKWITZ, 1978). Short day conditions retard gonad development in this type. Regarding the way in which the photoperiod influences gonad maturation in the spring breeders type 2, it seems improbable that they are related to the autumn-winter-breeder group. In all photoperiodically controlled dormancies of the latter group short day conditions are favourable for gonad maturation. The supposition that the spring breeders type 2 don't belong to the autumn-winter-breeder group is supported by another fact. Up to now spring breeders of type 2 are only known from the genus *Agonum*. In this genus there are no autumn breeders among 21 examined European species (LARSSON, 1939). Furthermore the species *Agonum marginatum*, known from river bank habitats of Central Europe, could be caught in the same habitats in North Africa. In North Africa *A. marginatum* probably belongs to the species with summer propagation (PAARMANN, 1975). Such species with summer propagation are able to reach their gonad maturity without dormancies under favourable temperature conditions within a range of short day to long day (up to LD 18:6). In summer breeders living in higher latitudes, possibly a retarding effect of short day conditions on gonad development evolved. This may have led to the evolution of spring breeders type 2 from summer breeders.

The last two types of annual reproduction rhythms (type 5 and 6) probably have to be associated again with the autumn-winter-breeder group. The beetles of type 5 (species with a development potentially free of dormancies) are able, like the adults of the autumn breeders type 3, to reach their gonad maturity without dormancies

(Löser, 1972). The larvae of this type have a dormancy comparable with that of the North African winter breeders (Paarmann, 1973). Thus, this type may have evolved either directly from winter breeders by loosing the aestivation dormancy, or, more probably, from autumn breeders type 3 by a reduction of the larval hibernation dormancy. Type 6 (two-year development), described by Lampe (1975), may also have evolved from the autumn breeders type 3. In both types we find a larval dormancy.

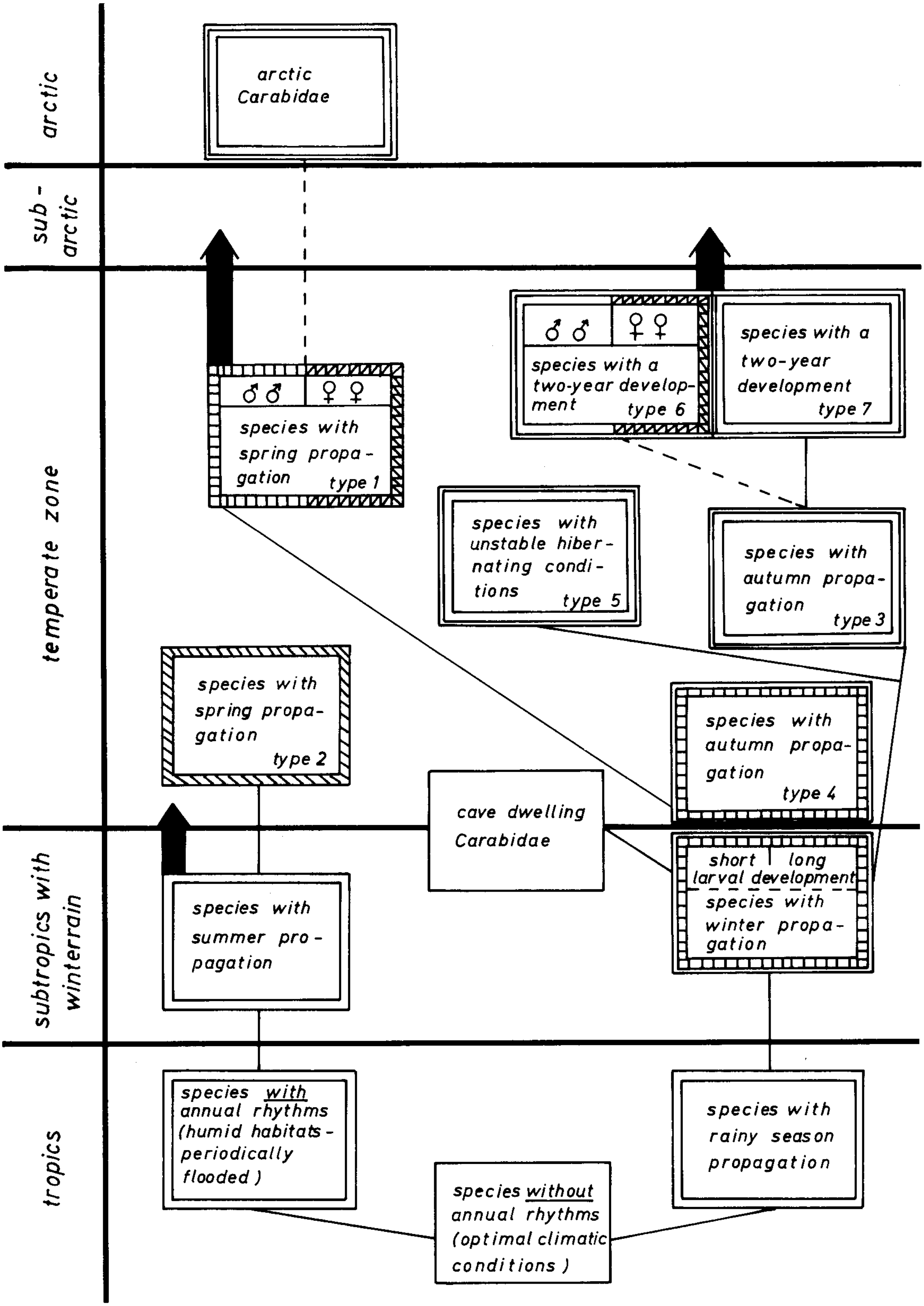
The ♂♂ of type 6 are able to reach their gonad maturity without dormancy, like the ♂♂ of type 3. Only in the females of type 6 do we find a gonad dormancy controlled by photoperiods comparable with that of the spring breeders of type 1. They reach their gonad maturity only after a change of day length from short day to long day. This kind of control mechanism in spring breeders is also supposed to have evolved in the autumn-winter-breeder group.

The annual rhythms in the Subarctic and Arctic zones

Only from one arctic species (*Pterostichus brevicornis*) is something known about its annual rhythm. *P. brevicornis* is able to develop free of dormancy during the arctic summer. The larva is able, however, to survive the arctic winter in a stage of dormancy. The same abilities are found in the imaginal stage (Kaufmann, 1971). Up to now nothing is known about the control mechanisms of these dormancies. Possibly this arctic type of annual rhythm evolved from spring breeders type 1 by the development of a facultative larval hibernation dormancy and a reduction of the gonad dormancy, controlled by photoperiods.

Conclusions

Although most of the relationships between the types of annual rhythms in carabids, discussed in this paper are of a more or less hypothetical character, there can hardly be any doubt, that autumn breeders of type 4 are closely related to the North African winter breeders. They obviously are the northern-most, respectively southern-most representatives of one type of annual reproduction rhythm, that finds its optimal conditions in a temperate Mediterranean climate. Larsson (1939), Lindroth (1949), and Heydemann (1962) discussed the fact, that autumn breeders are more numerous in areas with a warmer atlantic climate and that spring breeders are more abundant in areas with a more extreme continental climate. The geographical distribution of both types of annual rhythms as well as the results of my own investigations – mentioned above – support the idea that the autumn breeders belong to a more southern type of annual rhythm. This type has its distributional centre in areas where the winters are relatively warm. Larsson (1939) and Heydemann (1962) believe that in certain biotopes of the temperate zone with optimal climatic conditions the autumn breeders


arctic
sub-arctic
temperate zone
subtropics with winterrain
tropics
arctic Carabidae
♂♂ ♀♀
species with spring propagation type 1
♂♂ ♀♀
species with a two-year development type 6
species with a two-year development type 7
species with unstable hibernating conditions type 5
species with autumn propagation type 3
species with spring propagation type 2
cave dwelling Carabidae
species with autumn propagation type 4
short | long larval development
species with winter propagation
species with summer propagation
species with annual rhythms (humid habitats - periodically flooded)
species with rainy season propagation
species without annual rhythms (optimal climatic conditions)

evolved from spring breeders. In my opinion the spring breeders (type 1) seem to be the more advanced type, because of their more complicated control of the gonad dormancy in females. Therefore, it is more probable that they have evolved from autumn breeders under continental climatic conditions.

Fig. 1 shows the above postulated two 'lines of descent' in the types of annual reproduction rhythms of carabids from the different climatic zones. Related types are connected by a line. In the two 'lines of descent' we may also see two ways of successive adaptation, which the carabids may follow during their migration from the tropics to higher latitudes. These ways – as discussed above – probably were followed repeatedly by carabids of different systematic groups.

ACKNOWLEDGEMENTS

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Fig. 1.
The two 'lines of descent' in the annual reproduction rhythms of carabids from the different climatic zones. The different types are enclosed by differently formed frames:

───	(single)	– no dormancy
═══	(double)	– gonad dormancy or the ability to produce a gonad dormancy
≡≡≡	(threefold)	– larval and gonad dormancies or the ability to produce these dormancies.

The kind of gonad dormancy is recognizable by the shape of the surrounding frame:

═══	gonad dormancy only controlled by temperature or the ability to produce such a dormancy. This ability to produce a gonad dormancy controlled by temperature during hibernation is to be found in the species of the higher latitudes that are able to reach their sexual maturity potentially free of dormancies.	
▥	gonad dormancy controlled by photoperiods	– complete gonad development in SD (short day)
▨	gonad dormancy controlled by photoperiods	– complete gonad development in LD (long day)
▩	gonad dormancy controlled by photoperiods	– complete gonad development only after changing of day length from SD to LD.

The black arrows attached to some types of annual rhythm mean that members of the type also exist in the climatic zones to which the arrow points.

References

Ali, H. A.: The higher classification of the Carabidae and the significance of internal characters. Bull. Soc. ent. Egypte **51**: 211–231 (1967).

Bauer, T.: Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). Oecologia (Berl.) **14**: 139–196 (1974).

Darlington, P. J.: Area, climate, and evolution. Evolution **13**: 488–510 (1959).

Darlington, P. J.: The carabid beetles of New Guinea. Part. IV. General considerations; Analysis and history of fauna; taxonomic supplement. Bull. Mus. Comp. Zool. **142**: 129–337 (1971).

Dijk, Th. S. van: The significance of diversity in age-composition of *Calathus melanocephalus* L. (Col., Carabidae) in space and time at Schiermonnikoog. Oecologia (Berl.) **10**: 111–136 (1972).

Engelmann, F.: The physiology of insect reproduction. 307 p. Oxford, 1970.

Erwin, T. L.: A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). Quaestiones entomologicae **6**: 4–215 (1970).

Ferenz, H. J.: Steuerung der Larval- und Imaginalentwicklung von *Pterostichus nigrita* F. (Col., Carabidae) durch Umweltfaktoren und Hormone. Diss Köln. 112 pp. 1973a.

Ferenz, H. J.: Juvenile hormone – initiated sexual maturity in males of *Pterostichus nigrita* F. (Col., Carab.). Experientia **29**: 356 (1973b).

Ferenz, H. J.: Anpassungen von *Pterostichus nigrita* F. (Col., Carab.) an subarktische Bedingungen. Oecologia (Berl.) **19**: 49–57 (1975a).

Ferenz, H. J.: Photoperiodic and hormonal control of reproduction in male beetles, *Pterostichus nigrita*. J. Insect Physiol. **21**: 331–341 (1975b).

Ferenz, H. J.: Two-step photoperiodic and hormonal control of reproduction in the female beetle, *Pterostichus nigrita*. J. Insect. Physiol. **23**: 671–676 (1977).

Ferenz, H. J., Hölters, W.: Corpus allatum hormone induced maturation in males of three carabid species of the genus *Pterostichus* (Col., Carab.). Ent. exp. & appl. **18**: 238–243 (1975).

Heydemann, B.: Die biozönotische Entwicklung vom Vorland zum Koog. II. Teil: Käfer (Coleoptera). Abh. Akad. Wiss. Lit. Mainz, Math.-naturwiss. Kl. **11**: 765–964 (1962).

Hölters, W.: Untersuchungen zur Steuerung des Kurztag- und Langtag-Prozesses der Gonadenreifung bei *Pterostichus angustatus* Dft. (Col., Carabidae). Diss. Köln. 80 p., 1978.

Hůrka, K.: Fortpflanzung und Entwicklung der mitteleuropäischen *Carabus*- und *Procerus*-Arten. Studie CSAV **9**: 1–78 (1973).

Kaufmann, T.: Hibernation in the arctic beetle *Pterostichus brevicornis* in Alaska. J. Kans. Entomol. Soc. **44**: 81–92 (1971).

Könen, J.: Physiologisch-ökologische Untersuchungen zur Steuerung der Gonadenreifung und Fortpflanzungsperiodik von *Pterostichus oblongopunctatus* F. (Coleoptera, Carabidae) in Abhängigkeit von Temperatur, Fotoperiode und Juvenilhormon. Diss. Köln. 174 pp. 1978.

Kreckwitz, H.: Untersuchungen zur Fortpflanzungsbiologie und zum jahresperiodischen Verhalten in Temperatur- und Feuchtigkeitsgradienten an Wildfängen und Laborzuchten des Carabiden *Agonum dorsale* Pont. Diss. Köln. 137 pp. 1978.

Krehan, I.: Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagoüberwinterern der Gattung *Pterostichus* (Col., Carab.). Oecologia (Berl.) **6**: 58–105 (1970).

Lampe, K. H.: Die Fortpflanzungsbiologie und Ökologie des Carabiden *Abax ovalis* Dft. und der Einfluss der Umweltfaktoren Bodentemperatur, Bodenfeuchtigkeit und Photoperiode auf die Entwicklung in Anpassung an die Jahreszeit. Zool. Jb. Syst. **102**: 128–170 (1975).

Lamprecht, G. & Weber, F.: Die Circadian-Rhythmik von drei unterschiedlich weit an ein

Leben unter Höhlenbedingungen adaptierten *Laemostenus*-Arten (Col., Carabidae). Ann. spéléol. **30**: 471–482 (1975).

Larsson, S. G.: Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Entom. Medd. **20**: 277–560 (1939).

Lindroth, C. H.: Die Fennoskandischen Carabidae. No. 3, Allg. Teil, Kungl. Vetensk. Vitterh. Samh. Handling., Ser. **B 4**: 1–911 (1949).

Löser, S.: Art und Ursachen der Verbreitung einiger Carabidenarten (Coleoptera) im Grenzraum Ebene-Mittelgebirge. Zool. Jb. Syst. **99**: 213–262 (1972).

Luff, M. L.: The annual activity pattern and life cycle of *Pterostichus madidus* (F.) (Col. Carabidae). Entomol. Scand. **4**: 259–273 (1973).

Müller, H. J.: Formen der Dormanz bei Insekten. Nova Acta Leopoldina **35**: 1–27 (1970).

Neudecker, C., Thiele, H. U.: Die jahreszeitliche Synchronisation der Gonadenreifung bei *Agonum assimile* Payk. (Coleopt. Carab.) durch Temperatur und Photoperiode. Oecologia (Berl.) **17**: 141–157 (1974).

Paarmann, W.: Untersuchungen über die Jahresrhythmik von Laufkäfern (Coleoptera, Carabidae) in der Cyrenaika (Libyen, Nordafrika). Oecologia (Berl.) **5**: 325–333 (1970).

Paarmann, W.: Bedeutung der Larvenstadien für die Fortpflanzungsrhythmik der Laufkäfer *Broscus laevigatus* Dej. und *Orthomus atlanticus* Fairm. (Col., Carab.) aus Nordafrika. Oecologia (Berl.) **13**: 81–92 (1973).

Paarmann, W.: Der Einfluss von Temperatur und Lichtwechsel auf die Gonadenreifung des Laufkäfers *Broscus laevigatus* Dej. (Coleoptera, Carabidae) aus Nordafrika. Oecologia (Berl.) **15**: 87–92 (1974).

Paarmann, W.: Freilanduntersuchungen in Marokko (Nordafrika) zur Jahresrhythmik von Carabiden (Coleoptera, Carabidae) und zum Mikroklima im Lebensraum der Käfer. Zool. Jb. Syst. **102**: 72–88 (1975).

Paarmann, W.: Jahreszeitliche Aktivität und Fortpflanzungsrhythmik von Laufkäfern (Coleoptera, Carabidae) im Kivugebiet (Ost-Zaire, Zentralafrika). Zool. Jb. Syst. **103**: 311–354 (1976a).

Paarmann, W.: Die Trockenzeitdormanz der Carabiden des zentralafrikanischen Hochlands und ihre Steuerung durch Aussenfaktoren. Verh. Dtsch. Zool. Ges. **1976**: 209 (1976b).

Paarmann, W.:Die Bedeutung exogener Faktoren für die Gonadenreifung von *Orthomus barbarus atlanticus* Fairm. (Col., Carab.) aus Nordafrika. Ent. exp. & appl. **19**: 23–36 (1976c).

Paarmann, W.: The annual periodicity of the polyvoltine ground beetle *Pogonus chalceus* Marsh. (Col., Carabidae) and its control by environmental factors. Zool. Anz. **196**: 150–160 (1976d).

Paarmann, W.: Propagation rhythm of subtropical and tropical Carabidae (Coleoptera) and its control by exogenous factors. Advances in Invertebrate Reproduction **1**: 49–60 (1977).

Saunders, D. S.: Insect clocks. 280 p. Oxford, New York, Toronto, Sydney, Paris, Frankfurt, 1976.

Thiele, H. U.: Einflüsse der Photoperiode auf die Diapause von Carabiden. Z. angew. Entom. **58**: 143–149 (1966).

Thiele, H. U.: Formen der Diapausesteuerung bei Carabiden. Zool. Anz. Suppl. **31** (Verh. Dt. Zool. Ges. 1967): 358–364 (1968).

Thiele, H. U.: The control of larval hibernation and of adult aestivation in the carabid beetles *Nebria brevicollis* and *Patrobus atrorufus*. Oecologia (Berl.) **2**: 347–361 (1969).

Thiele, H. U.: Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren. Zool. Jb. Syst. **98**: 341–371 (1971).

Thiele, H. U.: Interactions between photoperiodism and temperature with respect to the control of dormancy in the adult stage of *Pterostichus oblongopunctatus* F. (Col., Carabidae). I.

Experiments on gonad maturation under different climatic conditions in the laboratory. Oecologia (Berl.) **19**: 39–47 (1975).

THIELE, H. U.: Carabid beetles in their environments. 369 pp. Berlin, Heidelberg, New York, 1977.

THIELE, H. U., KREHAN, I.: Experimentelle Untersuchungen zur Larvaldiapause des Carabiden *Pterostichus vulgaris*. Ent. exp. & appl. **12**: 67–73 (1969).

THE BEHAVIOURAL STRATEGY USED BY IMAGO AND LARVA OF *NOTIOPHILUS BIGUTTATUS* F. (COLEOPTERA, CARABIDAE) IN HUNTING COLLEMBOLA

THOMAS BAUER

Abteilung Biologie III, Universität Ulm, Oberer Eselsberg, D-7900 Ulm,
Federal Republic of Germany

ABSTRACT

Larva and imago of *Notiophilus biguttatus* are able to catch Collembola on the soil surface. The predatory behaviour was analyzed by means of film recordings at high speed. The imago belongs to the visually hunting type. Its hunting success depends on accurate visual location of the prey. In the larva the location of the prey as well as the attack result from tactile stimuli. The exceptional ability of *N. biguttatus* in catching Collembola is discussed in respect to the special demands of its ecological niche.

INTRODUCTION

The investigation of crop contents in Carabid beetles (DAVIES, 1953; 1959; KABACIK-WASYLIK, 1971; ANDERSON, 1972; LUFF, 1974; KOEHLER, 1977; HENGEVELD, in prep.) has shown that most of the smaller species feed to various degrees on Collembola. Hemiedaphic Collembola, however, are hard to catch because of their jumping ability. The predation tactics of most of the smaller species therefore probably consist in seeking them in soil cavities were springtails are unable to jump or where they are easy to catch because they are involved in moulting activities. The visually hunting species are the only type known to be able to catch springtails on the soil surface. This life form (BAUER, 1974) is characterized by its well developed compound eyes. In Central Europe the genera *Elaphrus*, *Asaphidion*, *Notiophilus* and some species of the genus *Bembidion* belong to this type.

Tab. 1. Success of various Carabid species in hunting Collembola (*Heteromurus nitidus*); illumination intensity: 700 lux; n = number of individuals observed per species (after BAUER et al., 1977).

Notiophilus biguttatus	59,5 %	(n = 5)
Asaphidion flavipes	3,3 %	(n = 6)
Asaphidion caraboides	–	(n = 5)
Elaphrus riparius	–	(n = 6)
Elaphrus aureus	2,3 %	(n = 4)

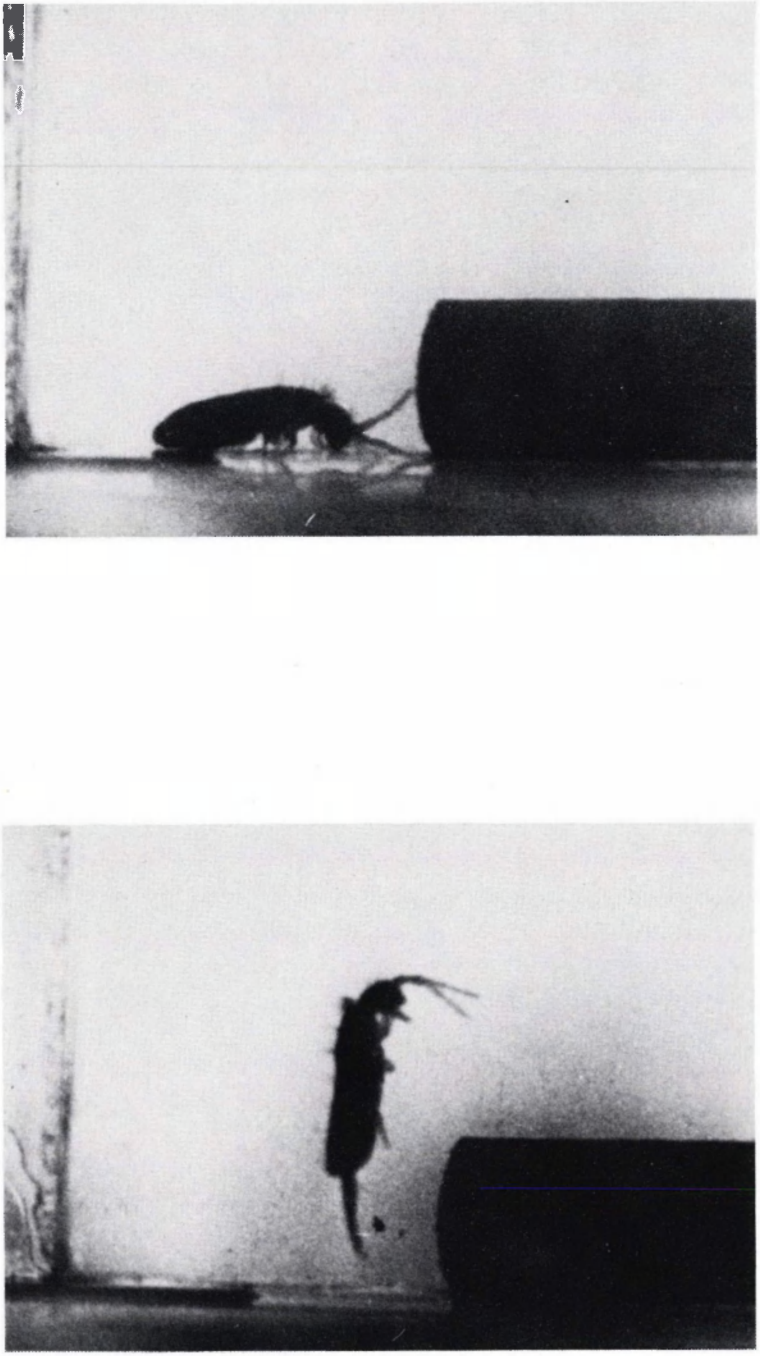

Fig. 1. Two frames from a film recording at high speed. 1: The springtail is touched by the wire-release. 2: It leaves the ground.

In a previous paper BAUER et al. (1977) compared the success of various species of visually hunting Carabidae in hunting a Collembolan species (*Heteromurus nitidus*). Fifty attacks of each beetle were observed and the number of captures was recorded (methods in: BAUER et al., 1977). Tab. 1 reveals that in this respect *N. biguttatus* is superior to the rest of the species. To find out the reason, the flight behaviour of the springtails and the hunting behaviour of *N. biguttatus* was analyzed by means of film recordings at high speed (BAUER & VÖLLENKLE, 1976).

THE FLIGHT BEHAVIOUR OF THE COLLEMBOLA

The jump of the springtails is released by various irritations e.g. by a sudden change in light intensity, by airflow or vibration of the soil. All species are particularly sensitive to being touched. The jumping distance usually amounts to some centimeters, in various Symphypleona to some decimeters. In every case this is sufficient to escape the reach of a predator of similar size – if the springtail succeeds in jumping. *Heteromurus nitidus*, the species used in the experiments, is stimulated to jump by touch. Therefore it is important to know the space of time between the initial mechanical stimulation and the moment when the animal leaves the ground. To find out this period of time the springtails were filmed while they were touched with a wire-release in a narrow cuvette (for methods cf. BAUER & VÖLLENKLE, 1976). Fig. 1 shows two frames from a recording at high speed: In picture 1 the springtail is touched, in picture 2 it leaves the ground. From the initial mechanical stimulation until the moment the animal leaves the ground an average of ca 26 ms elapses (min.: 14 ms, max.: ca 38 ms, 20–22°C, n = 56). This means, that *H. nitidus* after having been touched needs about 26 ms to evade the reach of a predator: this is very quick. The next question was, how does *N. biguttatus* cope with this flight efficiency.

Fig. 2. Shortly before reaching the critical distance of the attack the beetle turns its antennae backwards (recording at high speed).

The analysis of film recordings of 62 captures revealed that all components of the hunting behaviour are released by the movements of the prey: The turning towards it, every jerk approach and finally the actual capture (consummatory act) only occur, if the springtail moves. The distances of the jerky approaches vary, immediately before reaching the critical distance of the actual capture they are reduced to ca 0.2 mm. At a distance of about 5 mm from the prey the beetle turns its antennae backwards (Fig. 2). This is an infallible sign of its intention to attack the prey. During the approach the beetle directs its medio-sagittal plane to the body end of the springtal: It fixes its eyes upon the point with the highest optical contrast. If the beetle has reached a point which is ca 1.6 mm distant from the part of the prey's body it has fixed its eyes upon, the attack occurs: It hurls its body forward, mostly without lifting the middle and hind legs from the ground. The forward movement amounts to ca 2 mm, this is somewhat more than the critical distance, so that the beetle meets its prey with its mouthparts wide open (Fig. 3).

The mouthparts are closed at the end of the forward movement within ca 1.6 ms. As described earlier (BAUER & VÖLLENKLE, 1976) the attack is a fixed action pattern, consisting of three different phases. It takes ca 20–90 ms, the time seems to depend on the body temperature.

Not speed but accuracy in gauging distance and direction of the prey decides, whether the attack is successful or not. If the mouthparts get a good grasp at the moment of contact, the springtail has no chance of escaping (the mouthparts close within 1.6 ms). If, however, the springtail is only touched but not seized because of

Fig. 3. The rapid phase of the attack (recording at high speed).

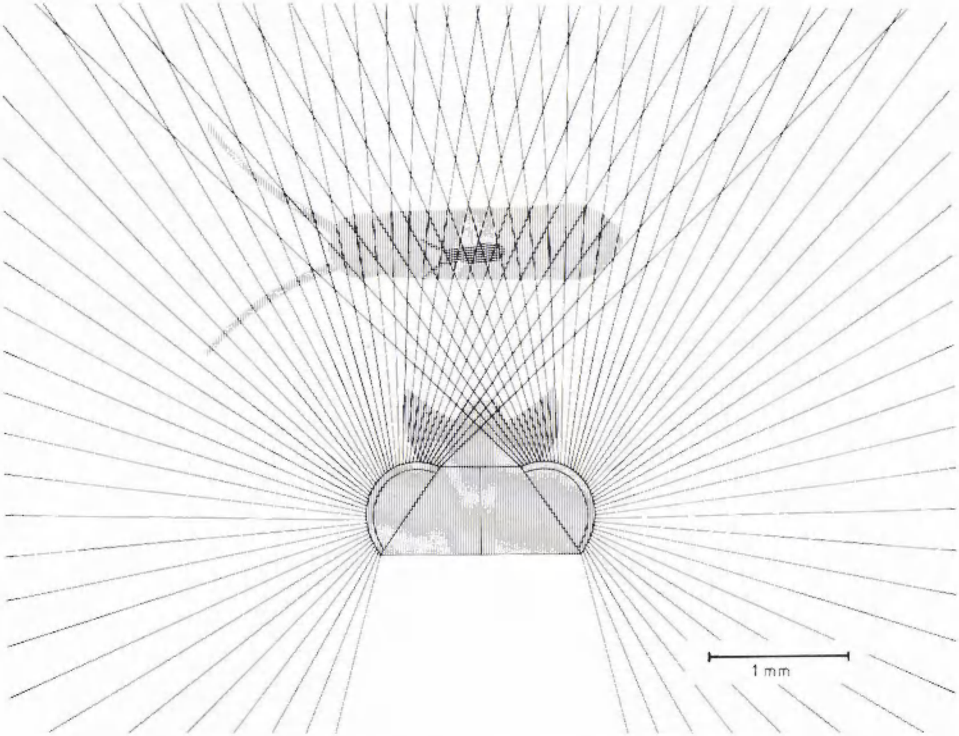

Fig. 4. The structure of the field of vision of *Notiophilus biguttatus*. The longitudinal and the transverse expansion of the quadrangels within the binocular field of vision is a measure of the depth and width of focus in different distances. A grown up and a newly hatched *Heteromurus nitidus* are plotted in the critical distance of the attack.

inaccuracy, a renewed attack is usually too late.

In *N. biguttatus*, the localization of the prey before it is attacked, is done exclusively by means of the compound eyes. If antennae, labrum, palpi maxillares and labium of a beetle are removed, it is still able to catch Collembola. The quality of localization therefore depends on the resolving power of the frontal parts of the compound eyes. The investigations up to now have shown that *N. biguttatus* has a 'fovea' in its frontal eyeparts with interommatidial angles of 3.5°. Depth and width of focus of the binocular field of vision (cf. BURKHARDT et al., 1973) are diminished to a large extent as the distance from the beetle is increased. In the critical range of attack (1.6 mm), however, the resolving power is sufficient to localize the smallest springtails (Fig. 4). This was proved experimentally: The success in hunting newly hatched *H. nitidus* (0.45 × 0.13 mm) amounted to 51.9% (668 attacks of 20 beetles were observed at 500 lux). In hunting adult *H. nitidus* (2.1 × 0.56 mm) the beetles succeeded in 52.9% of their attacks (365 attacks, 20 beetles).

The investigation of the binocular field of vision in other Carabidae of the visually hunting type will show, whether the high catching rate of *N. biguttatus* – compared with other species – can be attributed to the resolving power of its compound eyes.

THE HUNTING BEHAVIOUR OF THE LARVA

The larvae of *N. biguttatus* are remarkably quick and mobile. While running they perform gyratory movements with their head. Fig. 5 shows the long, sickle-shaped mandibles and the slim neck – untypical of Carabid larvae. Fig. 6. shows the long, thin hairs (trichobothria) on head and thorax.

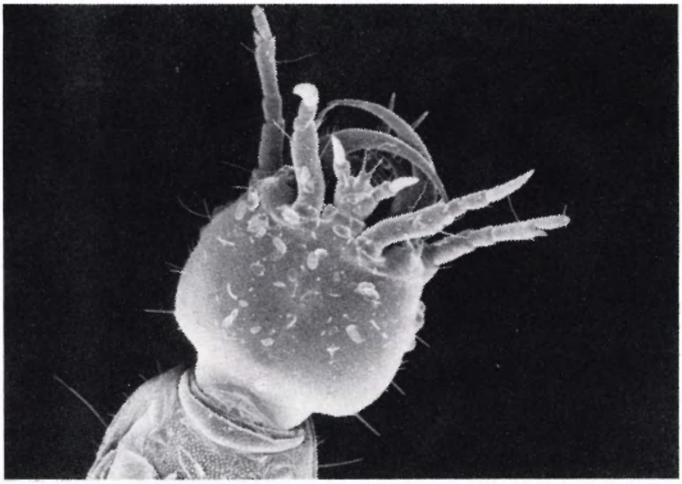

Fig. 5. The head of the *Notiophilus* larva: ventral view.

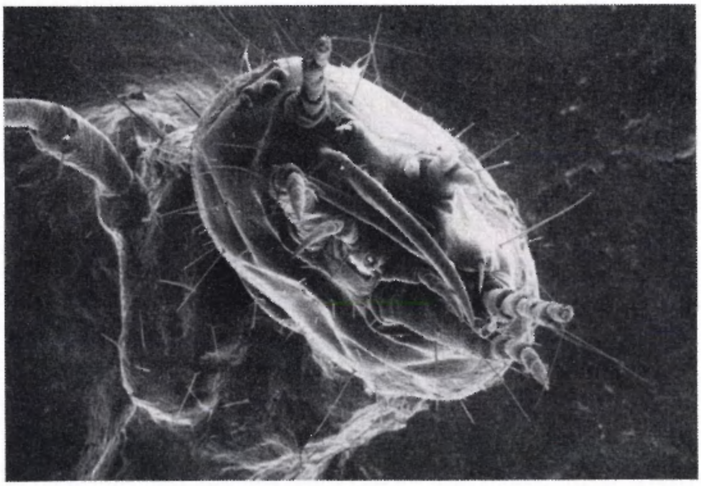

Fig. 6. The head of the *Notiophlus* larva: frontal view.

Like the imagines, the larvae are able to catch springtails on the soil surface. The attack occurs with lightning speed, but only when the larva has touched a springtail. The attacks are successful in total darkness, too, indicating that the larvae have no visual orientation during predation.

The fact that the attacks are only released by contact with the prey means that both the hunting behaviour of the larvae and the flight behaviour of the springtails are released by the same tactile stimuli. Therefore it was at first supposed, that the larva can only succeed, because its reaction time (from the contact until the mandibles are closed) is shorter than that of the springtail (from contact until it leaves the ground).

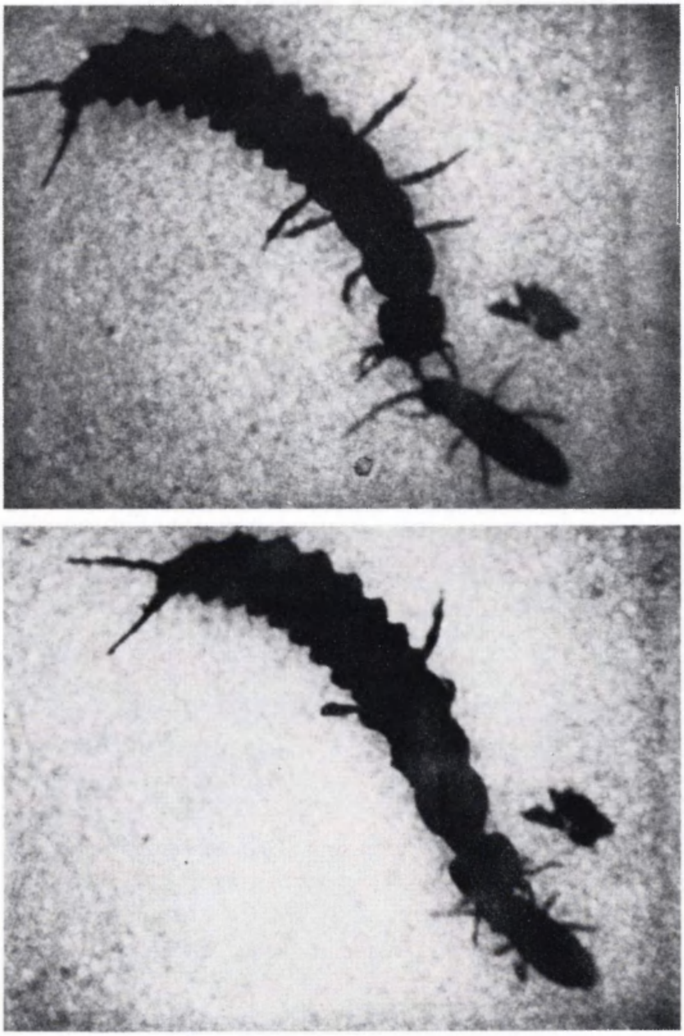

Fig. 7. Two frames from a film recording at high speed. 1: The larva touches a springtail. 2: The larva grasps in the direction where the contact occurred.

The analysis of the hunting behaviour by means of film recordings at high speed refuted this hypothesis. The analysis was carried out in the IWF, Göttingen (Institute of Scientific Film) with the following results:

The running with gyratory movements of the head is to be considered as a seeking behaviour (appetitive behaviour). The attack is only released when the trichobothria touch a springtail. The larva grasps in the direction where the contact occurred. Thus the localisation, too, results from tactile stimuli (Fig. 7).

As with the beetles, the attack of the larva comprises a slow phase, within which the mandibles are opened, and a rapid phase, within which the body is hurled forward. The duration of the slow phase varies widely, it took between 33 and 195 ms, on average 60 ms (n = 9). The rapid phase took 7–12 ms (n = 3). This means that the larva is not faster than the springtail after a tactile contact. The larva is only successful, because the touch by the trichobothria is too gentle to be a flight stimulus for the Collembola. All springtails on the film recordings throw out their furca ca 20 ms after having been pricked by the mandibles.

In contrast to the beetles, the mandibles of the larvae are not closed automatically at the end of the rapid phase but only if the prey is brought between them. In this case the closing is obviously based on a rapidly proceeding reflex, which is released by a tactile stimulus. It has not yet been established where between the open mandibles the contact has to take place.

DISCUSSION

The special ability of predation in larva and imago of *N. biguttatus* is to be regarded as specialization on a kind of prey which commands a highly effective flight mechanism. The evolution of a specialization of this kind can only be accounted for if one considers the special demands of the species' ecological niche.

N. biguttatus inhabits light forests and belongs to the small group of exclusively diurnal Carabidae (THIELE & WEBER, 1968; WILLIAMS, 1959; GREENSLADE, 1963; KASISCHKE, 1975; LUFF, 1978). As LUFF (1978) has pointed out, the larva of *N. biguttatus* is also diurnal. Diurnal and poikilotherm inhabitants of dry habitats are generally adapted to a higher temperature and a lower humidity than nocturnal inhabitants. *N. biguttatus* is an eurythermic and euryhygric species (BAUER, 1975). On the other hand the fauna of the leaf litter and, especially the hemiedaphic springtails have little resistance to desiccation. They normally leave the leaf litter only under favourable conditions of humidity, i.e. after rain falls and in the humid night hours (BOWDEN et al, 1976; BAUER, 1979). On the soil surface, however, they are hard to catch because of their jumping ability.

Thus *N. biguttatus* is confronted with two difficulties: On the one hand, encounters with suitable prey are not very abundant in its habitat during daylight, on the other hand its prey is especially hard to catch above the leaf litter. One may therefore assume that the high catching rate of this species is the result of its adaptation to these conditions.

ACKNOWLEDGEMENTS

I thank Theo Klimek for his assistance with the English manuscript.

REFERENCES

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

BAUER, TH.: Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). Oecologia (Berl.) **14**: 139–196 (1974).

BAUER, TH.: Zur Biologie und Autökologie von *Notiophilus biguttatus* F. und *Bembidion foraminosum* Strm. (Coleopt., Carabidae) als Bewohner ökologisch extremer Standorte. Zool. Anz., Jena **194**: 305–318 (1975).

BAUER, TH., VÖLLENKLE, W.: Hochfrequente Filmaufnahmen als Hilfsmittel bei der Analyse von Angriffs- und Fluchtverhalten in einer Räuber-Beute-Beziehung unter Bodentieren (Collembolenfang visuell jagender Carabiden). Wiss. Film (Wien) **17**: 4–11 (1976).

BAUER, TH., BRAUNER, U., FISCHERLEITNER, E.: The relevance of the brightness to visual acuity, predation, and activity of visually hunting ground beetles (Coleoptera, Carabidae). Oecologia (Berl.) **30**: 63–73 (1977).

BAUER, TH.: Die Feuchtigkeit als steuernder Faktor für das Kletterverhalten von Collembolen. Pedobiologia (1979) (in press).

BOWDEN, J., HAINES, I. H., MERCER, D.: Climbing Collembola. Pedobiologia **16**: 298–312 (1976).

BURKHARDT, D., DARNHOFER-DEMAR, B., FISCHER, K.: Zum binokularen Entfernungssehen der Insekten. 1. Die Struktur des Sehraumes von Insekten. J. comp. Physiol. **87**: 165–188 (1973).

DAVIES, M. J.: A contribution to the ecology of species of *Notiophilus* and allied genera (Col., Carabidae). Ent. mon. Mag. **95**: 25–28 (1959).

DAVIES, M. J.: The contents of the crops of some British Carabid beetles. Ent. mon. Mag. **89**: 18–23 (1953).

GREENSLADE, P. J. M.: Daily rhythms of locomotory activity in some Carabidae (Coleoptera). Ent. exp. appl. **6**: 171–180 (1963).

HENGEVELD, R.: Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). (in prep.).

KABACIK-WASYLIK, D.: Studies on the diet of three field species of Carabidae. Ekol. Pol. **19**: 502–508 (1971).

KASISCHKE, P.: Freiland- und Laborversuche zur Aktivitätsrhythmik der tagaktiven Carabiden eines Waldbiotops (mit besonderer Berücksichtigung der Gattung *Notiophilus*). Staatsexamensarbeit, Köln (1975).

KOEHLER, H.: Nahrungsspektrum und Nahrungskonnex von *Pterostichus oblongopunctatus* (F.) und *Pterostichus metallicus* (F). (Coleoptera, Carabidae), Verhdl. Ges. Ökol. Göttingen 1976. The Hague: Junk.

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

LUFF, M. L.: Diel activity patterns of some field Carabidae. Ecol. Ent. **3**: 53–62 (1978).

THIELE, H. U., WEBER, F.: Tagesrhythmen der Aktivität bei Carabiden. Oecologia (Berl.) **1**: 325–355 (1968).

WILLIAMS, G.: Seasonal and diurnal activity of Carabidae, with particular reference to *Nebria*, *Notiophilus* and *Feronia*. J. anim. Ecol. **28**: 309–330 (1959).

4. Behaviour and the dynamics of populations

POPULATIONS OF CARABID BEETLES AND INDIVIDUAL BEHAVIOUR. GENERAL ASPECTS

P. J. DEN BOER

Biological Station of the Agricultural University (Wageningen),
Kampsweg 27, 9418 PD Wijster, The Netherlands

Communication no 200 of the Biological Station

ABSTRACT

It is tried to outline the background of the investigations taking place at the Biological Station, Wijster: Because field populations are composed of individuals, population processes can only be understood by studying the differences in relevant properties between individuals living together in 'interaction groups'. The consequences of this view are illustrated by discussing the chances of survival of two carabid species at Kralo Heath.

The different contributions of our research group to this volume (DEN BOER, VAN DIJK, VAN HUIZEN, MOLS) are introduced within this general frame-work.

The main results of BAARS' work in this connection are also mentioned (have recently been published in Oecologia).

When we are occupied with population dynamics, population genetics, population ecology or population biology, sooner or later we will ask: 'What **is** a population?' This question appears to be difficult to answer: on the one hand, in theoretical studies 'the population' is generally treated as a uniform entity*; on the other hand, in the field we are mainly confronted with individuals, and therefore with the problem how to delimit 'our population', i.e. a group of individuals.

This delimitation will be greatly influenced by the problem one wants to study, but because of the widely diverging interests among ecologists field populations may thus be as different, as the population of larvae of some staphylinid species in a single mushroom is, from the stork population of Western Europe. Although such 'populations' are in no way comparable, both students may consider their 'population' as an entity, and wonder how it is 'regulated'. For, a holistic view of 'population' is widespread and as old as field biology, since it is based upon an assumption that carries us back to Darwin, namely the presupposition that the members of a population are somehow continuously competing and will thus keep abundance between certain limits.

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*This means: in theoretical studies population processes are generally described by differential equations, which tacitly assume that all members are equal and form a closed group in a homogeneous and generally constant environment.

Especially to test critically this competition hypothesis, one must be able to delimit comparable and natural population units, viz. groups in which the individuals can at least meet, and thereby possibly – but not necessarily – influence each other: interaction groups. If one does not take up a position in this competition/regulation question it seems nevertheless useful to work with 'interaction groups' as a kind of standardized units of population. This was already realized by BAKKER (1964, 1971), but met with the difficulty that ecologists did not see an easy way to generally delimit 'interaction groups' in the field. In the case of carabid beetles, however, working with interaction groups appeared to be not only feasible, but even inevitable.

Carabid beetles are generally sampled with the help of pitfalls, and therefore, the individuals caught in the same pitfall were potentially able to meet, i.e. form a sample from the same interaction group (see further: DEN BOER, 1977). The usefulness of this method was underlined by BAARS (1979b): at several sites on Kralo Heath and in several years, just before the start of reproduction, he fenced part of a locality and then trapped all individuals of two abundant species living there. The mean densities thus obtained were compared with the catches during that season in a nearby (20–120 m distant) standard set of pitfalls. In this way he could show that the catches in a pitfall, totalled over the whole season (or year), give a surprisingly accurate – but of course relative – measure of mean density, and at the same time a relative measure of the numerical size of the pertinent interaction group (note: within the same area different interaction groups of a certain species are apparently living on equally sized surfaces).

When we turn now to the whole area of the Heath of Kralo and Dwingeloo (1200 ha), which is more or less continually inhabited by *Pterostichus coerulescens* L. (= *versicolor* Sturm), one may wonder as to how far the numbers of individuals of this species, caught yearly in different sets of pitfalls, are samples from the same or from different interaction groups (subpopulations). Since the fluctuations of these numbers used to be quite different at the different sample sites (see: DEN BOER, 1971), we got the impression that especially in the more distant localities, i.e. more than 200–300 m apart, different interaction groups were sampled.

By marking individuals of *Pt. coerulescens* and of *Calathus melanocephalus* L. radioactively and localizing these individuals each day BAARS (1979a) was able to characterize and quantify the walking pattern of these species. This pattern was simulated in a computer model, after which he could not only test the reliability of this simulated pattern with the results of several independent field experiments, but also calculate what distances could be covered by average individuals during their lifetime. It then appeared that even very old individuals of *Pt. coerulescens* (3–4 years old) will not cover on an average more than 250–300 m (during the first breeding season about 150 m is covered). In the case of *C. melanocephalus* these numbers are much smaller: during the first breeding season an average of only 50 m, whereas old individuals (2–3 years old) will hardly cover 100 m. This means, that by the numbers of *Pt. coerulescens* caught, pitfall series that are more than 300 m apart will register population processes, that are highly independent of each other. In the case of *C. melanocephalus* this will already occur with pitfall series that are more than 100 m apart.

A pitfall estimates the fluctuations in composition and of numbers of the interaction group of which it automatically forms the centre; therefore pitfalls in different localities of the same more or less continually inhabited area, together give a reliable picture of the effects of the heterogeneity in the relevant conditions.

It thus appears, that for *Pt. coerulescens* the Heath of Kralo and Dwingeloo is very heterogeneous, i.e. the risks of large fluctuations are spread over a number of very different localities by which, in the area as a whole, the numbers are rather stable (see further: DEN BOER, 1968, 1971, 1973). For *C. melanocephalus*, on the other hand, the same area is much less heterogeneous; in different localities the fluctuations of numbers are more or less parallel, i.e. the risks are only poorly spread by which, seen over the whole area, the numbers fluctuate as heavily as in an arbitrary subpopulation (Fig. 1). Hence, under overall stationary conditions *C. melanocephalus* will run a much greater risk of dying out than *Pt. coerulescens*.

Now we have seen, that the numerical stability of a species over a large area can only be understood as being the result of the fluctuations of numbers of different interaction groups (subpopulations), the question of the causes of numerical fluctuations as such shifts, and the priority becomes: what are the processes that run within single but different interaction groups?, i.e. what are the processes that result from summing up the courses of life of the individuals? (see also DEN BOER, 1973).

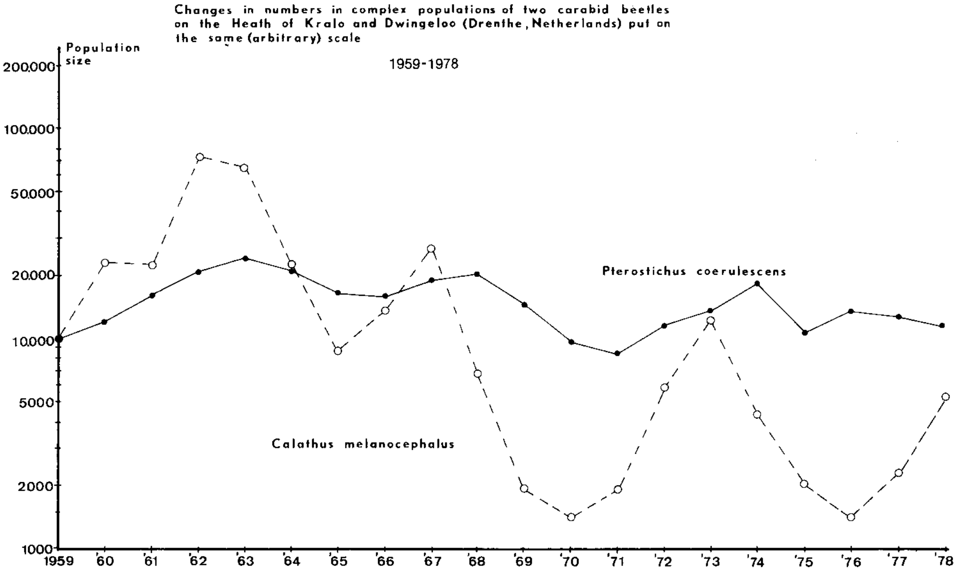

Fig. 1. Fluctuations of numbers in two carabid species on Kralo Heath to show the difference in magnitude, assuming that the subpopulations studied, together give a reliable estimate of the changes in numbers in the 'population as a whole'. To facilitate comparison it is assumed that in 1959 the two species were equally abundant.

Because abundance results from natality, mortality and migration, we are firstly interested in the conditions that determine or alter the chance of survival and/or the chance of reproduction of different individuals, at present especially of individuals of different ages. VAN DIJK, who took on this aspect, will deal with this subject in this volume. Next – in connection with migration – it will be important to know under what kind of conditions an individual will leave the area of the interaction group, either to contact other groups and possibly to contribute to a levelling of local differences in abundance (like in *Pt. coerulescens*, see above; see also: BAARS & DEN BOER, in prep.), or to disperse out of the habitat and possibly to contribute to the foundation of new groups (see further: DEN BOER, 1977, 1979). In the latter case in many carabid species the normal kind of locomotion, walking, will change into flying. Elsewhere in this volume VAN HUIZEN will report on both the morphological and the environmental conditions that determine frequency and level of flight behaviour in carabid beetles.

The numerical result of individual reactions (like feeding, copulating, egg-laying, sheltering, dying, walking or flying away) to different conditions – which can be partly studied in the laboratory – in the field will depend highly on the frequency by which each of these conditions is encountered. In the case of carabid beetles – like in many other animals – this frequency of encountering will directly be determined by the walking pattern. BAARS (1979a) showed that this walking pattern – by analysing the distances covered per day – is composed of two, randomly alternating elements: random walk, and directed movement. Most probably the random walk should be considered the generalized result of different kinds of searching behaviour, whereas the directed movement in some (unknown) way seems to be connected with dispersal (individuals that, while moving around, get out of their preferred habitat change over to an extreme kind of directed movement).

To further analyse the frequency of encountering some condition it was necessary to study the walking pattern more closely, viz. also within a day. Important questions are then: at what time-scale is random walk still random, and: at what distance do the beetles react to certain local conditions? Concerning encounters with prey this is now being studied by MOLS (see his contribution to this volume). We hope to study other aspects of individual behaviour along the same lines, e.g. egg-laying behaviour.

Again to get to grips with the processes behind the numerical changes of the interaction group we generally follow the strategy:

1. studying the relevant aspects of individual behaviour in such a way that each element can be quantified.
2. simulating this behaviour, and checking the model in independent experiments with real animals (the results of these experiments could be predicted): an example of this is discussed in this volume by MOLS (see also: BAARS, 1979a);
3. integrating the different, sufficiently tested submodels into a master-model with which eventually the numerical fluctuations of the interaction group – as they are found in the field – can be simulated and thus predicted.

4. Simplifying the master-model in such a way that the quantitative effects of the submodels are saved without the necessity of simulating all aspects of individual behaviour; this simplification will be repeated at different levels;
5. With such a simplified master-model we can also try to simulate the effects of integrating a number of different interaction groups (subpopulations), i.e. we can try to return to our observations from Kralo Heath, which were our starting point.

Meanwhile we will also have learned whether or not a 'population' should be considered a kind of entity to be able to understand the patterns of numerical fluctuations as they are observed in the field.

With similar arguments also KAISER (1979) advocates an individuals approach of population dynamics.

REFERENCES

BAARS, M. A.: Patterns of movement of radio-active carabid beetles. Oecologia (Berl.) **44**: 125–140 (1979a).

BAARS, M. A.: Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia (Berl.) **41**: 25–46 (1979b).

BAARS, M. A. & P. J. DEN BOER: Simulation experiments on populations of *Pterostichus versicolor* and *Calathus melanocephalus* on Kralo Heath to estimate the role of exchange between subpopulations for population stability (in prep.).

BAKKER, K.: Backgrounds of controversies about population theories and their terminologies. Z. ang. Entom. **53**: 187–208 (1964).

BAKKER, K.: Some general remarks on the concepts 'population' and 'regulation'. Proc. Adv. Study Inst. Dynamics numbers Pop. (Oosterbeek, 1970): 565–567 (1971). Pudoc, Wageningen.

DEN BOER, P. J.: Spreading of risk and stabilization of animal numbers. Acta Biotheor. (Leiden), **18**: 165–194 (1968).

DEN BOER, P. J.: Stabilization of animal numbers and the heterogeneity of the environment. The problem of the persistence of sparse populations. Proc. Adv. Study Inst. Dynamics numbers Pop. (Oosterbeek, 1970): 77–97 (1971). Pudoc, Wageningen.

DEN BOER, P. J.: Das Ueberleben von Populationen und Arten und die Bedeutung von Umweltheterogenität. Verh. D.Z.G., **66**. Jahresvers.: 125–136 (1973).

DEN BOER, P. J.: Dispersal power and survival. Carabids in a cultivated countryside. Miscell. Papers, Landb. Hogeschool Wageningen **14**: Veenman & Zn., Wageningen, 1977: 190 p.

DEN BOER, P. J.: The significance of dispersal power for the survival of species, with special reference to the carabid beetles in a cultivated countryside. Fortschr. Zool. **25**, 2/3: 79–94 (1979).

KAISER, H.: The dynamics of populations as result of the properties of individual animals. Fortschr. Zool. **25**, 2/3: 109–136 (1979).

THE INDIVIDUAL BEHAVIOUR AND POPULATION DYNAMICS OF SOME CARABID BEETLES OF FORESTS

P. J. DEN BOER

Biological Station of the Agricultural University Wageningen, Kampsweg 27, 9418 PD
Wijster (Dr.), The Netherlands

Communication no 201 of the Biological Station*

ABSTRACT

The development is described of a long-term experiment on the influence on population numbers of the individual reactions of carabid beetles towards surface temperature and humidity under natural conditions. The beetles are individually marked and (re)captured separately every hour during the night with time-sorting pitfalls, whereas at each catch site temperature and humidity of the surface layer (in which the eggs are deposited) is measured and recorded automatically. The processing of the data can be done by computer.

The sizes of the sampled interaction groups of four carabid species from the forest are estimated from capture-recapture data with Jolly's model and compared with the numbers of unmarked (new) individuals caught. These two estimates of population size appear to show a close linear relationship for all four species together, the consequences of which are discussed. All species are night-active with a maximum one or two hours after sunset. *Pterostichus oblongopunctatus* prefers the higher situated places and does not react to local differences in temperature. *Agonum assimile* prefers the lower situated places and reacts positively towards small differences in surface temperature. Many adults of both species reproduce again in a second year and some of them even in a third one. Males of the former species survive better after the first breeding season than females, whereas the latter species does not show differential survival of the sexes. Adults of *Nebria brevicollis* do not usually survive more than one breeding season. Overwintered adults of *Calathus piceus* reproduce again in the next spring, whereas juveniles reproduce for the first time in late summer.

When we realized for the first time, that the dynamics of a population can only be understood via individual reactions and adventures, we planned a long-term field experiment in which both certain aspects of individual behaviour and the fluctuations of numbers in the population could be recorded automatically. We reflected that: if in a small and isolated habitat many individually marked carabid beetles are moving around and repeatedly caught, while at the catch sites some relevant environmental factors are frequently measured, it should not only be possible to follow the numerical changes of the population but also to decide whether, under these natural conditions, the individuals behave randomly or more or less selectively towards these factors.

When investigating the behaviour of the woodlouse *Porcellio scaber* (DEN BOER,

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* This (and my other contributions to this volume) were typed by Mrs. G. H. Weijenberg-Boer.

1961) I had already discovered that studying preferences under field conditions may also give some insight into population numbers. I was moreover confronted with the question: What kind of choice situations are actually encountered by the animals in the field? This also means: How carefully should we study the field situation to be able to perform reliable (preference) experiments in the laboratory? Or the other way round: How could we translate the results of laboratory experiments (not only preference experiments) into individual chances of survival and reproduction in the field? In many cases it can hardly be expected that under field conditions there can actually be a choice, e.g. a ground-beetle can take an encountered prey or leave it; but if it has abandoned that prey, what will it meet afterwards? However, also concerning physical factors it is not clear in advance, what the choices are in the field and in what frequencies they occur. At the scale of the sizes of individuals we hardly know anything about spatial distribution and temporal variation of physical factors.

Hence, with the above long-term experiment we planned to find out what the real choice situations in the field were, how carabid beetles react to it, and how this works out dynamically in the population. Concerning the latter point it is specially important to find out what the predictive value is of the established individual reactions, e.g. if eggs are laid at moist places will then these places generally stay moist enough (but not be inundated) during larval development? Ten years ago we started step by step to realize such an experiment in a small and rather isolated deciduous forest close to the Biological Station.

At that time we not only had to start a biological experiment but at the same time we had to solve a number of technical problems*: how far could our wishes be translated into apparatus, which is able to stand up against diverse and often very severe weather conditions? Firstly, we wanted to work with time-sorting pitfalls, viz. 30 pitfalls in which the catches can be kept separately for each hour of the night (or for each two hours of a natural day). Secondly, we wanted to measure repeatedly (e.g. twice an hour, or even more frequently) and continually surface temperature and surface humidity at each catch site, and to record this data automatically.

After a short period (1968–1969) with initial defects the time-sorting pitfalls functioned satisfactorily or even excellently. However, we could only start measuring surface temperatures in 1973 and surface humidities in 1976 (at first only at 10 places, since 1977 at all 30 catch sites). Moreover, the processing of the punched (paper) tapes with data met with great, partly unsolvable difficulties. Since 1976 we have recorded our data on magnetic tape, and these problems have for the greater part disappeared. Although the measuring apparatus will never be foolproof as long as recording occurs in the field (this can only be further improved by recording telemetri-

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* Thus this experiment was realized in close cooperation with the TFDL (Technical and Physical Engineering Research Service), Wageningen, which had to develop the greater part of the apparatus and adapt it to our wishes. Special mention should be made of the novel development of a reliable and automatized measuring technique for soil humidity. As far as the time-sorting pitfalls are concerned, the TFDL modified a prototype that had already been developed at the Biological Laboratory of V.U. Amsterdam.

Photo 1. Our experimental forest, with four rows of time-sorting pitfalls. The central recording station is situated at the right (just out of the picture) November 1978.

Photo 2. A single time-sorting pitfall 'in situ' (covered with a transparent perpex roof). In the background the electronic unit for converting the primary signals concerning surface temperature and humidity.

Photo 3. The same as photo 2, but now the sensor for measuring surface humidity has been uncovered, and the perpex roof has been taken away to show the entrance of the (asymmetrical) funnel of the pitfall with a gitter to keep out litter and animals such as mice, shrews, frogs and toads.

Photo 4. The same as photo 2, but now the time-sorting pitfall has been taken out of its container and laid aside together with the loosened holder containing 13 catch-glasses. Note the asymmetrical outlet of the funnel.

cally in the laboratory), in the course of about ten years we have at least overcome the crucial technical difficulties attendent on such an experiment. At the moment we are greatly occupied in developing the processing of the many data with the help of the computer* and composing the necessary programs to make this possible.

Because of these time-consuming technical developments we do not yet have at our disposal the results of this series of preference experiments in the field, which were interrupted in December 1978 (for a number of years such experiments will be run now at another site and with the species *P. coerulescens* and *C. melanocephalus*). When these results are available, they should enable us to plan supplementary experiments, by which the suggested relations between individual behaviour and the chances to survive and to reproduce will have to be tested and be quantified further.

However, since this experiment intends to connect individual behaviour with population dynamics, I can already report the changes in numbers and composition of the interaction groups of the four carabid species of forest that were studied, viz. *Pterostichus oblongopunctatus* F., *Agonum assimile* Payk., *Nebria brevicollis* F., and *Calathus piceus* Mrsh. I will only mention briefly here some results that are of general interest to carabidologists, whereas a more balanced report will be reserved for more specialized publications.

1. To estimate the size of an animal population, at present the stochastic population model of JOLLY (1965; see also; SOUTHWOOD, 1971 and SEBER, 1973) is generally used. This model is an extension of the well-known Lincoln-index, in which catching, marking and releasing of the individuals is not restricted to a single experiment but is repeated several times. In this way it is possible to also estimate the size of the population several times, and even to estimate (but not very reliably) how many individuals have disappeared from, resp. joined the population (Fig. 1)**.

However, a basal assumption of all mark-recapture-models is, that during the whole sampling period every individual has and will keep the same chance of being caught. We already know that in many cases this assumption is not satisfied: a few individuals are recaptured too frequently (as compared with a Poisson-distribution of recaptures), whereas too many individuals are not recaptured at all during the season (because some of them reappear in the catches of the following year, we know that they have not all

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* Our data were at first processed with the CDC-3200 computer of the Department of Mathematics, and later with the DEC-10 system (and next the DEC-1090 system) of the Computing Centre, of the Agricultural University of Wageningen, in which we have been assisted by a number of people (we will only mention here the valuable and often extended help of B. A. Scholte). Thanks to the time-sharing DEC-systems we are able now to directly compose and test our programs and even to read in our magnetic tapes (A. Spee) directly from Wijster.

**A computer-program for this model was at first written for us by G. Sanders (for IBM-1670), revised by C. de Jonge (for CDC-3200), and adapted to DEC-systems by I. Madé Suwetja. Other versions, which can more easily be transformed in order to test the effects of some of the basal assumptions of the model, and which possibly can be corrected for part of these effects, are composed by R. H. van der Eijk and P. J. den Boer.

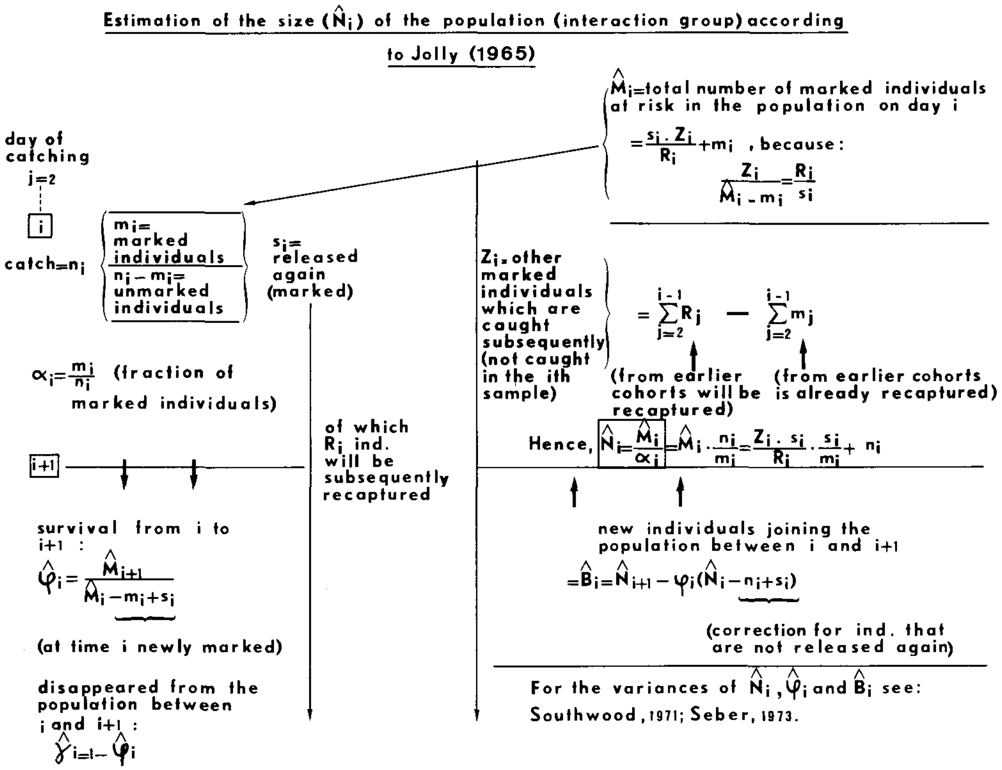

Fig. 1. Outline of the estimation of the running size of the interaction group during a capture-recapture experiment in which several successive samples are taken and all individuals caught are marked individually.

died), viz. about 10 % too many in both *P. oblongopunctatus* and *N. brevicollis*. We are now engaged in finding out whether, and how far, this phenomenon will influence our computations.

2. On the other hand we should like to know what kind of behaviour causes the above mentioned effects. It seems probable, that it is connected with differing individual preferences, which will keep some individuals for far too long a period within the catching area of 500 m^2, whereas others leave it too rapidly. However, when the whole catching area is fenced off – as in 1976 and 1977 – this phenomenon remained at least among young beetles of *N. brevicollis* in 1976 (other cases have not yet been checked). Hence, very variable lengths of the periods of individual activity and/or individually highly diverging intensities of activity apparently can also play a part.

Recently we got many indications (also in other species) which especially favour the latter hypothesis, and it is even probable that the individual level of activity is directly connected – via the frequency of encounters with prey – with the numbers of eggs produced (see also the contributions of Van Dijk and Mols).

A picture emerges of an apparently high level of variation of individual activity. To this can be added, that, at least in *P. oblongopunctatus*, old individuals (as far as they can be recognized, i.e. already marked during a preceding season) generally start their activities somewhat earlier in spring than do young ones (hatched last autumn). It seems important to study how far this will influence the amount of reproduction of old and young females respectively (via the influence of different temperatures on egg-production: Van Dijk, 1979). In the spring of 1978 Szyszko (as a guest-worker from Poland) discovered still another behavioural difference between individuals: ♂♂ of *P. oblongopunctatus* dispersed 3–4 times more frequently than ♀♀ into the adjacent pine forest, but also returned 3–4 times as frequently into our catching area, where in general the density of this species is many times higher than in the pine forest (see also: Szyszko, 1976).

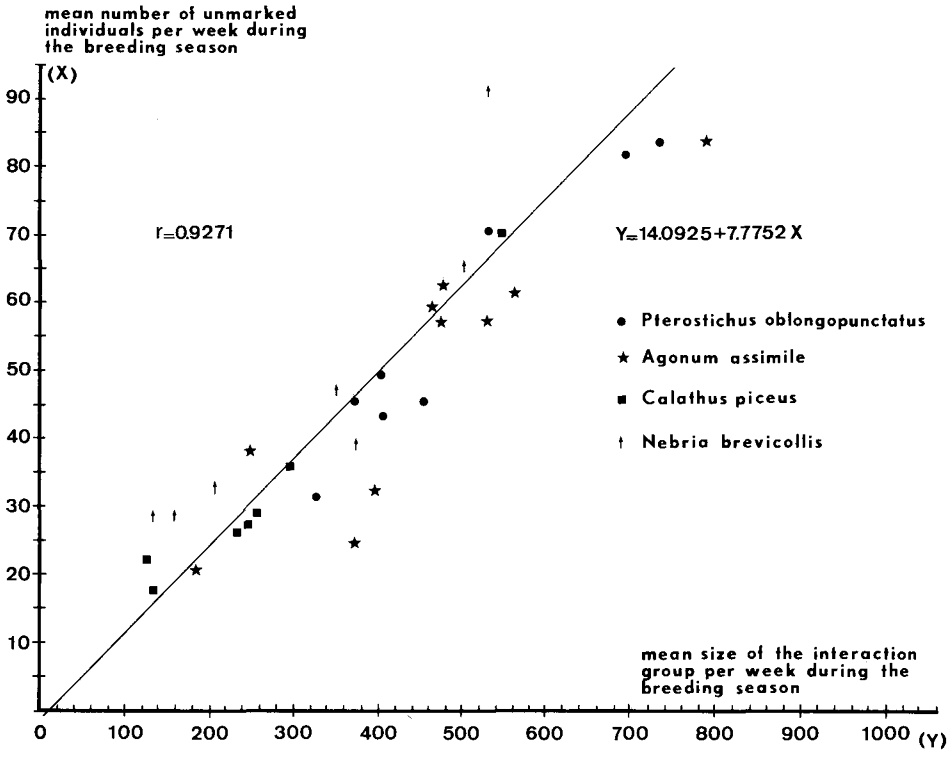

Fig. 2. Relationship between the size of the interaction group as estimated with Jolly's model (version of Sanders-De Jonge-Madé Suwetja) averaged over all weeks of the breeding season (Fig. 1) and the mean number of unmarked individuals (i.e. not captured before) caught during the same weeks. Each point for the pertinent species represents the results from uninterrupted pitfall sampling (see text) during one breeding season. For the different species this capture – recapture experiment was continued for 7–10 years.

3. It is very interesting now to learn that, in spite of the apparent individual differences in activity, the numbers of newly marked individuals totalled over the season gives a reliable relative measure of the size of the population as it can be estimated with JOLLY's model (cf section 1), not only within each species separately but even for all four species together, Fig. 2. This means, that individually determined differences in activity as well as changes of individual behaviour in time, when taken together both for the whole interaction group and over the whole season, work out statistically in such a way that the chance of an average individual being captured at least once does not differ very much between years and even between the species concerned, so that the size of the population is well reflected by the number of individuals caught. This phenomenon is treated more extensively by BAARS (1979). Even comparable data for some species of heathland (among which *P. coerulescens*, see the previous contribution) fit nicely into the relationship as it is picured in Fig. 2 for forest species only (see further DEN BOER, 1977; section 4.4, where a few exceptions are also mentioned). In this way, with JOLLY's model we correctly recorded the changes in numbers from year to year on a relative scale. We have only to find out now how far the JOLLY-calculations underestimate or overestimate the actual size of the interaction group. The necessary data for that was collected by enclosing the whole catching area in 1976 and 1977. There are several indications to suppose that JOLLY's model will generally underestimate the size of the population.

4. When we now look at differences and similarities in activity between the four species: they are all night-active, starting locomotory activities immediately after sunset and reaching a maximum (at least in the catches) one to two hours later after which they gradually decrease.

In general, *A. assimile* has a more restricted daily activity period and is more exclusively nocturnal than *P. oblongopunctatus*. However, during a number of nights the activity curves deviate substantially from this general pattern, e.g. in some nights a revival of activity occurs just before sunrise, especially in *N. brevicollis*. Although there are reliable indications that these deviations are connected with weather conditions the causal relations are not yet obvious. Because e.g. egg-production depends highly on the temperatures to which the females have been exposed, it will be important further to unravel these relationships.

5. Further differences and similarities in activity between the species are still hidden in our data on individual preferences, that are now being prepared for computer processings. However, a few provisional results can be mentioned. Although our experimental forest is rather homogeneous the captures are only as an exception distributed randomly (or even more or less equally) over the thirty pitfalls: usually the catches are more or less grouped. For the different species this clustering of the captures generally does not occur in the same part of the sampling area. Our experimental forest shows one spatially heterogeneous feature that time does not alter: There are small differences in elevation, by which the highest site is situated 27 cm above the lowest one. The two spring breeders apparently react (directly or indirectly) to these small differences in elevation: the catches of *P. oblongopunctatus* generally occur in the higher situated pitfalls, whereas those of *A. assimile* occur for the greater part in the ones situated in the lower sites. Because also the callow beetles in autumn often show this pattern, females of *P. oblongopunctatus* obviously deposit their eggs at other (more elevated) sites than females of *A. assimile*. Although the above pattern can generally be recognized, in different years the distribution of the captures may be quite different, probably because the beetles only react indirectly upon differences in elevation. We have still to find out how far spatial differences in surface temperature and/or humidity are correlated with these differences in elevation (some provisional tests suggest that a clear relationship does not exist).

As a first result of our data processing we have already established that *A. assimile* apparently prefers the warmer sites within our catch area – especially during the second part of the reproductive period – in the spring of 1973 to a very significant degree, and in 1974 to a lesser degree. How this preference is related to the higher catches in the lowest situated pitfalls has still to be investigated. These findings are especially interesting in the light of the results of the extensive preference experiments (in the laboratory) by NEUDECKER (1972): he showed convincingly that *A. assimile* is a species that prefers both cold and drought (at least under experimental conditions).

According to THIELE (pers. comm.) this contradiction with our findings can be removed by assuming that *A. assimile* in fact prefers a temperature of about 18 °C, whereas in our forest the surface temperatures at night only sometimes exceed 16 °C in May and June. Also the recorded drought-preference of this species promises to offer some complications: the densest population of *A. assimile* we ever sampled (during five years) inhabited a very wet site in the centre of a deciduous forest (cf. DEN BOER, 1977).

P. oblongopunctatus did not show any temperature reaction in the spring of 1973, and only a very weak positive reaction in 1974. From a population dynamical point of view it will be especially important to know how individuals of this species – and of *A. assimile* – react upon spatial differences in surface humidity during reproduction. This will be the more so because provisional analyses already show, that even within our experimental forest these humidity differences may be considerable and appear to have a much higher predictive value than spatial differences in surface temperature, with which they generally do not seem to be correlated*.

It will be as important, however, to learn how different individual preferences are, for these differences might contribute greatly to spreading of the risks of larval development and thus to the stabilizing of the numbers of young beetles from year to year (compare: DEN BOER, 1968).

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* These provisional analysis (and many others, e.g. those concerning night activity: section 4) have been done by my wife Wil Daanje. They show the kind of relationships that could most probably be expected, which again enables me to program the final computer operations more effectively.

6. Because we individually marked a great number of beetles during a succession of years* we got many reliable data about the survival time of individuals. It thus appeared, that many individuals of *P. oblongopunctatus* and of *A. assimile*, which have reproduced in spring, survive summer, autumn and winter, to reproduce again in a second spring, and sometimes also again in a third one (Table 1). A few individuals even survive a fourth winter.

The lowest estimates in Table 1 were derived from the individuals that could be recognized directly by their mark, whereas in the highest estimates also the chance of being recaptured has been taken into account (since this chance will generally be underestimated – see section 1 – these latter values will be too high). When in 1976 we enclosed the whole catching area, by which nearly all individuals could be recorded and marked, we established that the lowest estimates in Table 1 must be at least 6–8 % too low, whereas many highest estimates appeared to be about 6–8 % too high. Hence, the actual survival of old beetles will be about halfway between the lowest and highest estimates – or still somewhat higher –, i.e. to the second spring in *P. oblongopunctatus* about 30 % in most years, and in *A. assimile* still higher. A still better survival of old beetles (at least in some years) was found in the spring breeder *P. coerulescens* (cf. BAARS, 1979).

Contrary to the spring breeders *P. oblongopunctatus* and *A. assimile* in the autumn breeder *N. brevicollis* survival of beetles until the next reproduction period hardly occurs (Table 1). In this way *N. brevicollis* must also do without the important levelling influence which the survival of old beetles may have on the fluctuations of numbers. Fig. 3 indeed shows that in *N. brevicollis* the numbers tend to fluctuate more violently than in *A. assimile* and *P. oblongopunctatus*; compare the fluctuation characteristics (cf. DEN BOER, 1971), logarithmic range (LR) and variance R (Var R) of these three species: Fig. 3. Without the survival of old beetles (and a somewhat higher production of young beetles, so that the mean density is maintained at about the observed level during these eight years) our spring breeders would also have shown more violent fluctuations of numbers: *P. oblongopunctatus*, LR = 1.0034 (instead of 0.8069) and Var R = 0.265 (instead of 0.1685); *A. assimile*, LR = 1.4473 (instead of 1.1107) and Var R = 1.1213 (instead of 0.3085).

7. *C. piceus* represents a special case: DEN BIEMAN (a student from Wageningen) found that young and old beetles reproduce at different times of the year. Young beetles reproduce soon after hatching, in July–August. Between 7 and 22 % of these young beetles survive the winter (Table 1) and reproduce again in the next spring, in May–June. VAN DIJK (1972) found a comparable – but less extreme – situation in the related

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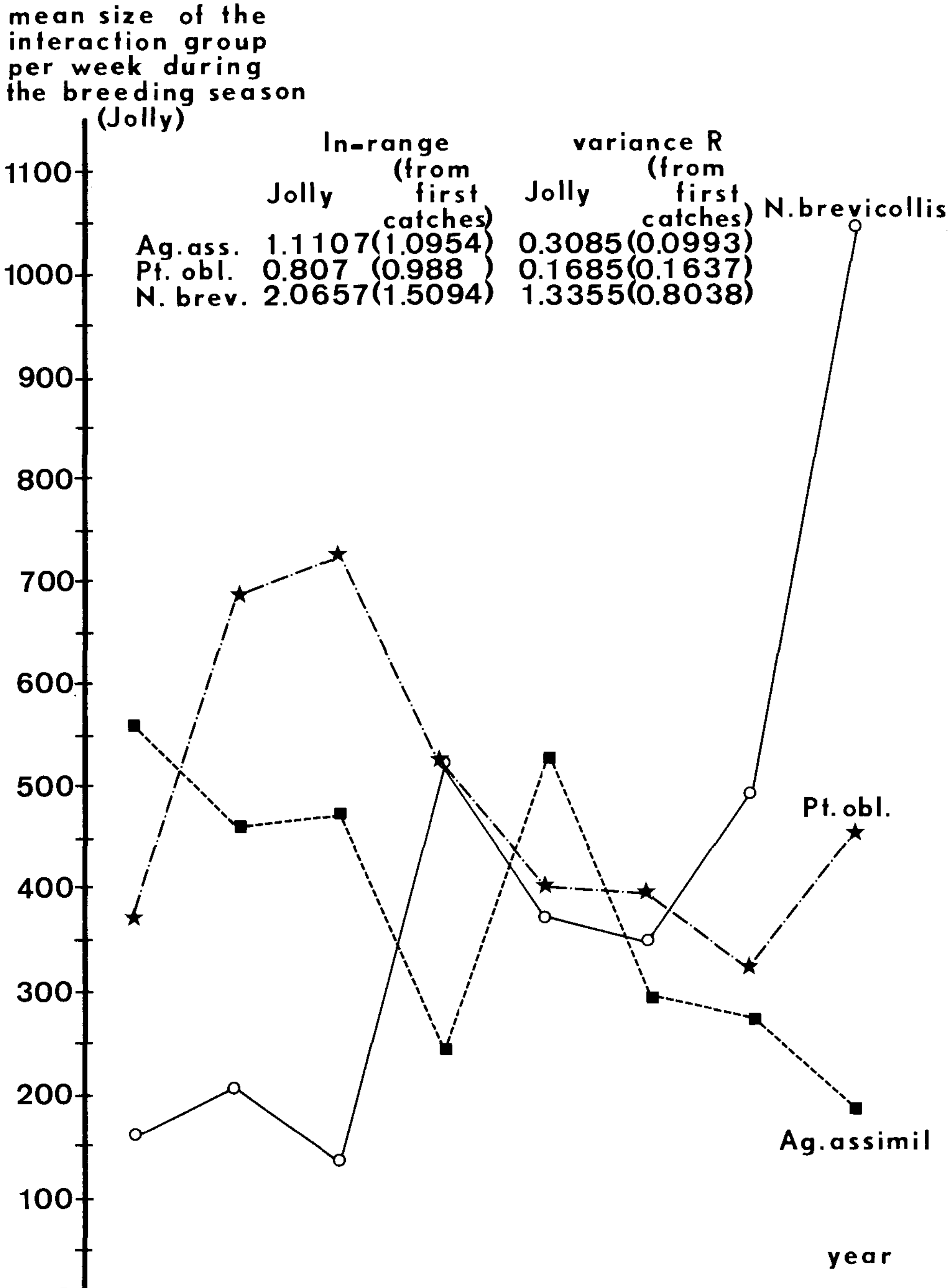
* During almost the whole period of ten years these markings were performed – and maintained often under difficult circumstances – by Arnold Spee (who also took the photographs and did the drawings for this paper). We make use of the technique of brand-marking, which was first described by SCHJØTZ-CHRISTENSEN (1965), and by which many thousands of beetles can be marked individually without loss of marks.

Table 1. Survival after the first breeding season in four carabid species of forests (lowest estimation–high estimation).

	Spring breeders			
	Pterostichus oblongopunctatus		*Agonum assimile*	
present in the population of	down to the 2nd breeding season	down to the 3rd breeding season	down to the 2nd breeding season	down to the 3rd breeding season
1968	17.0–58.9 %	?	18.0–41.2 %	?
1969	19.2–42.4 %	?	20.8–36.2 %	?
1970	11.0–33.6 %	2.3–7.4 %	16.6–35.0 %	2.1–4.5 %
1971	14.6–39.4 %	1.1–3.0 %	20.2–44.3 %	1.0–2.0 %
1972	11.7–30.1 %	0.5–1.3 %	15.5–33.2 %	4.0–8.5 %
1973	12.4–33.0 %	1.1–2.7 %	16.6–46.4 %	2.2–6.2 %
1974	13.6–36.4 %	0.7–1.9 %	13.8–35.5 %	2.4–6.1 %
1975	20.4–54.2 %	0.8–2.1 %	22.2–58.5 %	1.7–4.6 %

	autumn breeder		(spring) summer breeder	
	Nebria brevicollis		*Calathus piceus*	
present in the population of	down to the 2nd breeding season	down to the 3rd breeding season	down to the 2nd breeding season	down to the 3rd breeding season
1968	3.0– 6.3 %	?	?	?
1969	2.0– 4.9 %	(1.4–3.2 %)	8.3–33.2 %	?
1970	2.0– 3.4 %	0.4–0.7 %	4.7–19.5 %	1.2–4.9 %
1971	2.0– 3.9 %	0	6.3–32.0 %	0.7–3.4 %
1972	5.0– 9.7 %	0	4.5–30.6 %	0
1973	3.0– 6.5 %	0.3–0.6 %	2.0–11.6 %	0.7–4.1 %
1974	0.9– 1.8 %	0	2.8–14.6 %	0
1975	6.2–11.6 %	0.4–0.8 %	8.2–37.2 %	0.8–3.5 %



	ln-range Jolly	ln-range (from first catches)	variance R Jolly	variance R (from first catches)
Ag.ass.	1.1107	(1.0954)	0.3085	(0.0993)
Pt. obl.	0.807	(0.988)	0.1685	(0.1637)
N. brev.	2.0657	(1.5094)	1.3355	(0.8038)

Fig. 3. Changes in the size of the interaction group (averaged per week over the breeding season) during eight years for three carabid species of forest. The magnitude of the fluctuation of numbers is compared with ln-range (= ln greatest size minus ln smallest size) and with variance R (= variance net reproduction, i.e. variance of: size in year n/size in year n-1), both for Jolly-estimations and from first catches of individuals (compare Fig. 2).

C. melanocephalus on Schiermonnikoog: on the average overwintered individuals reproduce about one month earlier than young ones (in Drenthe in most years this difference is less, in *C. melanocephalus*). A further peculiarity of *C. piceus* is, that the reproductive season of the old beetles is nearly completely separated in time from that of the young beetles: when the young individuals start reproduction the few old beetles, that are still active, are already 'spent' again. Larvae born from eggs, that were laid early in spring, apparently have an uninterrupted development: at the end of August, when the young, reproducing beetles have already hardened their elytra, in most years once again a few callow beetles are caught. This somewhat unusual life-cycle among carabids may be connected with the fact, that *C. piceus* most probably is a comparatively new species in our regions (DEN BOER, 1962).

8. Among the four forest species studied *N. brevicollis* is remarkable because of the high level of locomotory activities shown by the non-reproducing stages (in this – and some other – respects it resembles the less abundant *Leistus rufomarginatus* Dfts., and possibly some other Carabinae). The first young individuals of this late-autumn breeder already hatch in May–June and are very active, allowing many hundreds to be caught and individually marked. After aestivation only about 40 % of these young beetles are recaptured, whereas in average 70 % of the individuals caught during the breeding period are still unmarked. Apparently, individuals of *N. brevicollis* are moving around in a much larger area than our experimental forest, and therefore the young beetles might make an important contribution to a thorough dispersal of the species. This was supported by enclosing the catching area in 1976: 58.6–68.4 % of the young individuals marked in spring were recaptured in autumn, whereas only 9.7 % of the beetles reproducing within the enclosed area were then unmarked.

Also the larvae – especially in the third stage – show a remarkably high level of locomotory activities, in this case during the winter. Part of the third stage larvae actively leave the forest, to return again early in spring (NELEMANS). To understand the life-cycle of *N. brevicollis* it may be important to note, that most other *Nebria*-species live under arctic and/or alpine conditions (see also: THIELE, 1969; TOPP, 1975).

9. As compared to the situation in *N. brevicollis* (section 8) the callow beetles of the spring breeders *P. oblongopunctatus* and *A. assimile* hardly show appreciable activities: in most autumns only some tens of callow individuals (of even less) are caught and marked (see also Table 2). Accordingly, the number of the young beetles that are then active is hardly correlated with the size of the population in the following spring. In order to find the significance of these locomotory activities it may be useful to note, that in most autumns also some marked individuals that have already reproduced in spring are moving around again. The latter are apparently unable to await inactively the next spring, possibly because they did not make enough fat (?). In any case – at least in *A. assimile* – the number of callow beetles active in autumn is positively correlated with the fraction of the old beetles that then reappear: $\tau = +0.67$ ($p = 0.025$, 7 years). There is

Table 2. Survival of the sexes.

Pterostichus oblongopunctatus

year	young beetles immediately after hatching in year n				the same young beetles during their first breeding in year n + 1				individuals in their 2nd (or later) breeding season in year n	
	estimation		recognized as callow		estimation		recognized individually		recognized individually	
(n)	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1968	159	166	104	110	67	65	44	54	23	13(*)
1969	100	80	18	16	35	33	4	4	71	37**
1970	32	36	9	17	14	9	5	3	101	39***
1971	58	46	37	26	10	8	7	5	115	63***
1972	28	54**	19	35(*)	6	10	5	6	87	27***
1973	31	22	19	9(*)	7	5	5	2	58	30**
1974	21	26	19	19	3	9(*)	2	8(*)	56	25**
1975	51	52	23	28					76	33***

Agonum assimile

year	young beetles immediately after hatching in year n				the same young beetles during their first breeding in year n + 1				individuals in their 2nd (or later) breeding season in year n	
	estimation		recognized as callow		estimation		recognized individually		recognized individually	
(n)	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1968	58	66	36	36	20	16	11	9	67	80
1969	63	65	18	15	27	27	3	7	90	105
1970	8	11	4	5	–	3	–	1	82	72
1971	30	31	14	18	7	14	3	8	92	70
1972	49	47	12	5	8	9	2	1	36	35
1973	15	17	7	4	4	8	1	2	72	72
1974	4	7	1	3	2	2	–	2	28	39
1975									41	33

(*) Nearly significantly different; * $p \approx 0.05$; ** $p \leqslant 0.005$; *** $p \leqslant 0.0005$

even a weak indication that this phenomenon is more apparent after a warm than after a cool summer ($\tau = +0.43$; $p = 0.119$).

10. In autumn equal numbers of young males and females are caught and marked of both *P. oblongopunctatus* and *A. assimile*: Table 2. During their first breeding period the sex ratio is still 1/1 in both species. Between the first and second breeding season, however, twice as many males as females of *P. oblongopunctatus* survive, whereas in *A. assimile* the survival of the sexes is then still similar: Table 2. It will be interesting to learn what causes this different mortality of the sexes in *P. oblongopunctatus*, since it may be connected with processes that significantly influence fluctuations of numbers. SZYSZKO (1976) suggests that the sex ratio in this species, which may again be different in different localities, might be connected with the favourability of the habitat.

The above are provisional notes on the population dynamics of four carabid populations studied for eight years, and we have discussed some first observations on relevant individual activities and preferences. During the same years VAN DIJK prepared the 'tools' with which these investigations will have to be continued, i.e. he developed the methods by which the egg-production of individual females and the survival of larvae can be measured under different sets of conditions (see his contribution to this volume, and VAN DIJK, 1979). First our observations on individual preferences will have to be worked out completely, and the experiments performed by which these reactions can be translated into individual chances to reproduce and survive (the latter especially during larval development). Then we can try to integrate all this data into simulation models which will have to produce the numerical changes of the interaction groups concerned as they were observed under the recorded field conditions.

REFERENCES

BAARS, M. A.: Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia (Berl.), **41,** 25–46 (1979).

DEN BOER, P. J.: The ecological significance of activity patterns in the woodlouse *Porcellio scaber* Latr. (Isopoda). Arch. Neerl. Zool. **14,** 283–409 (1961).

DEN BOER, P. J.: Vleugeldimorfisme bij loopkevers als indicator bij zoögeografisch onderzoek. Vakblad Biol. **42,** 110–119 (1962).

DEN BOER, P. J.: Fluctuations in morph frequency in catches of the ground-beetle *Pterostichus oblongopunctatus* F. and its ecological significance. Belmontia **13** II: Ecology (1968). Can be obtained from the Biological Station, Wijster.

DEN BOER, P. J.: Stabilization of animal numbers and the heterogeneity of the environment: The problem of the persistence of sparse populations. Proc. Adv. Study Inst. Dynamics Numbers Pop. (Oosterbeek, 1970), 77–97 (1971).

DEN BOER, P. J.: Dispersal power and survival: Carabids in a cultivated countryside. Miscell. Papers L.H. Wageningen **14,** 1–190 (1977).

JOLLY, G. M.: Explicit estimates from capture-recapture data with both death and immigration. Stochastic model. Biometrica **52,** 225–247 (1965).

NEUDECKER, CH.: Untersuchungen zur Steuerung der Jahresrhythmik, der Aktivität und zum Präferenzverhalten gegen Temperatur, Feuchtigkeit und Licht bei *Agonum assimile* Payk. (Col. Carabidae). Diss. Köln, 82 p., 33 Abb. (1972).

SCHJØTZ-CHRISTENSEN, B.: Biology and population studies of *Carabidae* of the *Corynephoretum*. Natura Jutlandica, **11,** 173 p. 89 tables (1965).

SEBER, G. A. F.: The estimation of animal abundance and related parameters. Griffin, London, 506 p., 1973.

SOUTHWOOD, T. R. E.: Ecological methods. Methuen, London 391 p. 3rd print, 1976.

SZYSZKO, J.: Male-to-female ratio in *Pterostichus oblongopunctatus* (Coleoptera, Carabidae) as one characteristic of a population. Pedobiol. **16,** 51–57 (1976).

THIELE, H. U.: The control of larval hibernation and of adult aestivation in the Carabid beetles *Nebria brevicollis* F. and *Patrobus atrorufus* Stroem. Oecologia (Berl.) **2,** 347–361 (1969).

TOPP, W.: Biozönotische Untersuchungen in einem Kar der östlichen Hohen Tauern. Carinthia **II,** 165–185 (1975).

VAN DIJK, TH. S.: The significance of the diversity in age composition of *Calathus melanocephalus* L. (Col., Carabidae) in space and time at Schiermonnikoog. Oecologia (Berl.) **10,** 111–136 (1972).

VAN DIJK, TH. S.: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. (Coleoptera, Carabidae). Oecologia (Berl.) **40,** 63–80 (1979).

REPRODUCTION OF YOUNG AND OLD FEMALES IN TWO CARABID BEETLES AND THE RELATIONSHIP BETWEEN THE NUMBER OF EGGS IN THE OVARIES AND THE NUMBER OF EGGS LAID

TH. S. VAN DIJK*

Biological Station of the Agricultural University (Wageningen).
Wijster, Kampsweg 27, 9418 PD, The Netherlands

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ABSTRACT

In many ecological studies on carabid beetles the amount of reproduction of a population is often considered to be a rather fixed characteristic. However this paper emphasizes the large variability of this characteristic caused by individual differences and even more so by environmental factors such as food and temperature. In this connection the use of the number of eggs in the ovaries as a measure for the amount of reproduction is criticized. For a correct estimate of the amount of reproduction of a (sub)population it is necessary to determine exactly the egg-production of many single individuals. In this way reliable values for the variability of such population characters can be obtained, which are again needed in comparative studies on the differences between and changes in (sub)populations.

1. INTRODUCTION

In comparative ecological studies the amount of reproduction is often considered a character of a population (or a species), such as: 'high breeders' or 'low breeders'. Besides the question whether the amount of reproduction of carabid beetles should be defined as the number of eggs laid or as the number of eggs in the ovaries, it is necessary to study critically what kind of information can be obtained from such measurements of reproduction in carabid beetles.

To get a reliable estimate of the amount of reproduction, the total number of eggs laid by many individual females of different ages should be determined. The number of eggs was determined continuously from the start of the reproduction period in one group of females kept at constant temperatures in laboratory experiments, and in females sampled weekly during the whole reproduction period and kept under field (i.e. changing) conditions in a culture house outside the laboratory for a period of one or more weeks.

*This paper could only be accomplished because of the daily and intensive assistance of Mr. Y. Jongema in all the experiments.

In this way the influence of several factors on the amount of reproduction as well as the relationship between the number of eggs in the ovaries and the number of eggs laid is studied, and will be discussed in this paper.

Moreover, it was possible to verify whether the amount of egg production of a population of carabid beetles is indeed of a rather fixed character, or a highly variable quantity as was expected because it results from the reproduction of many different individual beetles living in an environment that is changing daily.

2. MATERIAL AND METHODS

The amounts of reproduction of *Pterostichus coerulescens L.* (a spring breeder and day-active) and of *Calathus melanocephalus L.* (an autumn breeder and night-active) have been determined during several years.

2.1. The estimation of the amount of reproduction in P. coerulescens

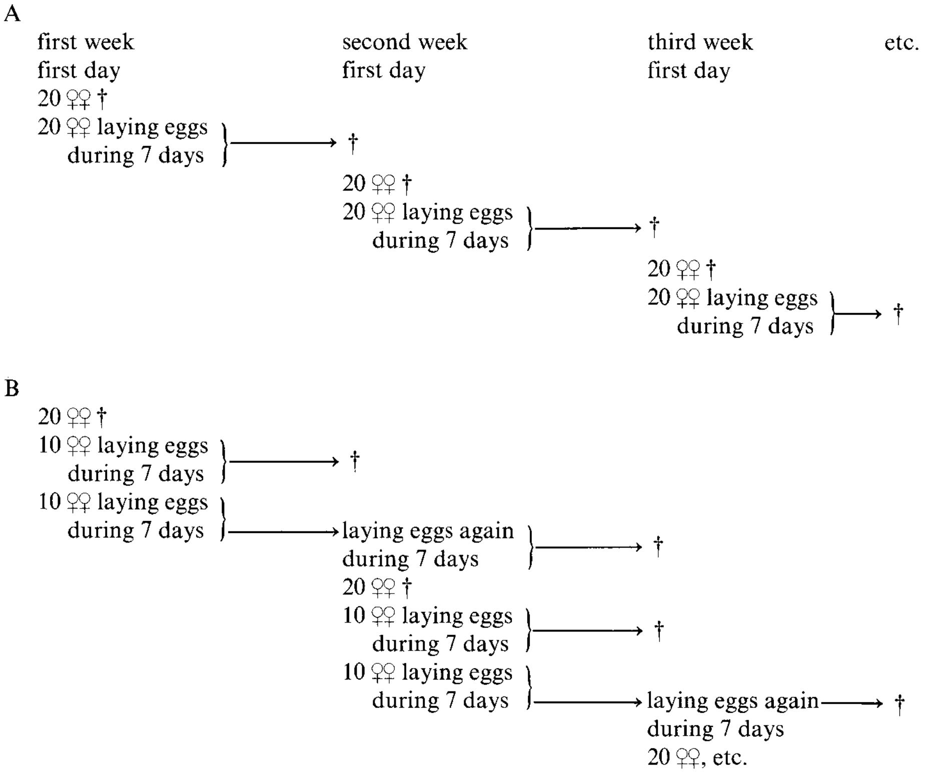
Starting on 21 April 1975 every week two groups of beetles were sampled from the same place at Kralo Heath. One group of 20♂♂ and 20♀♀ were kept during one week in 20 glassjars with some peat (1♂ + 1♀ per glass) outside in a culture house under the daily changing temperature conditions of the field ('outside' experiment). The beetles were fed three times a week with pieces of mealworm. After 7 days the beetles were killed and the number of eggs in the ovaries counted (Fig. 1A).

At the same time the number of eggs laid by each female was estimated (for the method, cf. VAN DIJK, 1979). The second group of 20 ♀♀ (Fig. 1A) were killed immediately after sampling to determine the total number of eggs in the ovaries at the moment the first group in our experiment started egg-laying. In this way every week the number of eggs in the ovaries of females collected in the field was known together with the number of eggs laid by each individual female in one week. The number of eggs in the ovaries after the egg-laying under field conditions and with optimal food (culture house) was also known.

The beetles were fed optimally because starvation of three or more days greatly influences reproduction (cf. 3.3.). In the field and over a ten year period starvation only occured once namely in 1976. Besides, it is difficult to quantify food between an optimal situation and starvation.

In 1975 the females were laying few eggs (cf. 3.1.), and to be sure that this was not caused by too early killing (after 7 days) the experiment was repeated in 1976, starting on the 21st of April, but now it was enlarged by adding a third group of beetles which were allowed to live on for 14 days; after the end of egg-laying these females were then also killed (Fig. 1B). Halfway this period (i.e. after seven days) the eggs were counted and taken away (for method, cf. VAN DIJK, 1979). In 1977 this experiment was repeated for a third time.

Figure 1. Scheme of the weekly sampling of females that either laid eggs during one week (A + B) or during two weeks (B) after which they were killed, or were already killed at the start of the week.



2.2. *The relationship between temperature and egg production*

In 1976 (starting on 29 April) the relationship between temperature and egg production was determined by counting the number of eggs every week laid by each of 5 groups of females kept in glasses with peat (1♂ + 1♀ per glass) at 5 different temperatures viz. 8.5, 15, 20, 25 and 30°C. All the beetles were fed three times a week.

2.3. *The relationship between food and egg production*

In 1975 two experiments were executed to determine the relationship between starvation and egg development resp. egg production. On 21st May a number of beetles was sampled from Kralo Heath and divided in 7 groups of 1 ♂ and 7 ♀♀ each. All the beetles were fed every day until 26th May, after which feeding was stopped. One group of females was dissected on 26th May to determine the number of eggs in the ovaries (control group), after which every two or three days another group was dissected and the number of eggs counted. This type of experiment was repeated starting on 6th June 1975.

In 1978 again every week a group of 10 females was sampled from the field (cf. 2.1.). The beetles were treated in the same way as in 1975, but did not get any food. At the end of every week these 10 females were killed and dissected. The number of eggs in the ovaries together with the number of eggs laid in the preceding week could only be related now with the quantity of food taken in the field before sampling. The females stayed maximally two days in the pitfalls before they were collected.

2.4. *The relationship between age and egg production*

Starting in 1976 with 30 ♂♂ and 30 ♀♀, over a period of two or three years – dependent on the females surviving the winter in the field – every week egg-laying of each female was estimated in the laboratory at 19°C. After reproduction was over

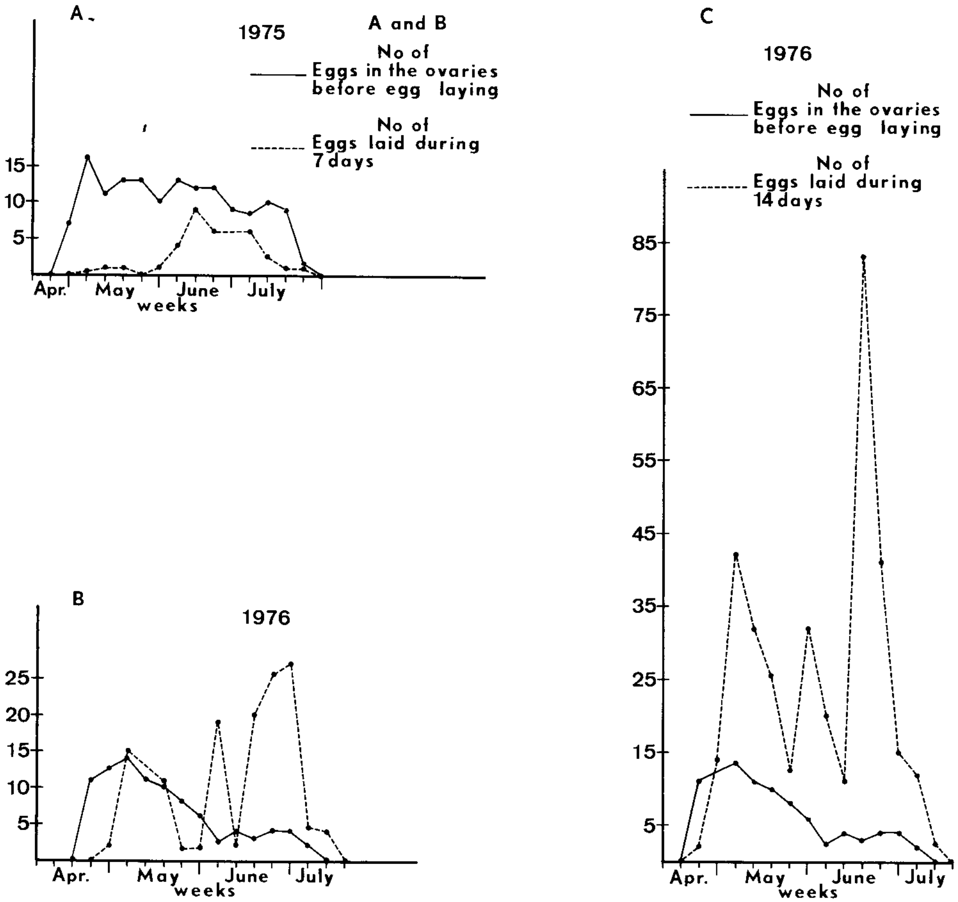


Fig. 2. *P. coerulescens*: the number of eggs in the ovaries and the number of eggs laid during the reproduction period.

the beetles were released inside fences to overwinter and were recaptured the next year at the start of reproduction (for details, cf. Van Dijk, 1979).

2.5. As to *C. melanocephalus* the same types of experiments were executed as described in 2.1. and 2.4., starting in the last week of July or the first week in August, with the aim of comparing the reproduction of an autumn breeder with that of a spring breeder. Because we had to restrict ourselves, these experiments will not be discussed here and only some results will be mentioned for comparison with *P. coerulescens.* The experiments with *C. melanocephalus* will be treated more extensively in a seperate paper.

3. RESULTS

3.1. The relationship between the number of eggs in the ovaries and the number of eggs laid in P. coerulescens.

In 1975 during the whole month of May eggs were present in the ovaries, but none or only very few eggs were laid (Fig. 2A). Only during the last half of the reproduction period eggs were laid (starting in the second week of June). Rank-correlations were calculated weekly between the number of eggs laid by every female during different weeks and the number of eggs in the ovaries at the end of each week; only very incidently did we find a positive and significant correlation (when combining the S-values and variances for different weeks, no significant correlation was found either: $z = 1.45$, $\bar{\tau} = 0.12$, $p = 0.073$). Moreover, no correlation was found between the mean number of eggs in the ovaries before egg-laying started and the number of eggs laid in the next week (only for the last 7 weeks a rather good correlation was established: $r = 0.74$, $df = 5$, $p \approx 0.05$). A great individual variation appeared to exist in the numbers of eggs in the ovaries and in the number of eggs laid within one week, as well as between the weeks.

The main conclusions from this experiment are, that:

a. when the females have eggs in the ovaries, it does not follow as a matter of course that at the same time they are laying eggs (during the whole month of May no eggs were laid). Hence, the reproduction period should be defined as the period in which eggs are actually laid, and not as the period in which the females have eggs in the ovaries.

b. the temperature at which egg-development starts and continues is apparently different from that at which the eggs are laid (cf. 3.2.).

c. as a consequence of the first two points the number of eggs in the ovaries is not correlated with the number of eggs laid.

However, to be sure that the situation in 1975 was not an exceptional one we repeated the experiment in 1976 (cf. 2.1.). In that year, contrary to 1975, egg-laying started immediately at the end of April, whereas also a rapid decline in the numbers of eggs in the ovaries was observed. In the same period many eggs were laid in the

'outside' experiment (Fig. 2B). These two years thus appeared to be quite opposite to each other, viz.:
in 1976, when the numbers of eggs in the ovaries were very low (June, July), many eggs were produced, whereas in 1975, when the numbers of eggs in the ovaries were high (May) almost no eggs were laid. Hence once again we can conclude, that the reproduction period of a carabid beetle is not necessarily the period in which the females have eggs in the ovaries. And once again, no relationship will occur between the numbers of eggs in the ovaries and the number of eggs laid (tested in the same way as in 1975: Kendall combination test: $z = 1.19$, $\bar{\tau} = 0.10$, $p_L = 0.117$).

Finally, under the same food conditions as in 1975, in 1976 a much higher number of eggs was laid by the same number of females.

Both the early start of egg-laying and the high egg production in 1976 were apparently caused by the higher temperatures in 1976 as compared with those in 1975 (cf. 3.2.).

In 1977 we once more repeated this type of experiment, but again no relationship between the number of eggs in the ovaries and the eggs laid was found, as contrasted with *C. melanocephalus*, in which both in 1975 and in 1976 a good correlation between the number of eggs in the ovaries before egg-laying and the number of eggs laid was found (in 1975 $r = 0.74$, $df = 8$, $p < 0.02$; in 1976 $r = 0.90$, $df = 10$, $p < 0.001$).

3.2. *Influence of temperature on the amount of reproduction*

Our results during the last four years have shown that in the 'outside' ex-

Table 1. Mean maximum temperatures and the mean day temperatures (measurements every hour of a natural day) per week between March and July at Eelde.

	Mean maximum temp.				Mean day temp.			
weeks	1975	1976	1977	1978	1975	1976	1977	1978
1/4–7/4	6.4	11.0	7.8	9.8	2.8	6.9	4.5	5.6
14/4	7.9	14.2	7.6	8.0	4.6	7.3	3.2	4.0
21/4	12.5	14.3	9.9	12.2	8.0	8.0	5.2	6.8
28/4	12.8	10.4	12.9	11.7	8.6	5.3	9.0	6.8
5/5	13.8	13.0	14.7	17.3	9.3	8.0	10.3	11.3
12/5	14.5	24.1*	14.7	14.3	10.6	16.3*	10.0	10.0
19/5	16.7	19.7	14.8	14.6	12.1	12.8	10.0	9.3
26/5	13.6	17.1	19.0*	14.1	9.2	12.0	12.8*	11.3
2/6	13.6	14.4	16.6	25.6*	8.4	11.2	10.8	17.2*
9/6	18.8*	21.0	15.9	22.9	12.9*	14.9	11.6	17.2
16/6	21.2	20.8	24.1	16.2	15.3	15.6	17.2	12.1
23/6	22.7	21.0	17.4	20.8	16.9	15.2	13.5	14.1
30/6	18.4	28.6	18.4	15.1	13.8	21.5	13.7	12.1

*The temperature at which reproduction started in the 4 succeeding years.

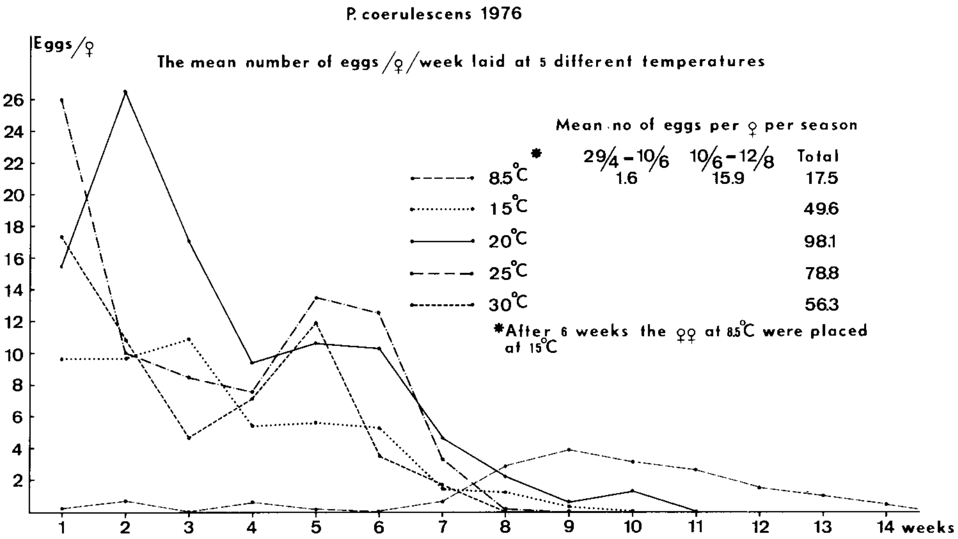


Fig. 3

periment egg-laying only started if in a certain week the mean maximum temperature per week reached or exceeded 19–20°C (or the average temperature in 24 hours reached or exceeded 13°C or more): Table 1. Below this mean temperature only an incidental female starts reproducing. This is confirmed by our temperature experiments, by which it could be shown that below a constant temperature of 10°C none or only a few eggs were laid, whereas egg-laying started immediately when the temperature was raised (Fig. 3). It may be concluded, that not only the sequence of short day followed by long day is needed for the development of the ovaries of *P. coerulescens* (KREHAN, 1970; THIELE, 1977), but also that certain temperatures must be exceeded.

During the whole reproduction period of 1976 the mean maximum temperature per week was highly correlated with the weekly number of eggs laid per ♀ ($r = 0.85$, $p = 0.01$). It may thus not only be concluded that below a certain temperature (8 to 9°C) no eggs are developed in the ovaries, but also that eggs are only laid after a certain temperature-total has been reached (MOLS, personal communication; BURSELL, 1974; ENGELMANN, 1970). This means, that the higher the temperature in early spring the sooner egg-laying will start, although the length of the period of egg-laying is not clearly influenced by temperature (in contrast with *C. melanocephalus*, in which a high positive correlation between temperature and the length of this period was found; cf. VAN DIJK, 1979). The length of the period of egg production of *P. coerulescens* is much more influenced by the age of the beetles (cf. 3.4.).

The number of eggs laid not only depends on the temperature, but also on the amount of food the females can get (or as in our experiments is offered to the beetles; cf. 3.3.).

Table 2. *P. coerulescens:* The difference between the mean number of eggs per 10 ♀♀ per week in the first part and in the second part of a 14 days egg laying-period in 1976 respectively. The reproduction period has been divided in two parts of 5 weeks each.

3 May until 7 June The mean number of eggs per 10 ♀♀ in the first week	 in the sec. week	7 June until 12 July The mean number of eggs per 10 ♀♀ in the first week	 in the sec. week
155.6 ± 93.12	109.2 ± 41.50	158.2 ± 146.00	221.0 ± 141.22

To show that the amount of egg production is especially determined by temperature, we tried to predict the numbers of eggs laid every week in the 'outside' experiment. To this end the graphs of Fig. 3 were used which show the mean number of eggs laid per female under constant temperature conditions in the successive weeks of the reproduction period, to calculate (by linear interpolation) the numbers of eggs which should be laid under influence of the changing maximum temperatures that were measured in the 'outside' experiment (in *C. melanocephalus* – a night active species – we used the differences between the daily minimum and maximum temperatures for this calculation). It thus appeared that, when the females were fed optimally, these predictions were very accurate for both species (for example, in *C. melanocephalus* in 1976: 86 eggs/♀/season predicted, and 85 eggs/♀/season actually laid).

3.3. The relationship between food and egg production

As indicated in section 2.1., in 1976 we also observed groups of females for 14 days. It was found, that the mean number of eggs laid per ♀ per day was somewhat higher in the second week (2.4 eggs per ♀ per day) than in the first week (1.7 eggs per ♀ per day). In fact, when the reproduction period of 1976 is divided in two parts of 5 weeks each (5 weeks from 3/5–7/6 and from 7/6–12/7 resp.) the above differences appeared to be found especially in the second part of the reproduction period (Table 2).

We have reasons to conclude that in 1976 the beetles were underfed when they were sampled from the field, so that because of the feeding in our experiment

Table 3. *P. coerulescens:* The mean number of eggs laid per ♀ per week in three succeeding years.

year	the mean max. temp. during the period May, June and July	the mean number of eggs per ♀ per week
1975	18.8 °C	2.7
1976	21.5 °C	8.8
1977	18.4 °C	2.0

new eggs were immediately developed, and were laid after some days. Especially in June, 1976 almost no eggs were present in the ovaries, whereas in the 'outside' experiment (cf. 2.3.) within one week (and especially during the second week) many eggs were laid (Fig. 2B, 2C).

Because of the high temperatures in 1976, especially at the end of June and during July (Table 1), in the 'outside' experiment a much higher number of eggs could be developed in one week than in the same period of 1975 in the same type of experiment: Table 3.

Especially at high temperatures new eggs develop very rapidly (cf. also the paper of P. MOLS). Apparently, in 1976 it was very difficult for the females to get enough food in the field during the periods with high temperatures (most small arthropods retired deeper into the soil), and as a consequence a reversed process started, viz: stopping of egg development and/or starting of egg resorption. In fact, even in June and July, 1976 a high percentage of the females had 'spent' ovaries, which is an indication of food shortage. The latter was shown in experiments, in which females, sampled from the field, were fed during 4 days and then starved (Table 4). After 7 days almost all females were spent or had only a single egg in the ovaries. The same results were reached with *Agonum fuliginosum* in starvation experiments (MURDOCH, 1966). From the start 7 ♀♀ of the starvation groups were dissected every two days to determine the reaction (Table 4). It may be concluded that both the increase and the decrease of the number of eggs in the ovaries are very rapid processes depending on temperature and on the quantities of food taken.

Table 4. Influence of starvation on the number of eggs in the ovaries.

A. 7 groups of beetles (1 ♂ + 7 ♀♀ each) were fed between 21/5 and 26/5, 1975.
Start of starvation: 26/5/'75.
Mean number of eggs on the day(s)

at the start of starvation	after the start of starvation					
26/5	27/5	29/5	2/6	4/6	6/6	9/6
19.3	16.0	14.9	6.4	0.6	4.9	1.9

B. 4 groups of beetles (2 ♂ + 8 ♀♀ each), fed between 6/6 and 9/6, 1975.
Start of starvation: 9/6/'75.
Mean number of eggs on the day(s)

at the start of starvation	after the start of starvation		
9/6	12/6	14/6	18/6
22.8	12.8	1.4	1.3

As expounded in 3.1. in 1976 we also did not find any relationship between the number of eggs laid during a week and the number of eggs in the ovaries after that week. But in 1975 in our 'outside' experiment we also followed groups of females for 14 days after sampling from the field (cf. 2.1. and Fig. 1B). In these groups the numbers of eggs laid in the second week were indeed correlated to the numbers of eggs in the ovaries after the 14 days ($z = 2.63$, $\bar{\tau} = 0.22$, $p_L = 0.004$). Hence, only under special food conditions (excess of food) is this relationship realized. Because the beetles from the field are generally not satisfied, the number of eggs in the ovaries will readily change at any moment, depending on the frequency of encounters with food, by which the number of eggs in the ovaries is not representative for the number of eggs laid. In 1978

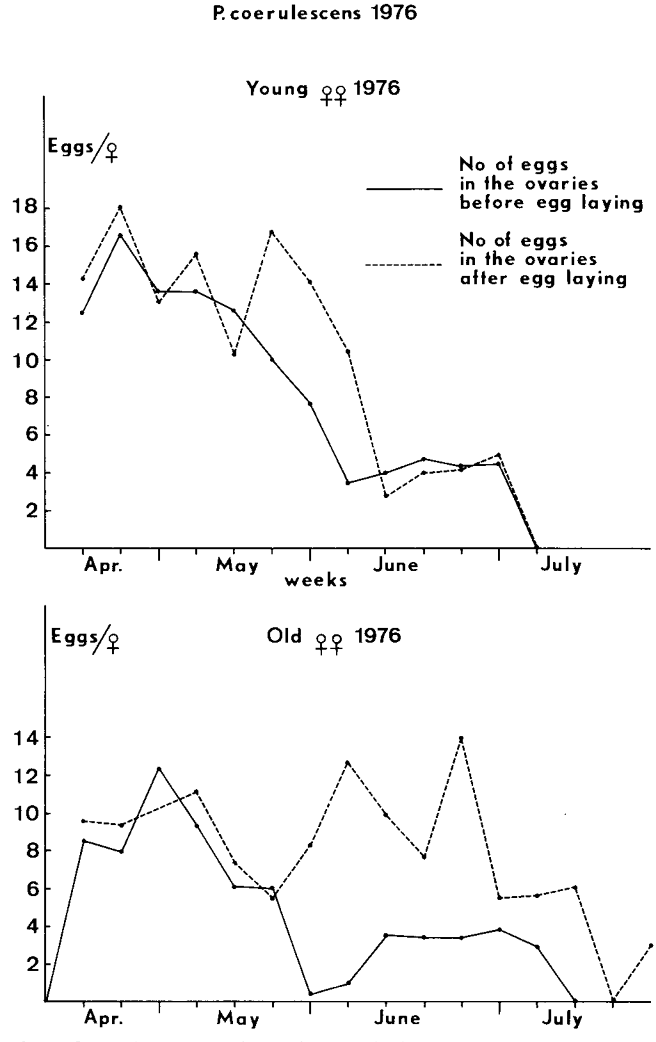


Fig. 4: The number of eggs in the ovaries before and after egg laying.

we did the same experiments as in the previous three years, but now the females did not get any food (cf. 2.3.). The result was, that during the first two to three days most females did not lay eggs or only very few (1.2 egg/♀/week) and there was not even a slight relationship between the number of eggs in the ovaries and the eggs laid.

A further conclusion is, that although *P. coerulescens* generally does not suffer from food shortage on Kralo Heath, the beetles are apparently never satiated, and therefore will eat more if the opportunity arises. It will be clear that this situation will promote a high level of individual variability in the number of eggs in the ovaries both in time and space.

As to *C. melanocephalus* it has been established that the beetles are generally better satiated and that therefore the above relationship could be found in this species.

3.4. The significance of the age of the beetles for the level of reproduction

The ovaries of the females contained almost no eggs in June/July 1976. But when we kept these females for a period of 14 days with food in our 'outside' experiment, it was ascertained that only the old females were able to recommence egg development, resulting in a rather high number of eggs in the ovaries at the end of the 14-days period (Fig. 4). The young beetles on the contrary were unable to do this and so most young females were 'spent' at the end of the 14-days feeding. Apparently, if the conditions remain suitable, the old beetles can reproduce during a longer period than the young ones and only the old beetles can recommence egg development after an unfavourable period.

From our experiment with 30 young beetles that were followed for three years (cf. 2.4.) it appeared that the older the beetles the longer their egg-laying period and the higher the number of eggs laid per female per week (Table 5). In fact, at the same temperature the old beetles start to reproduce some days earlier than the young ones. Hence, the longer the beetles survive the greater will be their individual contribution to reproduction. Apart from the above results several other conclusions may be drawn from this experiment:

At first, like in all other experiments, even in those with a constant temperature, the number of eggs laid per female per week is highly variable (at the start of reproduction the standard deviation of the number of eggs is about as large as the mean and in the middle of the reproduction period about half the mean): Table 6.

Secondly, if females start with a high or low egg production respectively they more or less maintain this level during all the weeks of the breeding period, although a rather high variation will remain between the number of eggs laid per week (VAN DIJK, 1979): Table 6.

Thirdly, the females with the highest mean number of eggs laid per week also have the longest period of reproduction in weeks.

The position of individual old beetles in the population may thus be important, and as shown in Table 7 even three or four year old beetles are present in our populations (see also BAARS, 1979). However, a high or low number of old beetles in a population is

Table 5. *P. coerulescens:* The number of eggs laid in three succeeding years by the same females (young in 1976) at 19 °C.

	The number of eggs in						Total No of eggs
	1976	† in winter	1977	† in winter	1978		
1	0		92		0	†	92
2	0	†	–		–		
3	1		3		224		228
4	1		98		59	†	158
5	3		72	†	–		
6	5		61		164		230
7	9		2		94		105
8	11		5		87		103
9	25		18		31	†	74
10	42	†	–		–		
11	45		89		171		305
12	48		276		291		615
13	72		50		169		291
14	79		1	†	–		
15	79		10		204		293
16	81		88		278		447
17	83		169	†	–		
18	93		215	†	–		
19	93		32		292		417
20	95	†	–		–		
21	112		87		0	†	199
22	115		17		89		221
23	119		280		146		545
24	122		114		114		350
25	124		95	†	–		
26	128		54		70	†	252
27	134		252		0		386
28	147	†	–		–		
29	197	†	–		–		
30	261		315		98		674
Σ of eggs	2324		2495		2581		5985
x̄	77.5 ± 63.63		99.8 ± 96.29		129.05 ± 94.10 (151.82 ± 82.71)		
No of ♀♀	30		25		20		
Σ of eggs for 20 ♀♀	1461		1943		2581		5985
x̄. 20 ♀♀	73.1 ± 65.84		97.2 ± 100.98		129.05 ± 94.10 (151.82 ± 82.71)		299.3 ± 172.39

(between brackets x̄ without ♀♀ not laying eggs)

Table 6A. *P. coerulescens*, young females: The number of eggs laid by each female at 19 °C in the successive weeks of the breeding period of 1976 (see also the anova table 6B).

	Total number of eggs laid																											
	0	0	1	1	3	5	9	11	25	42	45	72	79	79	81	83	93	93	95	112	115	119	122	124	128	134	147	261
week																												
1	0	0	1	0	0	0	0	0	0	0	16	0	0	1	0	0	21	0	3	0	22	0	4	0	0	0	0	20
2	0	0	0	1	1	3	4	0	3	1	24	8	37	2	20	8	23	26	39	3	39	31	46	33	21	42	24	40
3	0	0	0	0	2	1	5	8	10	7	3	26	32	20	33	36	15	21	15	4	21	39	29	41	32	37	36	51
4	0	0	0	0	0	1	0	3	12	8	2	18	10	31	14	18	19	36	23	17	24	26	24	24	28	24	37	38
5	0	0	0	0	0	0	0	0	0	22	0	15	0	18	13	18	15	10	15	21	9	18	19	24	25	26	43	41
6	0	0	0	0	0	0	0	0	0	4	0	0	0	7	1	3	0	0	0	18	0	5	0	2	18	5	7	32
7	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	29	0	0	0	0	4	0	0	33
8												0								15					0	0	0	6
9																				5								0
10																				0								

Table 6B. Anova table. (for data cf. Table 6A)

source of variation	DF	SS	MS	Expected MS	F_s
among groups (between ♀♀)	27	17045.5	631.31	$\sigma^2 + n\sigma^2_A$	$\frac{631.31}{70.08} = 9.01$
within groups [replicates in time of the number of eggs in 4 succeeding weeks (week 2–5) of each female]	84	5886.5	70.08	σ^2	
Total	111	22932.0			

σ^2_A = the added variance component due to differences between ♀♀ (for explication cf. Sokal and Rohlf, 1969).
$F_{0.001}$ [30.120] = 2.26 $F_{0.001}$ [24.60] = 2.69
There is a highly significant added variance among ♀♀ as to the number of eggs laid.

$S_A{}^2 = {}^1/n\,(631.31-70.08) = 140.31$ $S^2 + S^2_A = 70.08 + 140.31 = 210.39$
$S_A{}^2$ = 66.7% of this sum. Much more variation occurs among groups (the numbers of eggs of ind. ♀♀) than within groups (the number of eggs in the succeeding weeks of one ♀).
R_I = coefficient of intraclass correlation = 66.7%.

Table 7. Survival of *Pterostichus coerulescens*, estimated with marked individuals in the field between 1974 and 1978.

Released as 1 year old beetles in the reproduction periods of 1974 and 1975 resp.	Recaptured as 2, 3 or 4 years old beetles in the reproduction periods of 1976, 1977 and 1978		
	2e years	3e years	4e years
240 exx	131 (54.6%)	27 (11.3%)	7 (2.9%)

Survival of *Calathus melanocephalus*, estimated with marked individuals in the field between 1975 and 1978.

Released as 1 year old beetles in the reproduction period of 1975	Recaptured as 2 or 3 years old beetles in the reproduction periods of 1976, 1977 and 1978		
	2e years	3e years	4e years
200	94 (47%)	53 (26.5%)	1 (0.5%)

1 year old beetles = beetles reproducing for the first time
2 year old beetles = beetles reproducing for the second time in the next year
etc.

not simply related to the amount of reproduction of that population (VAN DIJK, 1979). Summarizing, the old beetles especially the two and three year old ones may be very important in the populations, because they can start reproduction at lower temperatures, and if they survive the whole breeding period under optimal conditions (much food and optimal temperatures) they can produce a higher number of eggs than the young ones and for a longer period. Hence, young and old beetles react differently to environmental conditions with low or high levels of reproduction.

4. SUMMARY AND DISCUSSION

It is difficult to estimate the amount of reproduction of such carabid beetles as *P. coerulescens*, since for several reasons as shown in this paper it is incorrect to use (especially within a rather short period of one breeding season) the number of eggs in the ovaries as a measure of egg production (compare e.g. MURDOCH, 1966a, b; LUFF, 1973). The possible occurrence of such a relationship over longer periods e.g. when comparing the amount of reproduction of one population in succeeding years, is now being studied. Also the assumption of a constant oviposition rate per species during the whole breeding season is not realistic (GRÜM, 1972).

In *P. coerulescens* only under special food and temperature conditions a relationship between the number of eggs in the ovaries and the number of eggs laid could be obtained. In *C. melanocephalus*, however, such a relationship occurs more generally. The difference in the time of activity between these two species (resp. by day and at night) may be a possible explanation (see below). At Kralo Heath individuals of *P. coerulescens* are generally not satiated and will therefore eat more if abundant food is available, especially at higher temperatures (as in our experiments), after which many eggs can be produced. On the other hand, the beetles from the field are not starved; if they were, we would find many 'spent' females in the field during the reproduction period (as can be concluded from our experiments cf. 3.3.). On the contrary, during the breeding season spent females are only present in very low percentages in field populations (with the single exception, recorded so far, the summer of 1976). The increase and decrease of the number of eggs in the ovaries are very rapid processes, generated especially by the temperature and by food consumption. Because every individual beetle will be in a state somewhere between satiation and hunger (cf., also WHITE, 1978) it will react very sharply upon each change in temperature and in the availability of food both of which vary greatly in time and space in the localities where *P. coerulescens* is active. Hence a high temporary variation in the egg production of individual females (and of whole subpopulations) as well as between individual females (and between whole subpopulations) could be expected.

The *C. melanocephalus* beetles from Kralo Heath are much better fed, and a further improvement in the availability of food will generally not be followed by a significant increase in number of eggs. This situation together with more even night temperatures is very different to the daytime situation of *P. coerulescens*. This may be an explanation of the more general existence of a relationship between numbers of eggs in the ovaries and the number of eggs laid by *C. melanocephalus* as compared with *P. coerulescens*.

Not only in the field, but also under constant conditions (food and temperature) the individual egg production varies highly, but in spite of this variation it is possible to roughly distinguish groups of females with a high or low mean egg production per week respectively. LUFF arrived at a same conclusion for *Pterostichus madidus*, although he supposed, that some exceptional factors such as parasitism by nematodes caused low egg production in some females (LUFF, 1973). The females with a high mean egg production per week also lay eggs during more weeks than the other females.

The start of egg-laying is influenced highly by temperature (in 1976 egg production started 4 weeks earlier than in 1975), and also in this respect individual females react differently. Especially old females may start some days earlier than the young ones. Moreover, in our experiments the length of the reproduction period in weeks was much greater in old females than in young ones (especially in *P. coerulescens*, but also in *C. melanocephalus*). In *C. melanocephalus* a high correlation exists between the length of the reproduction period and the temperature. Finally, the old females of *P. coerulescens* lay a higher number of eggs per week than the young ones.

In contrast with the literature (cf. THIELE, 1977) the percentage of old individuals (2–4 years old) in a population can be very high (up to 80 %) in *P. coerulescens*, but also in *C. melanocephalus* (especially two year old beetles): BAARS (1979); see also the contribution of DEN BOER to this volume. Hence, in connection with the above differences between old and young beetles the age-composition of a population of carabid beetles has an important influence on egg production.

A complex of factors (some are discussed in this paper) causes a high variation in both the number of eggs per week per female, the length of the reproduction period, and the time of commencing of the reproduction, which will again influence the changes in numbers of individuals within (and between) subpopulations. Hence, the amount of reproduction of a population cannot be considered as a fixed quantity (not varying in time and space), by which the value of statements about level of reproduction of populations (species) in comparative ecological studies cannot be high. A significant part in the process of evolution is played by the variation in many characters between the individuals within (sub)populations. By comparative studies of the differences and changes in the amount of variation of various characters (especially those of ecological significance) between (sub)populations can lead to a deeper insight into this process.

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REFERENCES

BAARS, M. A.: Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia (Berl.), **41**: 25–46 (1979).

BURSELL, E.: Environmental aspects – temperature, p. 1–41. In the physiology of Insecta sec. ed., vol. II, ed. M. Rockstein. London: Academic Press, 1974.

DIJK, TH. S. VAN: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus L.* and *Pterostichus coerulescens L.* (Coleoptera, Carabidae). Oecologia (Berl.) **40**: 63–80 (1979).

ENGELMANN, F.: The physiology of insect reproduction. Oxford: Pergamon Press Ltd., 1970.

GRÜM, L.: Egg production of some Carabidae species. Bull. Acad. Pol. Sci. Cl. II, **21**: 261–268 (1973).

KREHAN, I.: Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagoüberwinterern der Gattung *Pterostichus* (Col., Carabidae). Oecologia (Berl.) **6**: 58–105 (1970).

LUFF, M. L.: The annual activity pattern and lifecycle of *Pterostichus madidus F.* (Col., Carabidae). Ent. Scand. **4**: 259–273 (1973).

MURDOCH, W. W.: Aspects of the population dynamics of some marsh Carabidae. J. Anim. Ecol. **35**: 127–156 (1966a).

MURDOCH, W. W.: Population stability and life history phenomena. Amer. Nat. **100**: 5–12 (1966b).

SOKAL, R. R. and F. J. ROHLF: Biometry. The principles and practice of statistics in biological research. San Francisco: W. H. Freeman and company, 1969.

THIELE, H. U.: Carabid beetles in their environments, pp. 369, 152 fig. Berlin: Springer, 1977.

WHITE, T. C. R.: The importance of a relative shortage of food in animal ecology. Oecologia (Berl.) **33**: 71–86 (1978).

MOTIVATION AND WALKING BEHAVIOUR OF THE CARABID BEETLE *PTEROSTICHUS COERULESCENS* L. AT DIFFERENT DENSITIES AND DISTRIBUTIONS OF THE PREY.

A PRELIMINARY REPORT

P. J. M. Mols

Biological Station of the Agricultural University (Wageningen), Wijster.
Kampsweg 27, 9418 PD, The Netherlands

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Abstract

In this study it is tried to analyse and partly to quantify the most important factors which govern the predatory and walking behaviour of the polyphagous carabid beetle *Pterostichus coerulescens* L. in relation to the distribution of the prey. Hunger, defined as the gut capacity minus the actual gut content is assumed to be the most important factor influencing the behaviour of the beetle. Hunger is determined by ingestion and digestion but its effect is also influenced by the quantity of the fatbody and by the ovarial activity. To integrate the most important factors affecting the hunger of the beetle a computer model is constructed according to the state variable approach (De Wit & Goudriaan). With help of this model the 'motivational state of the predator' can be computed continuously. An outline of the components of predatory and walking behaviour is given. The walking patterns can be divided roughly into two types: a random walking pattern, and a walking pattern with a high frequency of turning movements following feeding, the latter of which is similar to the pattern described in literature for many insect predator and parasitoid species.

1.1. Introduction

Prey populations may occur aggregated in different places depending on their preferences (Southwood, 1966). There are strong indications that predators can react to this by concentrating in the most profitable sites (Royama, 1970, 1971; Cook and Hubbard, 1977; Hassell et al., 1976). The predation risk of a clumped prey would thus be higher than is expected with a homogeneous prey distribution.

Three processes have been proposed to explain this phenomenon. The first process is, that a sensory detection threshold is most likely to be exceeded when preys are encountered in locally high densities (Krebs, 1973). The second explanation is, that many predators decrease their moving speed after feeding, simultaneously with an increase of the rate of turning (Fleschner, 1950; Banks, 1957; Dixon, 1958; Mitchell, 1963; Murdie and Hassell, 1973; Evans, 1976; Hassell and May, 1974). This behaviour should be an obvious adaptation to hunting aggregated prey, by which encounters with prey are expected to increase. The third process that is often proposed, is the development of learned searching patterns, such as specific search images, which appears to proceed more rapidly when preys are clumped (TINBERGEN, et al, 1967; CROZE, 1970). The latter occurs especially in vertebrates because of their high learning ability.

A higher predation of clumped prey will thus result only, of course, when the prey has not developed an effective group defence or warning behaviour.

1.2. THE AIM OF THE INVESTIGATION

Our studies are concentrated on the following questions: Does a polyphagous predatory beetle like *P. coerulescens* change its walking behaviour depending on the prey distribution pattern, and does this result in a change of the predation rate?

2.1. PREDATOR

Pterostichus coerulescens (L.) is chosen for this investigations as it is a polyphagous predator whose autecology has already been studied several times (KREHAN, 1970; VAN DIJK, 1979). The beetle is easy to manipulate and is abundant around the Biological Station at Wijster where our experiments are carried out. It lays its eggs in the spring; these hatch without dormancy after which the larvae grow up in summer, pupate in late summer and moult into adults in autumn. Hibernation occurs in the adult stage. The beetle is usually active during the day (GREENSLADE, 1963; LAUTERBACH, 1964). The species is abundant in moist-dry heathlike vegetations but also lives in more weedy vegetations. It is macropterous but the wings are generally small and are usually unsuitable for flying. Thus walking is the normal way of movement.

2.2. PREY

The studies are restricted to preys which do not show any kind of group defence.

3.1. APPROACH OF THE PROBLEM

To gain insight into relations between the predator and its preys answers to the following questions have to be found:

a. Which are the dominant components of behaviour of the predator in the predation process?
b. What is the 'motivation' of the predator?

c. Which relationships exist between the motivation and the relevant components of behaviour of the predator?

As soon as we have the information on the motivation, on the relevant components of behaviour and on their interactions, we can integrate this knowledge into a model. Such a model describes the sequence of events at the level of the input information, but can also have a predictive value at a higher level. With the help of this model we can try to simulate the behaviour of the predator with several densities and distributions of the prey from its behaviour with respect to a single prey individual. Comparing the model output with experimental results will increase our insight into the processes involved, and thus we hope to understand the interactions between predators and prey in the field.

3.2.1. The state variable approach

The models are constructed according to the state variable approach (DE WIT & GOUDRIAAN, 1978). This implies that the state of the system at any particular time can be expressed quantitatively and that the changes in the system can be described in mathematical terms. In state determined models, state variables, driving or forcing variables, rate variables, auxiliary variables and output variables can be distinguished.

State variables characterize and quantify all properties that describe the current state of the system. Examples of state variables are amount of biomass, number of animals, amount of food, water content, temperature of the soil, and so on. The values of all state variables have to be known at the onset of simulation. In mathematical terms they are quantified by the contents of integrals.

Driving or forcing variables are those that are not affected by processes within the system but characterize an influence from outside. These may be macrometeorological variables, the amount of food added in the course of time, and so on. It should be realized that depending on the boundaries of the system to be simulated, the same variables may be classified either as state or as driving variables.

Rate variables quantify the rate of change of the state variables. Their values are determined by the state variables and the driving variables according to rules formulated from the knowledge of the underlying ecological, physiological and physical processes. These processes may be so complicated that the calculation process becomes much more lucid when use is made of properly chosen intermediate or auxiliary variables.

Output variables are the quantities which the simulation produces for the user. Sometimes they are state variables, sometimes rates and sometimes auxiliary variables that may be calculated especially for this purpose.

3.3. SENSITIVITY ANALYSIS

To determine the relative importance of the rates, the parameters and the initial values, and to evaluate structural changes in a model, a sensitivity analysis is executed. Concerning rates, parameters and initial values such a sensitivity analysis consists of varying the values within a certain range and comparing the relative changes of the values with the relative changes in the output of the model. A sensitivity analysis on structural changes consists of eliminating parts of the program and evaluate the influence on the output.

This is done to validate the model concept we have in mind. If the influence of a certain parameter input or structural change is comparatively small a further analysis in that direction may be delayed, but if the influence is great, the features of these parameters or input should be analysed thoroughly. The result of such an analysis should be a guide-line for further experiments and programming.

Finally the output of the model has to be compared with the results of realistic field experiments in order to estimate the explanatory value of both the input data and the structure of the model.

4.1. MOTIVATION OF THE PREDATOR

In HOLLING'S (1966) model of the mantid *Hierodula crassa* the motivation for feeding behaviour is hunger defined as the degree of emptiness of the gut. Hunger increases through the combined action of assimilation and defecation, and declines during feeding approaching a minimal value when the gut is filled completely. Feeding behaviour is governed by the hunger level in which thresholds for different components of behaviour may be distinguished, such as the search, pursuit, capture and consumption of the prey. FRANSZ (1974) considered the satiation level, which is opposite to hunger, of the predatory mite *Typhlodromus occidentalis* to be the driving force for its behaviour. In other investigations it has also been shown that the satiation level of predators is a factor which significantly influences both the predation activity and the preference for different prey species (RABBINGE, 1974; JOHNSON et al., 1975).

From these studies it was concluded that insight into the predation activity and the prey preference of the groundbeetle *P. coerulescens* could be obtained only when the predation process is studied in relation to the hunger level of the predator.

The hunger level may also be influenced by other physiological factors, for example the fatcontent of the body and the ovarial activity, and these on their turn may be regulated by hormonal and neural processes. Thus we have to integrate the most important factors that will govern the hunger level in what may be called 'the state of the predator'.

4.2. STATE OF THE PREDATOR

In fig. 1 a simple relational diagram of the feeding, digestion and reproduction of the

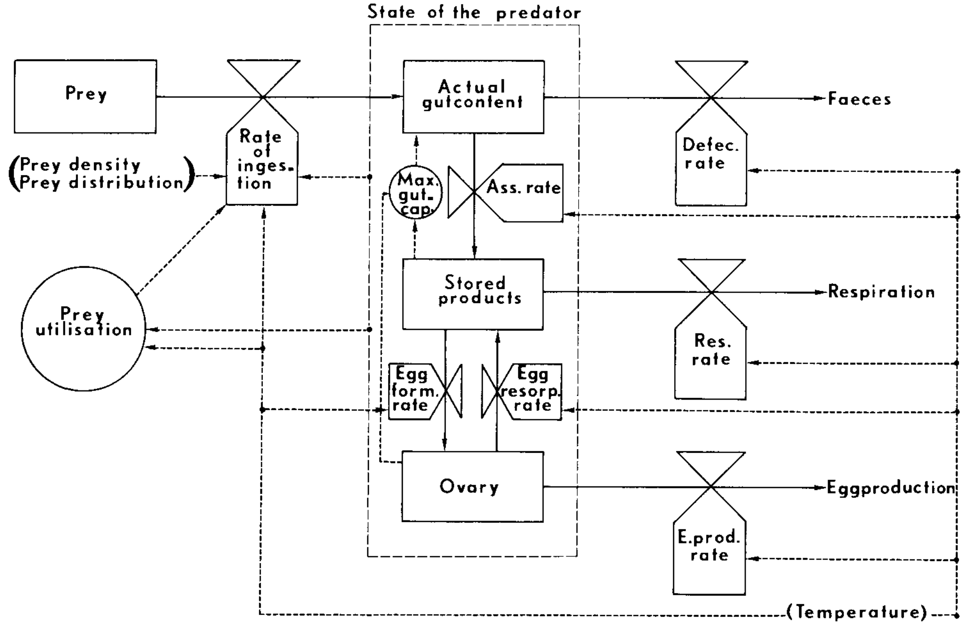

Fig. 1. Relational diagram of the state of the predator, according to the conventions of FORRESTER (1961).
☐ state variables, ⧗ rates of change, ○ auxiliary variables → flow of material, ---→ flow of information.

beetle is given. The predator consumes a captured prey at a certain rate: the ingestion rate. The food enters the gut until the beetle is completely satiated: the gut capacity. The indigestible parts leave the body by defecation and the remainder is assimilated. This assimilated fraction is partly respired or can be stored in the fatbody or be used for egg production. Hunger, for practical reasons it is defined as the gut capacity minus the actual gut content, is used as the motivation for the components of feeding behaviour. In this paper we will treat superficially the different factors that influence the hunger level of the predator. Other aspects will be published separately.

4.2.1. *The ingestion rate*

The ingestion rate of a captured prey depends on temperature, the hunger level of the predator and the prey species. Prey with thick and hard integuments require a longer handling time and thus the ingestion rate is decreased. The handling time becomes more important as a greater proportion of the predation time is spent on this activity.

4.2.2. *The gut capacity*

In the laboratory the gut capacity is measured, at 20 °C, by weighing initially starved beetles before and after periodic feeding till satiation. Experiments in which young hungry beetles were fed sequentially (fig. 2) showed that the gut capacity is not a

Fig. 2. Mean weight of 10 young female beetles fed periodically at 20°C.

constant but is greatly affected by the volume of the fatbody (fig. 3a + b).

The same relation is found to exist between gut capacity and the volume of the reproductive organs, especially the number of the eggs (fig. 4). In the breeding season the fatbody is reduced so that the abdomen of the females is nearly completely filled with eggs.

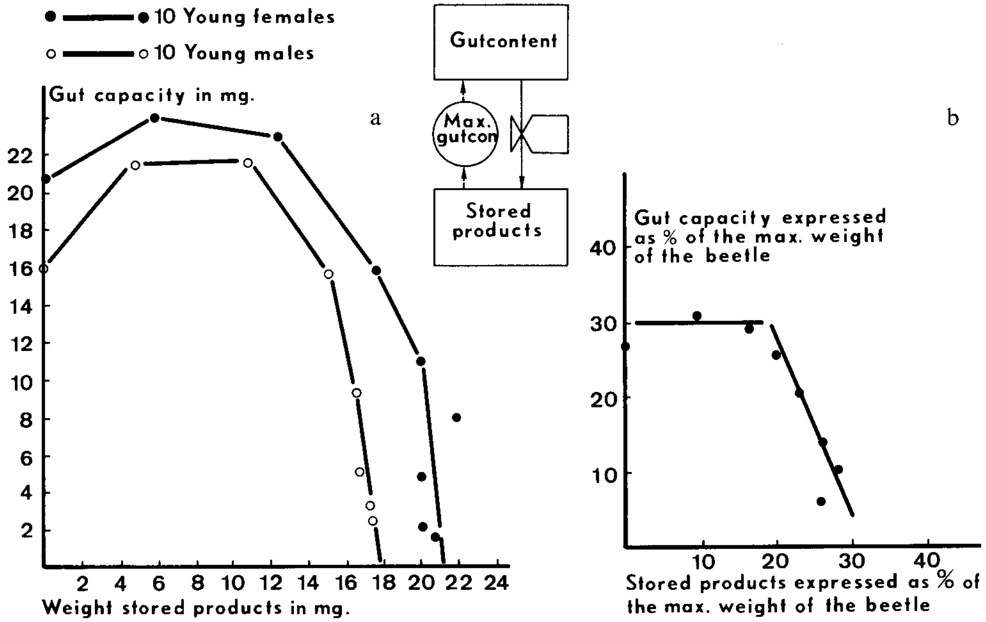

Fig. 3a, b. The relation between the gut capacity and the weight of stored products in young beetles expressed in (a) mg fresh weight and (b) as a proportion of the maximum weight of the beetle.

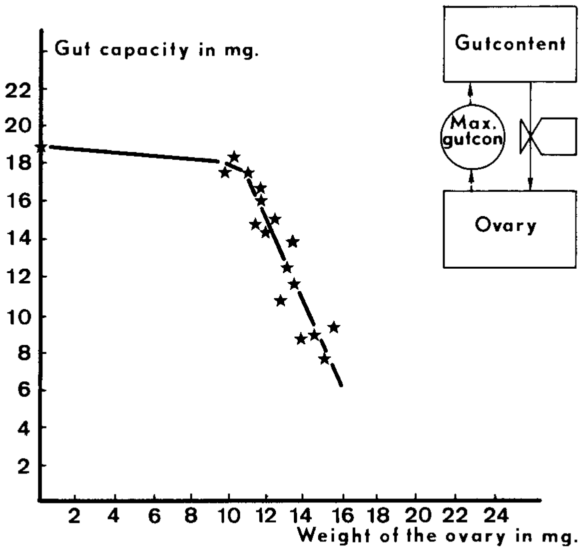

Fig. 4. The relation between the gut capacity and the weight of the ovaries during the reproduction period.

We assume that at the start of adult life the actual size of the crop will be the factor restricting the amount of food ingested, but when the fatbody or the ovarioles grow the available space in the abdomen is reduced and the crop cannot expand to its maximum size.

4.2.3. *The digestion rate*

The relative digestion rate is defined as the reciprocal of the mean residence time of the food in the gut. To measure this residence time hungry beetles are fed until they are satiated. After a few hours, depending on the temperature, the production of faeces starts. The period needed for the production of 50 % of the total amount of faeces is used as the average residence time of the food in the digestive tract, assuming that the digestion rate is proportional to the actual gut content. An illustration of this process is given in fig.'s 5a + b which show the decrease in weight caused by defecation and respiration. The corresponding accumulation of faeces pellets is given in the same figure. The presented rates are highly dependent on temperature, therefore the experiment is done at a constant temperature of 20 °C.

4.2.4. *The assimilation rate*

Calculation of the assimilation rate is only possible when the food utilisation by the beetle is known. The food utilisation is defined as: the increase in weight of the beetle after having completely digested the ingested food, corrected for by the weightloss caused by respiration during digestion, and divided by the total amount of food ingested. In our experiments with larvae of a blowfly (*Calliphora* sp.) as prey the food

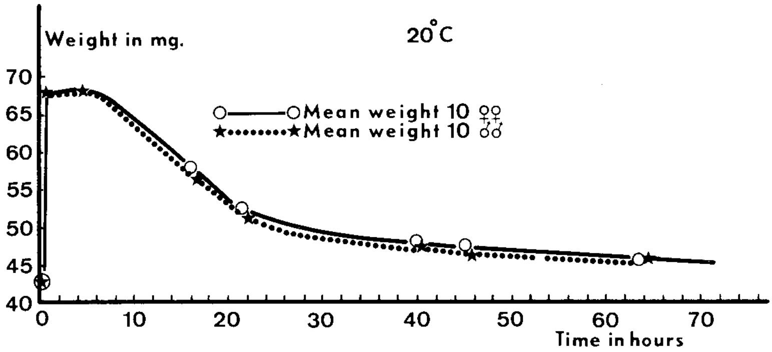

Fig. 5a. The loss in weight of the beetle by digestion and respiration.

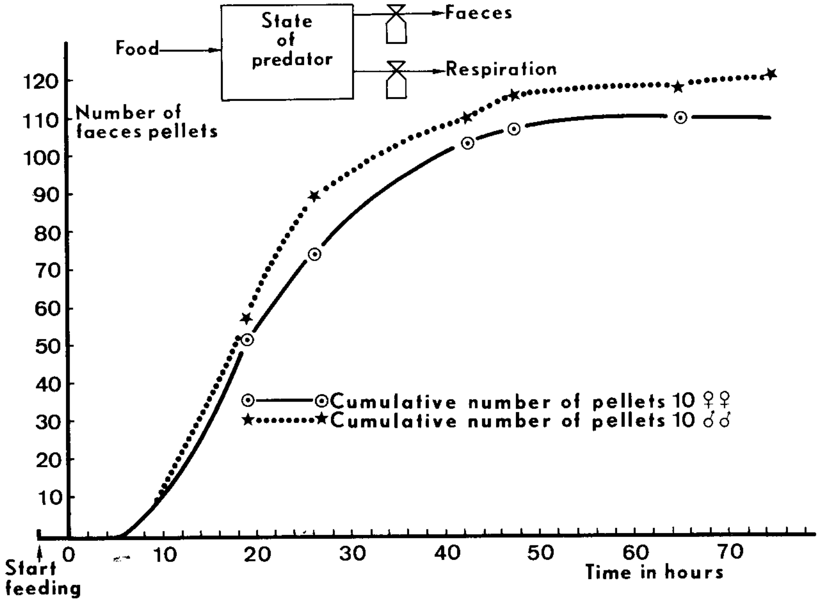

Fig. 5b. The production of faeces pellets after satiation and without further feeding.

utilisation is about 30 %, but other more chitineous prey species may give very different results. The assimilation rate is thus assumed to be 30 % of the digestion rate using blowfly larvae as prey.

4.2.5. *The respiration rate*

The respiration rate is affected by temperature and by the physiological stage of the beetle. Therefore, measurements were done both with young beetles, with beetles in hibernation and during aestivation, and with preovipositing females at several temperatures. Preovipositing beetles and young active beetles before hibernation have about the same respiration rate. The results of those measurements are shown in fig. 6.

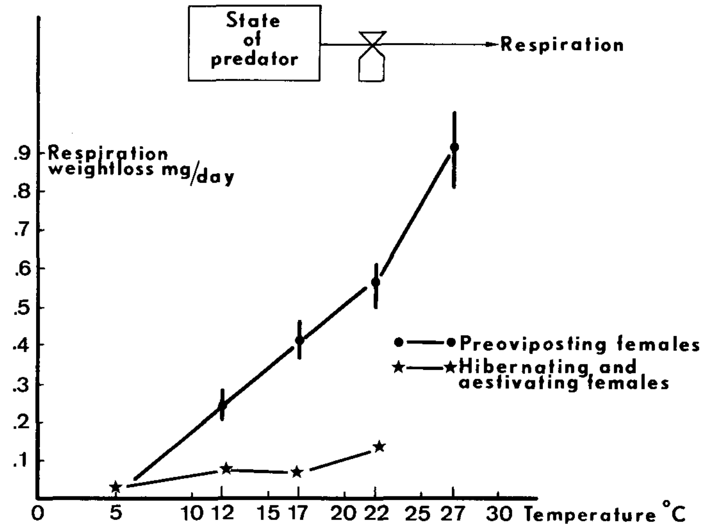

Fig. 6. Weightloss by respiration in relation to temperature.

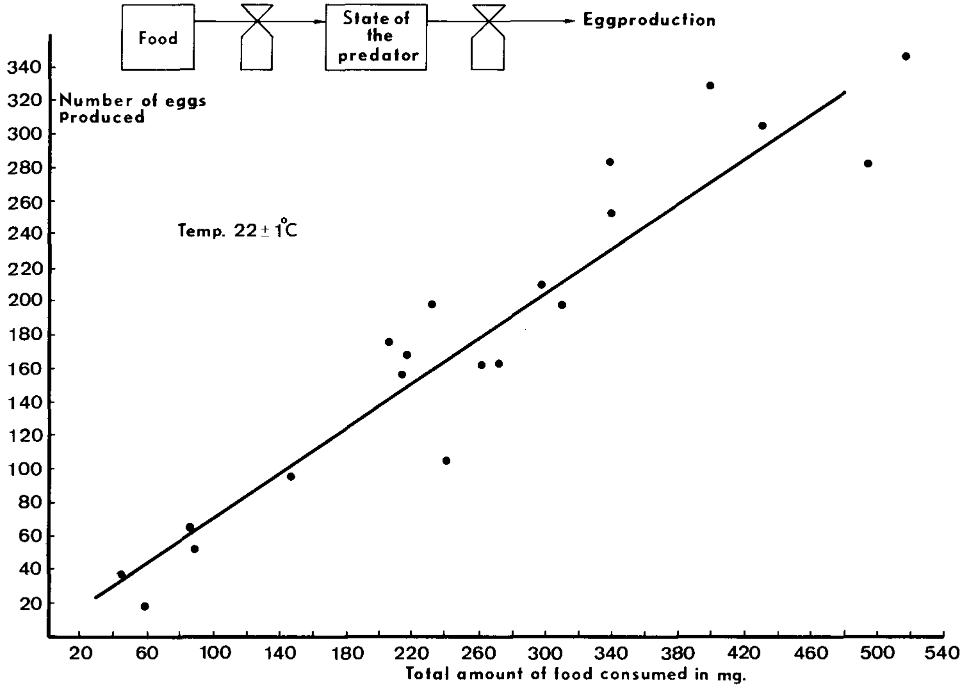

Fig. 7. Relationship between the total amount of food consumed during the reproduction period and the number of eggs produced.

Hibernating and aestivating beetles have a much lower respiration rate than active ones, due to a low level of activity and probably of other metabolic processes.

4.2.6. *The reproduction rate*

The reproduction rate depends on food consumption, but food consumption is greatly affected by the size of the ovaries in the abdomen of the beetle. Voluminous ovaries diminish the gut capacity and thus the food consumption, so that at each temperature the actual reproduction rate is greatly influenced by a negative feed back-loop dependent on food availability. For each quantity of available food and for each temperature a different equilibrium value for reproduction and food consumption occurs. The relation between egg production and food consumption at 22°C is given in fig. 7. The weight of one egg is about 0.5 mg.

The food conversion into eggs, using this egg weight, thus has an efficiency of about 30 %. This is equal to the efficiency of the conversion of food into fat.

5.1. COMPONENTS OF THE BEHAVIOUR OF THE PREDATOR

Closely looking at a beetle when it walks in the field or in an artificial arena gives us a first impression of the most eye-striking components of its behaviour. An active beetle viviously walks around with a certain velocity. The velocity of this walking depends

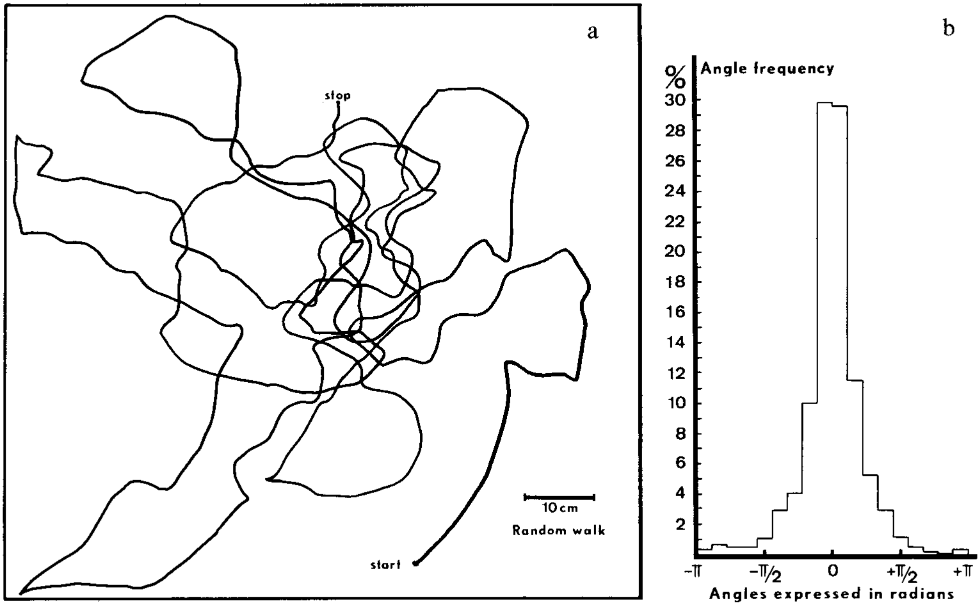

Fig. 8. (a) An example of a random walk pattern with (b) the angle frequency distribution, analysed with 1 cm steps. Total N = 946 steps $\sigma/\sqrt{N} = .012$.

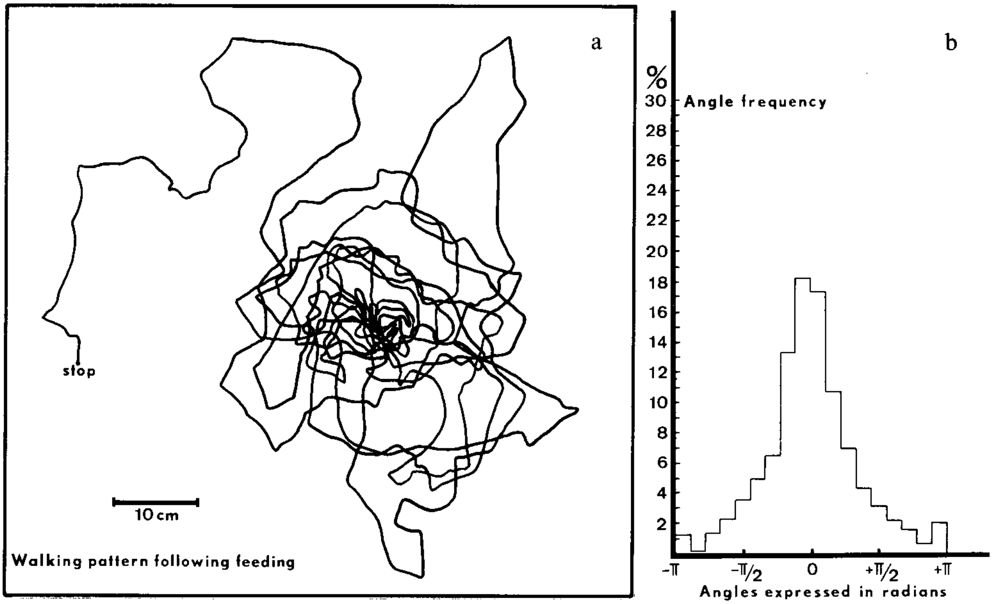

Fig. 9. (a) An example of a walking pattern following feeding with (b) the angle frequency distribution, analysed with 1 cm steps. Total of N = 945 steps, $\sigma/\sqrt{N} = .020$.

on external factors such as the surface structure, the vegetation, temperature, and also on the motivational state of the beetle.

Another aspect of walking is that it occurs in an almost continuously changing direction. The degree of change of these directions depends probably also on the above mentioned external factors, and on the motivational state of the predator. Both changing speed and direction result in walking patterns in which we can roughly distinguish two types. The first is a more or less random walking pattern as pictured in fig. 8a, b, whereas the second is characterized by a high frequency of turning movements following feeding (fig. 9a, b). If no prey is encountered during the latter way of walking it will gradually turn into the first type of walking. The duration of the second pattern has appeared to depend on the hunger level of the beetle.

Periods of walking alternate with periods of cleaning, resting, mating or ovipositing, usually at sheltered places under vegetation cover or in litter. The proportion of time spent walking is called the predator activity. A randomly walking beetle keeps its antennae stretched forward, whereas a searching beetle frequently bends the antennae downward and moves them over the surface. A potential prey may be perceived either by direct contact with the antennae or by visual perception. The latter implies a distance of perception which may vary with the hunger level of the predator (Holling, 1966), with the size of the prey, with the mobility of the prey, and with light intensity (Bauer, 1977; Ernsting, 1978). The number of encounters with prey per time unit is called the encountering rate. An encounter is successful when it results in killing of the prey. The number of successful encounters divided by the total number of encounters is thus named the success ratio. The success ratio is greatly affected by the hunger level of the predator (FRANZ, 1974; RABBINGE, 1976). Capturing a prey is followed by a period of handling the prey, which includes a period of feeding. The predation rate can be formulated as follows:

Predation rate = activity predator × encountering rate × success ratio × coincidence in space.

The last factor accounts for the phenomenon that in vegetation predator and prey may walk on different horizontal levels and thus pass over or under each other.

Summarizing we can state that also in carabid beetles the most relevant components of predatory behaviour are influenced by the motivational state of the beetle, i.e. hunger.

6.1. FURTHER ASPECTS OF THE INVESTIGATION

The purpose of our study is to quantify the relevant components of predatory and walking behaviour in relation to the motivational state of the beetle. The walking behaviour is recorded with the help of a video-outfit (SABELIS, in prep.) and the walking patterns are analysed concerning the distributions of velocities and of angle-frequencies at different hunger levels. The success ratio, distance of perception, period of handling the prey are quantified in experiments with different prey species and at different hunger levels.

The results of these experiments are incorporated into a computer model which aims to simulate the walking and predatory behaviour. The simulated walking behaviour is based on the assumption that the direction of each step deviates from the direction of the previous step. The angle of this deviation is taken from an experimentally established frequency distribution. Autocorrelation is taken into account by way of a correction factor that is based on a detailed analysis of the autocorrelations (RUARDY, in prep.). With the help of this model we hope to predict the rate of successful encounters at different distributions of preys and thus to gain more insight into the effect of clustering of preys on their predation risk.

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REFERENCES

BANKS, C. J.: The behaviour of individual coccinellid larvae on plants. J. Anim. Behav. **5**: 12–24 (1957).

BAUER, T.: The relevance of the brightness to visual acuity, predation, and activity of visually hunting ground-beetles (Coleoptera, Carabidae). Oecologia (Berlin) **30**: 63–73 (1977).

COOK, R. M. and S. F. HUBBARD: Adaptive searching strategies in insect parasites. J. Anim. Ecol. **46**: 115–125 (1977).

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

DIJK, TH. S. VAN: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. (Coleoptera, Carabidae). Oecologia (Berlin) **40**: 63–80 (1979).

DIXON, A. F. G.: A study of the searching behaviour of certain insects feeding on aphids. D. Phil. thesis, Oxford, 1958.

ERNSTING, G.: Predation of springtails. Drukkerij Ernsting, Wageningen, 88 p., 1978.

EVANS, H. F.: The searching behaviour of *Anthocorus confusus* (Reuter) in relation to prey density and plant surface topography. Ecological Entomology **1**: 163–169 (1976).

FLESCHNER, C. A.: Studies on the searching capacity of the larvae of three predators of the Citrus red mite. Hilgardia **20**: 233–264 (1950).

FORRESTER, J. W.: Industrial Dynamics. MIT-press, Boston, 1961.

FRANSZ, H. G.: The functional response to prey density in an acarine system. Pudoc, Wageningen, 149 p., 1974.

GREENSLADE, P. J. M.: Daily rhythms of locomotory activity in some carabidae (Coleoptera). Ent. Exp. Appl. **6**: 171–180 (1963).

HASSELL, M. P., LAWTON, J. H. & BEDDINGTON, J. R.: The components of arthropod predation I. The prey death rate. J. Anim. Ecol. **45**: 135–164 (1976).

HASSELL, M. P. and R. M. MAY: Aggregation in predators and insect parasites and its effect on stability. J. Anim. Ecol. **43**: 693–726 (1974).

HOLLING, C. S.: The functional response of invertebrate predators to prey density. Memoires Entomol. Soc. Canada, no **48**: 86 p. (1966).

JOHNSON, D. M., AKRE, B. G. and P. H. CROWLEY: Modelling arthropod predation: Wasteful killing by damselfly Naiads. Ecology **56**: 1082–1093 (1975).

KREBS, J. R.: Behavioural aspects of predation. In Perspective in ethology (P. P. G. Bateson, P. H. Klopfer eds.) New York: Plenum Press, 73 p. 1973.

KREHAN, I.: Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagoüberwinterung der Gattung *Pterostichus* (Col. Carab.). Oecologia (Berlin) **6**: 58–105 (1970).

LAUTERBACH, A. W.: Verbreitungs- und aktivitätsbestimmende Faktoren bei Carabiden in sauerländischen Wäldern. Abhandl. Landesmus. Naturkunde Münster **26**: 1–100 (1964).

MITCHELL, B.: Ecology of two carabid beetles *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). 1. Lifecycles and feeding behaviour. J. Anim. Ecol. **32**: 289–299 (1963).

MURDIE, G. and HASSELL, M. P.: Food distribution, searching succes and predator prey models. The Mathematical Theory of the Dynamics of Biological Populations. Academic Press London, 87–101, 1973.

RABBINGE, R.: Biological control of the fruit-tree red spider mite. Pudoc, Wageningen, 228 p., 1976.

ROYAMA, T.: Factors governing the hunting behaviour and food selection of the great tit (*Parus major*). J. Anim. Ecol. **39**: 619–688 (1970).

ROYAMA, T.: Evolutionary significance of predators response to local differences in prey density: a theoretical study. In P. J. den Boer and G. R. Gradwell (ed.) Proc. Adv. Study Inst. Dynamics Numbers Popul. Oosterbeek, 344–357, 1971.

RUARDY, P.: Intern rapport from Theoretical production ecology. Agricultural University, Wageningen.

SABELIS, M. W.: Evaluation of predatory mites for the control of spider mites. (In prep.)

SOUTHWOOD, T. R. E.: Ecological methods. Methuen, London, 391 p., 1966.

TINBERGEN, N., M. IMPEKOVEN and D. FRANCK: An experiment on spacing out as a defence against predation. Behaviour **28**: 307–321 (1967).

WIT, C. T. DE and J. GOUDRIAAN: Simulation of ecological processes. Pudoc, Wageningen, 175 p., 1978.

INDIVIDUAL AND ENVIRONMENTAL FACTORS DETERMINING FLIGHT IN CARABID BEETLES

T. H. P. VAN HUIZEN

Biological Station of the Agricultural University Wageningen, Kampsweg 27, 9418 PD
Wijster, The Netherlands

Communication no. 202 of the Biological Station, Wijster

ABSTRACT

In this paper it is shown that flight behaviour in carabid beetles may only be expected if the daily max. temperature rises above 16 °C, rainfall ⩽0.1 mm/day and wind velocity ⩽7 m/sec. Spring breeders show their main flight activities in spring around midday, whereas late summer–winter breeders tend to fly later on in the year and at twilight. Daylight flight activity has also incidentally been observed in strictly nocturnal species. The number of days available for flight varies considerably from year to year. Form properties of the window-traps used to measure flight activities will influence the catch results. Dissection of females has revealed, that during the flight period of the investigated species fertilized individuals with or without eggs regularly take part in flight activities. It could be demonstrated that within a number of species only part of the individuals are able to (re)build flight muscles, and this phenomenon is not restricted to macropterous species only.

The possibility of settling of carabid species in suitable localities depends on their dispersal capabilities. 'Dispersal' is that kind of movement of individuals –flying or walking – that results in leaving the population area (DEN BOER, 1977). In this paper attention will be paid to the morphological and environmental conditions that determine frequency and level of the flight behaviour in carabid beetles. Flight activity data have been obtained by sampling flying insects at different sites by means of window-traps, from 1969 up to now. Every year this sampling is started in April and is continued until November. Weather-data from the nearest meteorological station Eelde (± 50 km) were used to establish the physical conditions favouring flight. The state of reproduction (e.g. presence of spermatozoa in the spermathecae) of individuals caught in the window-traps was compared with that of individuals caught by means of pitfalls together with the degree of flight muscle development of the latter individuals, to learn what place flight takes in the life cycle and survival strategy of the species (DEN BOER, 1977, VAN HUIZEN, 1977).

1. ENVIRONMENTAL CONDITIONS

1.1. *Daily maximum temperature (measured in °C at about 1.5 m above ground level)*

To find the lower take-off threshold, all daily max. temperatures, as they occurred in May + June during 7 years, were compared with the frequencies of catches in window-traps. The first carabid individuals are generally caught at the beginning of May. The peak of the flight activities is reached within three weeks after the first catch, followed by a gradual decrease of catches till the end of June. According to TAYLOR (1963) not the number of carabid beetles in a catch should be evaluated, but only the fact whether or not a catch has occurred, by which 'activity' is zero below the take-off threshold when flying does not occur, and unity above it when one or more individuals fly. Such an ordination avoids the need to consider aerial numbers as affected by population changes.

A comparison of the frequency of the daily max. temperatures with that of the occurrence of catches (fig. 1) shows a sharp increase of temperature frequency between 12° and 16 °C which is not reflected in the frequency of catches. However, as soon as the temperature rises above 16°–17 °C, the catch frequency suddenly increases. This means that the take-off threshold coincides with an air temperature between these values. Above 17 °C the temperature frequency decreases again, whereas the frequency of the catches continues to rise until 20 °C. The best temperatures for an effective dispersal occur for the different species between 18°–22 °C, because both the

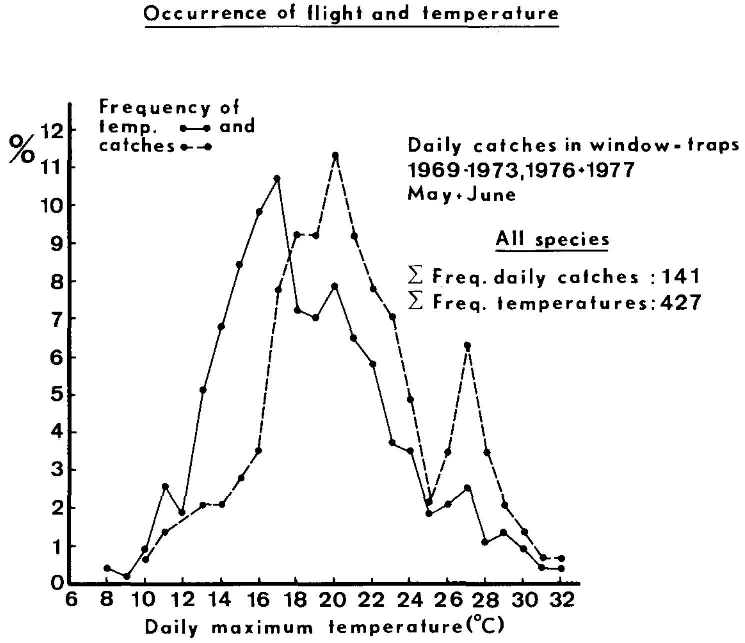

Fig. 1

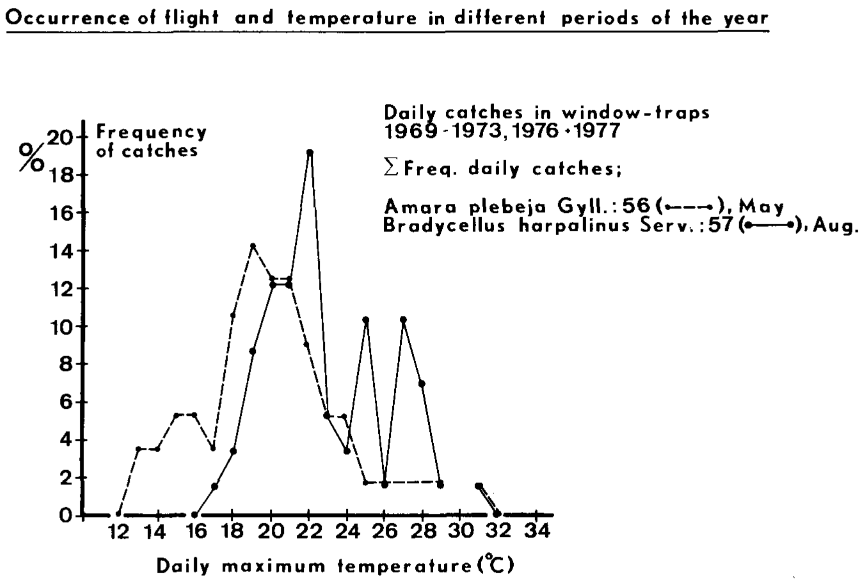

Fig. 2

frequencies of the temperatures and those of the catches are then very high. See also fig. 2, where the frequencies of daily catches of two species – with quite different flight periods – are plotted and can thus be compared. Above 24 °C the frequency of catches for the different species increases sharply again (figs. 1 + 2), in spite of the low frequencies of the temperatures. Perhaps then the general environmental conditions become unfavourable and the beetles may try to escape.

1.2. *Rainfall – Wind velocity/Temperature*

About the influence of rain we can be very short: if the weather is rainy (> 0.1 mm/day), usually no catches occur. Moreover, max. temperature then often decreases below the take-off threshold. Apart from this the wet animals will become too cold to fly even when the max. air temperature remains above 17 °C. The body of the insect may also be cooled by wind, especially when it tries to take off. It will be clear from table 1 that the frequency of catches decreases considerably when the wind velocity increases.

During a field experiment concerning flight activity and orientation upon the sun, at first small groups of beetles were able to take off from a petri-dish (∅20 cm). In the afternoon wind velocity increased and the take-off failed; the air temperature probably fell below the threshold value. After that, spontaneous flights only occurred when the petri-dish was covered and thus warmed up for a while in the sun. From another experiment, in which every 15 minutes window-traps were controlled and max. temperature and wind velocity were measured, it appeared that on very warm days

Table 1. Frequency of catches at different wind-velocities. Daily catches in window-traps, May + June: 1969–1973, 1976–1978.

Wind-velocity (m/sec.)	Frequency of wind-velocity (days)	Number of these days with catches	Fraction of these days with catches
0–1	10	6	0.60
2	64	28	0.44
3	155	65	0.42
4	123	42	0.34
5	83	25	0.30
6	36	10	0.28
7	11	3	0.27
8	4	0	–
9 and >	2	0	–

(max. temp. about 26 °C) catches occurred only if the wind velocity decreased for a moment below 4 m/sec. The wind velocity has a direct take-off influence and especially at high values when it prevents flying.

1.3. *Flight activities by day and at night – orientation by the sun*

In papers published by LINDROTH (1945, 1949) only little information concerning flight activities by day (and also during the night) can be found. He refers for that to a publication by MC. CLURE, who in Kentucky systematically sampled flying insects during the morning and evening. However, only 4 of the 88 carabid individuals (belonging to 20 species) present in his samples were caught in the morning, whereas 84 were captured in the evening. These observations were the main source of information for LINDROTH in combination with his own experiments on flight-direction (orientation by the sun). Our results (fig. 3), however, agree only partly with his findings. The most important deviation is, that about 90 % of the total catch (N = 180; 26 species) occurred between 11.00 and 16.00 o'clock with a top between 13.00 and 14.00 o'clock. During this latter period at our latitude the temperature also reaches a top, and not around midday when sun's altitude is highest and thus radiation is most intense.

The flight activity as it occurs in April–June starts rather late in the morning and falls off again towards the end of the afternoon. However, more than once the max. temperature had already passed the take-off threshold (17 °C) at 07.00 o'clock, although catches did not occur before midday. With the help of experiments we will have to estimate whether in such cases radiation or temperature is more important to warm up the insect body.

During late summer however early in the morning (08.00 o'clock), some specimens belonging to species different from the above are found in the window-traps. In most of the cases observed the max. temperature (± 14 °C) was below the threshold for take-off then, but the night before at about 21.00 it reached 20 °C, so we can conclude that the

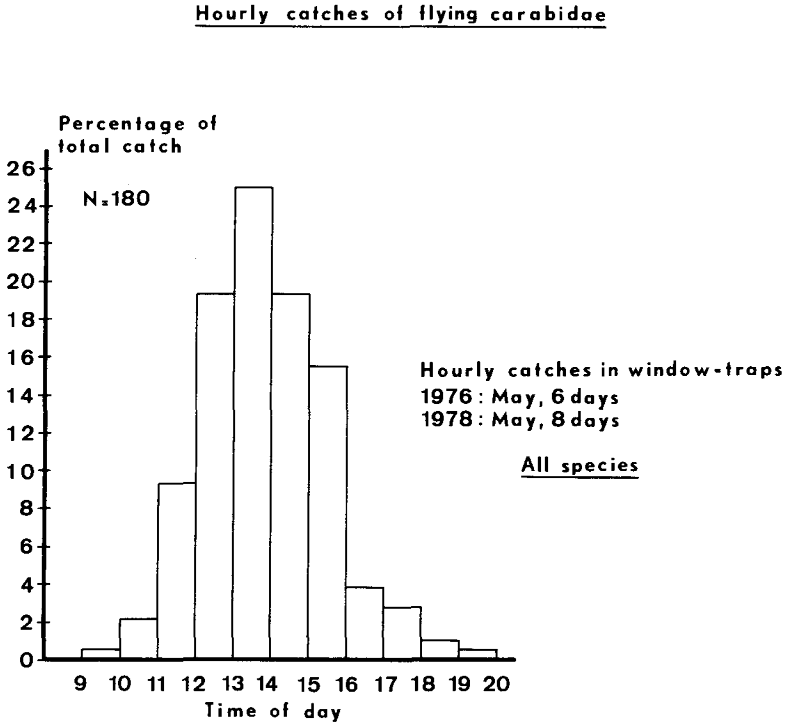

Fig. 3

pertinent flight activities occurred after 21.00 o'clock (shortly before 21.00 o'clock the window-traps were emptied). These observations have been made from the second week of July until October, and agree with the experiences of entomologists collecting with light-traps (e.g. KERSTENS, 1961; BRIGGS, 1965).

Results from a field experiment indicate that the majority of flying carabids (± 75 %) indeed follow the movement of the sun in the course of the day. But flight direction will also be influenced by the direction of the wind, which during the experiment mainly came from the North-N.E. with a mean velocity of about 3.5 m/sec. LINDROTH supposed that the flight of carabids is more directed towards the sun the nearer the sun is to the horizon. He thus explains the tendency to fly in western direction of those carabid beetles, which show their flight activities mainly during twilight and in the course of the night. This agrees only with our findings concerning some species which fly rather late in the year, and deviates from the general pattern as shown in fig. 3. Although the flight activities of most species in Drenthe occur around midday, LINDROTH may be right as far as the more northerly latitudes of Sweden are concerned.

Our window-traps also taught us that individuals of some forest species that showed walking activities during the night are able to fly by day between 12.00 and 16.00 o'clock (viz. *Nebria brevicollis* F., *Pterostichus oblongopunctatus* F. and *Calathus piceus* Marsh.). So we can conclude that reversal of the night activity rhythm can also occur under natural conditions, comparable with the laboratory findings of PAARMANN (1966) concerning *Pterostichus angustatus* Dfts.

1.4. *Seasonal periodicity*

To illustrate the possible differences between the species as to the timing of the flight period in the course of the year (fig. 4), some representative examples are given. The first graph, *Amara aenea* de Geer, shows a flight activity period which consists of two

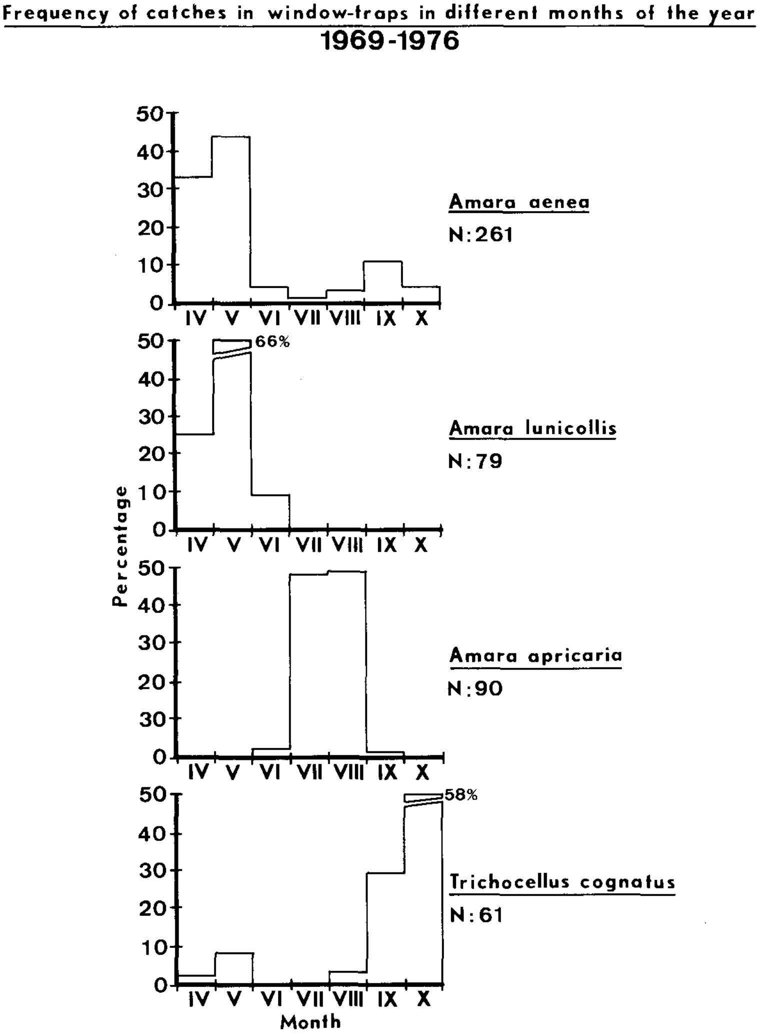
Frequency of catches in window-traps in different months of the year
1969-1976

Fig. 4

parts, an important activity in spring and a lesser one in late summer. This pattern applies to about 20 species, among which *Anisodactylus binotatus* F. (FRAENKEL, 1932, refers to an observation by WALCH concerning the autumn flights of this species) and *Acupalpus dorsalis* F. Particularly individuals of the latter species were caught around midday, this is contrary to the findings of LINDROTH (1949). During the second flight period mainly young but also some old individuals were caught. The frequency pattern illustrated by *Amara lunicollis* Schiödte represents a group of about 24 species. They show a single flight period in spring in which both young (after overwintering) and old beetles take part. Among both groups discussed so far mainly spring breeders (e.g. *Amara* spp.) but also some winter breeders (e.g. *Trichocellus placidus* Gyll.) are represented. The frequency patterns of a group of about 23 spp. is illustrated here by those of *Amara apricaria* Payk. and *Trichocellus cognatus* Gyll., which are partly late summer breeders (e.g. *Amara majuscula* Chaud), partly autumn breeders (e.g. *Amara bifrons* Gyll.) or even winter breeders (e.g. *Bradycellus ruficollis* Stephens, *Bradycellus harpalinus* Serv.). Until now, only individuals belonging to different species within this group had been caught by us during twilight (compare 1.3).

1.5. In the foregoing sections it has been indicated to what extent the flight activities of carabid beetles might be determined by some environmental factors. On this basis, it seems possible to say something about the conditions for dispersal. By accepting the conditions: (1) Max. day temperature $\geqslant 17$ °C (cf. 1.1); (2) Rainfall $\leqslant 0.1$ mm/day (cf. 1.2); (3) Mean wind velocity $\leqslant 4$ m/sec. (cf. 1.2), as necessary the frequency of 90 % of

Table 2. The influence of different sampling techniques on the sex ratio in catches of *B. harpalinus*.

Sample technique	Site	Years	Number of ♀♀	Number of ♂♂	♀♀/♂♂	χ^2	P
Window-traps (T-type)		1969–1977	1874	1267	1.48	0.28	n.s.
*Pitfall-traps		1957–1967	495	350	1.41		
**Window-traps							
Trough-type (T-type)	BZ	1977	187	148	1.26	0.64	n.s.
Funnel-type (F-type)	BZ	1977	34	10	3.40	5.31	<0.05
Trough-type	BZ	1974–1977	475	402	1.18	3.24	n.s.
Funnel-type	CE	1974–1977	368	176	2.09	11.18	<0.001

* The expected value for the different tests is derived from the sex ratio (1.41), which dominated in pitfall catches.
** A description of the two types of window-traps can be found in VAN HUIZEN (1977).
BZ: Meadow with cattle, bordering heath.
CE: Meadow that was dunged for the last time in 1970, situated between forest and heath.

Table 3. Comparison of the numbers of individuals caught in T- and F-type (cf. table 2) window-traps respectively. The catches in the two types of window-traps are made comparable by converting them to the same 'window surface' ($T = 2.16 \times F$).

		Type of window trap			Type of window trap	
1977	A	T	F	B*	T	F
	Number of ind.			Number of ind.		
	(18 spp.)	217	101	(16 spp.)	33	46
	expected	159	159	expected	39.5	39.5
		$\chi^2 = 21.13$	$P \ll 0.001$		$\chi^2 = 0.77$	P. n.s.
1973	C	T	F	D*	T	F
	Number of ind.			Number of ind.		
	(21 spp.)	84	142	(20 spp.)	55	60
	expected	113	113	expected	57.5	57.5
		$\chi^2 = 7.0$	$P < 0.01$		$\chi^2 = 0.04$	P. n.s.

*B After subtraction of the numbers of individuals of *B. harpalinus* and of *A. aenea* caught.
*D After subtraction of the numbers of individuals of *A. plebeja* caught.

our catch data is explained. This result is the more conclusive because it enables us also to understand why the number of flight days varies from year to year: the number of days avaible for flight varies considerably between years (1969, May + June: 16 days and for the same period in 1976: 34 days).

1.6. Besides the environmental factors treated so far also the form properties of the window-traps used may influence the numbers of individuals caught. In table 2 we give an example of a species in which the sex ratio is influenced, and in table 3 we demonstrate that also the overall numbers caught of some species may be influenced by the technique used to measure flight activities.

2. INDIVIDUAL CONDITIONS

Besides the changing abiotic factors and their influence upon the flight activities of Carabidae (cf. section 1), also variable properties of the individuals themselves (crop content, development of reproduction organs and flight muscle system resp.) within species as well as between species must be considered. During the period 1969–1977, about 8000 specimens belonging to 80 species have been caught by means of window-traps, i.e. during the act of flying. Contrary to the first findings in this field mentioned by DEN BOER (1971) we can now establish that among 16 species studied so far there are at least 15 in which some or more females are still able to fly after having copulated (table 4). Some of these females showed that they could even fly with fully developed ovaries, partly filled with ripe eggs (in these cases the number of eggs in the ovaries varied between 1 and 10). We agree with DEN BOER (1971) that older beetles (that had reproduced at least once: i.e. with Corpora Lutea) also usually take part in flight activities.

2.1. To reconstruct the life-history of a species, the conditions of individuals caught during the act of flying are compared with the data derived from individuals caught by means of standard sets of pitfalls, sometimes supplemented (during winter time) by those from specimens collected by hand. An example of this kind is treated in VAN HUIZEN (1977) for *A. plebeja*. Besides habitat change by means of flight activities, also flight muscle autolysis-reconstruction is shown to exist in this species. During hibernation no individuals with developed flight muscles could be found. In spring the muscles are built up again and flying activities start (during this flight period also about 90 % of the individuals from pitfall catches show fully developed flight muscles). After this period, when reproduction starts, the flight muscles autolyse. At the end of the reproductive season the muscles are rebuilt or built up for the first time (in late summer) and both old and young beetles fly towards overwintering sites. The whole cycle can be repeated by the same individuals in the next year.

Table 4. Catches in window-traps between 1969 and 1977. Reproductive state of females caught during the act of flying (without C.L.* = before having laid any eggs; with C.L. = after having reproduced at least once).

Species	Total number of ♀♀		Among which:			
			number of fertilized ♀♀		number of ♀♀ with ripe eggs	
– : without C.L + : with C.L.	–	+	–	+	–	+
Agonum dorsale Pontopp.	2	–	2	–	1	–
Amara aenea de Geer	5	2	5	1	1	–
Amara apricaria Payk.	2	5	2	–	–	–
Amara bifrons Gyll.	7	1	2	–	–	—
Amara communis Panz.	2	1	2	1	–	1
Amara familiaris Dfts.	74	12	29	9	16	6
Amara lunicollis Schiödte	29	14	3	–	–	–
Amara plebeja Gyll.	91	11	–	–	2	–
Anisodactylus binotatus F.	26	9	6	8	5	3
Bradycellus harpalinus Serv.	75	27	20	27	7	–
Calathus mollis erythroderus G & H.	7	1	2	–	1	–
Calathus piceus Mrsh.	1	–	1	–	–	–
Loricera pilicornis F.	6	–	4	–	4	–
Pterostichus vernalis Panz.	13	1	4	–	4	–
Trichocellus cognatus Gyll.	1	1	1	–	–	–
Trichocellus placidus Gyll.	2	1	1	1	–	–

* C.L.: Corpora Lutea.

2.2. An entirely different and much more complicated case is represented by the macropterous species *A. lunicollis*. During the flight period in spring only about 16 % of the beetles caught by means of pitfalls show fully developed flight muscles (compare *A. plebeja*: 90 %). This phenomenon does explain why dispersal power of this species is lower than expected (see DEN BOER, 1971, 1977: page 61). Although the frequency distribution of the relative surfaces of the alae of specimens caught by means of window traps is different from that of specimens captured in pitfall-traps at different sites and in different years, the wings of most individuals must be large enough to allow flying. During the reproduction period no individuals with fully or even partly developed flight muscles have been found. But some beetles from window-traps possessed Corpora lutea, which indicates that after reproduction and overwintering within the same habitat, at least some individuals rebuild their flight muscles. This is supported by the fact that only during both the beginning and the end of the flight period some individuals with partly developed flight muscles are present. This phenomenon, that only some of the individuals have the capacity to (re)build flight muscles, may be considered a kind of flight muscle-dimorphism, analogous to wing-dimorphism.

2.3. We have indications now that this phenomenon of flight muscle-dimorphism is not restricted to macropterous species only, as was shown by e.g. DEN BIEMAN (1977, unpublished report). During an investigation into the degree of dispersal of some carabid species he found that the wing-dimorphic forest species *C. piceus* showed two reproduction periods: the first in spring (old beetles) and the other in summer (young beetles); see also DEN BOER, this volume. 5.4 % of the old beetles and 25 % of the young individuals then had fully developed flight muscles as well as ovaries with ripe eggs. DEN BIEMAN demonstrated that some of these beetles succeeded in flying under special conditions at the beginning of August. One of these was a female with developed ovaries, spermcells in the spermatheca and without Corpora lutea. This observation agrees with the properties of a specimen caught on 21-8-'78 in a window-trap that was erected at a distance of about 20 m from the nearest *C. piceus* population.

The flight muscle-dimorphism phenomenon exists also within the wing-dimorphic carabid species *C. mollis erythroderus* (VAN DIJK, 1978) of which both a few young and some old individuals have been caught in window-traps. The earliest and latest catches of these occurred on 21 VI and 14 VIII respectively, so that the flight period ends more or less when the development of the reproductive organs has already started (VAN DIJK, 1978); see also table 4. Individuals sampled by means of pitfall-traps – mainly during the reproductive period – did not possess fully or even partly developed flight muscles. These contradictory findings may be understood as a combination of the oogenesis-flight syndrome (JOHNSON, 1969) and flight muscle-dimorphism (see 2.2).

2.4. *Pterostichus versicolor* Sturm is a macropterous species in which the wings are rather small (DEN BOER, 1977). Two window-trap catches could be recorded however, both in May and in different years, but the wing-surfaces of these individuals were larger than usual. Dissection of beetles from pitfall catches (different year-samples, but same site, N = 200), showed that two among them – caught in May – had fully developed flight muscles combined with wing surfaces that were as large as those from the individuals caught in the window-traps. TIETZE (1963) mentions one female among 16 individuals, caught in the course of June or July that might have been capable of flying. Also LINDROTH (1945) refers to three observations of spontaneous flights between the end of May and the end of July in this species.

Flying individuals of *N. brevicollis* were caught in window-traps twice during the month of June, but in different years and sites. These catches occurred in the middle of the first activity period of this species when only young individuals are active, which agrees with the findings of LINDROTH (1945). From the middle of September onwards during the second activity (reproductive) period, some beetles have been caught in pitfalls with fully developed flight muscles and ripe eggs in their ovaries. Whether or not flying is restricted to the first activity period is therefore not yet clear.

At the beginning of June at a distance of about 40 m from the nearest population one male of *P. oblongopunctatus* was caught in a window-trap. The flight muscles were fully developed, of course, and the wing surface was relatively large. As far as we know this is the first observation which supports LINDROTH's statement (1945) that flight ability occurs in this species with rather small wings (as in *P. versicolor*, see above).

At the end of June 1977 also a single specimen, a female, of *Harpalus latus* L. has been caught with the help of a window-trap. The ovaries were not developed and no Corpora lutea were present. The wing-surface was large as compared with those of individuals caught in pitfalls. The flight period agrees with the findings of LINDROTH (1945).

2.5. Finally some notes on the macropterous species *Loricera pilicornis* F. In this species TIETZE (1963) only found individuals with fully developed flight muscles and thus concluded that autolysis could not occur, by which this species should be one of the few carabid species in which all individuals should be able to fly during their whole life (as the *Cicindela*-spp., and some *Bembidion*-spp.). Contrary to his findings we recently saw some individuals with completely reduced flight muscles; see also SMITH (1964). Some of these beetles had well developed ovaries, filled with ripe eggs.

2.6. Summarizing the notes in this and in the foregoing section we may conclude that within the family of Carabidae the occurrence of seasonal, diurnal and nocturnal flight activities depends greatly on the presence of fully developed flight muscles. With respect to this, considerable differences may exist among macropterous as well as among dimorphic species, which is complicated again by the occurrence of the phenomenon of flight muscle-dimorphism. The latter phenomenon apparently goes together with the more universal cyclic reduction and reconstruction of flight muscles, by which flight activities are generally restricted to periods outside the reproduction season of the species. However, within many species flying of fertilized individuals, with ovaries in different stages may also occur more or less frequently (cf. table 4).

LINDROTH (1949, p. 596) supposes that within the Carabidae fertilized females would only fly in exceptional circumstances. Up to now we randomly investigated only 20% of the species caught in window-traps (16 species); this showed that within 15 of them flying of fertilized females could be demonstrated. However, the two females of *A. plebeja* (viz. table 4), each with one ripe egg, were not fertilized.

Hence we will have to review the current ideas concerning this subject. Fertilized females that fly may be of great importance for the (re)founding of populations, (also see LINDROTH (1949, p. 595)). Also JOHNSON's (1969) statements concerning the universality of the oogenesis-flight syndrome will have to be modified somewhat as far as carabid beetles are concerned: apparently copulation and ovary development don't exclude flight activities completely, by which already developed eggs may be laid outside of the original habitat. A close examination of the flight activities of the individuals from different populations, in different years and in different species in its relations to the reproductive period will be continued. Apart from this it has already been shown in the first part of this paper that flight activities occur when weather conditions are suitable, which agrees with the findings of PAJUNEN (1970), RICHTER (1971) and SOLBRECK (1976).

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REFERENCES

BRIGGS, J. B.: Biology of some ground beetles (Col., Carabidae) injurious to strawberries. Bull. Entomol. Res. **56,** 79–93 (1965).

DEN BOER, P. J.: On the dispersal power of carabid beetles and its possible significance. Miscell. Papers, L. H. Wageningen **8**, 119–137 (1971).

DEN BOER, P. J.: Dispersal power and survival. Miscell. Papers, L. H. Wageningen **14**, 1977.

FRAENKEL, G.: Die Wanderung der Insekten. Ergeb. Biol. **9,** 1–238 (1932).

JOHNSON, C. G.: Migration and dispersal of insects by flight. London: Methuen 1969.

KERSTENS, G.: Coleopterologisches vom Lichtfang. Entomol. Bl. **57,** 119–138 (1961).

LINDROTH, C. H.: Die Fennoskandischen Carabidae I. Göteborgs kgl. Vetensk. Handl. **4** (1), 1–709 (1945).

LINDROTH, C. H.: Die Fennoskandischen Carabidae III. Göteborgs kgl. Vetensk. Handl. **4** (3). 1–911 (1949).

PAARMANN, W.: Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*Pterostichus angustatus* Dft. und *Pterostichus oblongopunctatus* F.) an ihre verschiedenen Lebensräume. Z. Wiss. Zool. **174,** 83–176 (1966).

PAJUNEN, V. I.: Adaptation of *Arctocorisa carinata* (Sahlb.) and *Callocorixa producta* (Reut.) populations to a rock pool environment. Proc. Adv. Study Inst. Dynamics numbers Pop. (Oosterbeek, 1970), 148–158 (1971).

RICHTER, C. J. J.: Some aspects of aerial dispersal in different populations of wolf spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). Miscell. papers L.H. Wageningen **8**, 77–88 (1971).

SMITH, D. S.: The structure and development of flightless Coleoptera: A light and electron microscopic study of the wings, thoracic exoskeleton and rudimentary flight musculature. J. Morph., **114**: 107–184 (1964).

SOLBRECK, C.: Flight patterns of *Lygaeus equestris* (Heteroptera) in spring and autumn with special reference to the influence of weather. Oikos **27**, 134–143 (1976).

TAYLOR, L. R.: Analysis of the effect of temperature on insects in flight. J. Anim. Ecol. **32**, 99–117 (1963).

TIETZE, F.: Untersuchungen über die Beziehungen zwischen Flügelreduktion und Ausbildung des Metathorax bei Carabiden, unter besonderer Berücksichtigung der Flugmuskulatur (Coleoptera: Carabidae). Beitr. Ent. **13**, 88–167 (1963).

VAN DIJK, TH. S.: *Calathus mollis erythroderus* Gemminger & Harold in Drenthe (Coleoptera, Carabidae). Ent. Ber. **38**, 151–153 (1978).

VAN HUIZEN, T. H. P.: The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). Oecologia (Berl.) **29**, 27–41 (1977).

SOME REMARKS IN RETROSPECT

P. J. den Boer

Biological Station of the Agricultural University (Wageningen), Kampsweg 27, 9418 PD Wijster, The Netherlands

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Evolution, as the unifying concept of biology, is the result of an immense collection of generally unique historical processes, which have left only very few direct records. Moreover, the records we need to reconstruct some of the more interesting parts of these histories are usually lacking. On the other hand, evolutionary processes will not be restricted to the past, and if we support the 'principle of topicality' (according to Occam's razor), we should still be able to study such processes as they are occurring at present. If we are interested in the evolution of behaviour this is even the only way to get some insight, since behaviour only in exceptional circumstances leaves any direct fossil records. There remains one major difficulty, however: significant evolutionary changes, as they occurred in the past, apparently took an enormous amount of time. Hence, once again we have to use Occam's razor: important evolutionary changes are assumed to result from an accumulation of smaller changes as these are actually studied by population biologists.

This very concise formulation of the necessary presuppositions for the realization of direct evolutionary research is needed to pose an interesting question: What kind of changes are sufficiently small to be successfully traced and experimented upon during the short period of active life of a field biologist? From the older work on polymorphism (e.g. Cain, Dowdeswell, Ehrlich, Ford, Kettlewell, Sheppard; see Ford, 1964) already it became evident, that in field populations selection processes sometimes may happen surprisingly quickly and may thus result in striking changes, also in organisms with only one generation a year. We have similar experiences with some newly founded populations of wing dimorphic carabid species: within a few years the percentage of fullwinged specimens decreased rapidly (in a young and numerous population of *Calathus mollis erythroderus* Gemm. & Har. in the course of five years the percent macropterous ind. decreased from 80–90 % to 65 %; see also *Trechus obtusus* Er. in Haeck, 1971: Table 6). Hence, also under natural conditions some selection processes may happen fast enough to distinctly alter the composition of the population within the period of observation. On the other hand, Nagel (this volume) mentions that the outward appearance of some Paussinae did not alter for 50 million years. Apparently, in evolution varying rates are possible.

In the above cases of wing dimorphic populations it does not seem very difficult to understand the speed of this process: especially in rather isolated populations the loss of fullwinged specimens flying away will generally be higher than the gain of macropterous individuals appearing from elsewhere (see further: DEN BOER, 1970). In some of the cases discussed by FORD (1964) however, the observed selection pressure upon certain morphological features could not be understood at first sight. Selection must have worked indirectly upon such features, i.e. they must somehow have been genetically closely connected with some vital property of the individuals. Such a situation becomes especially interesting if the morphological features concerned are also decisive taxonomic characters to separate the species from related ones. Measurable changes in such characters would then be indicators of a selection process that might be a reasonable model for processes that have led to speciation among the kind of organisms concerned. An example of this was found in the number of pits on the elytra of *Pterostichus oblongopunctatus* F. (DEN BOER, 1962). This species is taxonomically separated from the closely related *P. angustatus* Dfts. (with 3 pits on each elytron in 89.8 % of 971 ind. studied, or at least with 3 pits on one elytron: 98.4 %) mainly because it has five, six or even more pits on each elytron (in 7 % of the ind. only 4 pits on one of the elytra). The number of pits is partly genetically fixed and the ratio 'low pitters' (4 or 5 pits)/'high pitters' (6 or more pits) in the populations of this forest species is changing from year to year under the apparent (direct or indirect) influence of the yearly changing moisture content of the litter during the period of larval development: 'low pitters' are relatively favoured under dry conditions and 'high pitters' under moist conditions (these correlations were provisionally confirmed by some field experiments and a breeding experiment by THIELE; more data are being studied, and more experiments are planned). In confirmation of this *P. angustatus* (an 'extreme low-pitter', see above) is living in dryer localities than *P. oblongopunctatus*, especially in places were the forest has recently been burned. Hence, the diagnostic character of the number of pits on the elytra is closely connected with habitat preference in these species (see also: MOSSAKOWSKI, this volume). The above example was not only mentioned to illustrate that also among carabid beetles interesting selection processes may sometimes happen fast enough to be studied under field conditions and to be manipulated in experiments, but also to illustrate two other points:

1. Natural selection does not operate on separate genes, but on whole individuals. Therefore, the result of selection will always be a compromise, not only because of the obvious restrictions imposed by the starting material, but also because of the restricted number of combinations of traits that can be realized and/or will be sufficiently viable (e.g. in the above case, the combination of a high number of pits with a high tolerance of dry conditions is apparently impossible). BRANDMAYR (this volume) gives good examples of such compromises among a number of closely related carabid species. Hence, simple optimality models of evolutionary processes will almost necessarily be biologically unrealistic (see also: STEARNS, 1976).
2. Selection can only operate within restricted (local) groups of phenotypically different individuals (and not within 'gene-pools'), thus relatively favouring the survival of the gene-combinations of the best of the available individuals. However, the

above example already illustrates that under different circumstances (e.g. in years with different moisture conditions, but also in different places within the habitat of the same population) different individuals may be the 'best' ones. This means, that it can hardly be expected that natural selection will often be an unidirectional process, although we all hope to have the opportunity of studying such cases (see FORD, 1964). More generally, natural selection will be a complicated, multicausal process the direction of which will often change, because it comprises the integrated result of a number of varying factors that in each generation anew together determine the different magnitudes of the mortality and reproduction of a number of different individuals.

The above remarks not only point to the kind of difficulties one may expect to meet when studying selection processes that occur under field conditions, they also indicate another phenomenon: When natural selection is not unidirectional, but follows a very tortuous route, many different kinds of genes will be preserved in the population in an increasing number of combinations (genotypes). In this way, by continually 'testing', so to speak, the members of the population against a wide variety of different combinations of environmental factors, natural selection will broaden its own base, i.e. the genetic heterogeneity of the population as it is distributed between individuals. It can be expected, that in the long run (when the environment does not change fundamentally) the influence of natural selection will thus become more and more subtile, just as the differences in many characters between the resulting individuals, i.e. in spite of an enormous genetic heterogeneity between individuals the phenotype will have a tendency to become more and more uniform (at least in many features), or to split in a few quite distinct types (polymorphism) with a not very different overall selective value. Note, that the existence of polymorphism within natural populations (which need not to be restricted to morphological features, but is especially very common – and theoretically very important – at many enzyme-producing loci, (see e.g. SCHARLOO, VAN DIJKEN, HOORN, DE JONG & THÖRIG, 1977) already shows that simple optimality models must generally be inadequate (STEARNS, 1976): apparently, in nature there are more 'solutions' for the same 'problem'. In many cases these 'different solutions' will have the significance of 'spreading the risks' that are connected with living in a heterogeneous and/or fluctuating environment over different gene-combinations, (DEN BOER, 1968), e.g.: in our example no larva of *P. oblongopunctatus* is apparently able to tolerate every humidity-value that may occur in the natural environment of the larvae, but by 'dividing' the range of tolerances between 'low-pitters' and 'high-pitters' respectively, the population can nevertheless survive under fluctuating moisture conditions. In this connection it would be very interesting to study the level of polymorphism of populations which have already lived for many generations in nearly constant environments, e.g. deep into caves (see JUBERTHIE, this volume, and WEBER, this volume).

When in the same population natural selection already preserves 'different solutions for the same problem', this may be expected to occur still more between related species living together in the same habitat (in spite of the general belief in 'competitive

Table 1. Life tactics of carabid species that occur together in the litter of oak-birch forests in Drenthe (stable habitat).

Species	breeding season[3]	mean number of eggs in ovaries[4]	larvae in	young adults in[3]	length of life of adults	size class adults[5]	active during the	feeding habits	dispersal power[6]
1	2	3	4	5	6	7	8	9	10
Pterostichus oblongopunctatus F.[1]	spring	13	summer (in the soil)	autumn	> 1 year til 3-4 y.	III	mainly night	polyphagous	(macr. ?) flies only rarely
Agonum assimile Payk.[1]	spring	27	summer (in the soil)	autumn	> 1 year till 3-4 y.	III	night	polyphagous	(macr. ?), no flying ind. so far
Pterostichus strenuus Panz	spring	7	spring (in the soil)	summer	> 1 year	II	night	polyphagous	dim: 23 % m., flies regularly
Carabus nemoralis Müll.	spring	8?	summer (at the surface)	autumn	> 1 year	IV	night (and day?)	oligophagous: worms, snails, etc.	brach.
Loricera pilicornis F.	spring	18	? (at the surface?)	autumn?	only one year?	II	day (and night?)	oligophagous: Collemb., mites	macr., flies regularly
Amara brunnea Gyll.	summer	3	winter? (in the soil)	spring	> 1 year	I-II	night (and day?)	polyphagous, prefers ants?	macr., flies only rarely
Carabus problematicus Hbst.	late in summer	9	winter (at the surface)	June	> 1 year til 3-4 y.	IV	night	oligophagous? snails?	brach.
Abax ater Villers[2]	spring and summer	few	eggs laid in mud cell made by ♀	spring and autumn	> 1 year developm. in two years?	IV	night	oligophagous? mainly worms?	brach.
Calathus piceus Mrsh.[1]	spring (old ind.) summer (juv.)	±7	winter (summer?) (in the soil)	summer (+ few in autumn)	> 1 year till 2 y.	III	night	polyphagous?	dim: 93 % m., flies only rarely
Notiophilus biguttatus F.	spring and autumn	±4	mainly summer (at the surface)	late in spring and in autumn	> 1 year?	I-II	day	oligophagous: Collemb.	dim.: 79 % m., flies infrequently

Notiophilus rufipes Curt.	autumn, winter, spring	±4?	? (at the surface)	?	? > 1 year?	I-II	day	oligophagous? (Collemb.?)	macr., no flying ind. so far
Nebria brevicollis F.[1]	late in autumn	19	winter (at the surface)	spring (aestivation)	only one year	III	night	polyphagous prefers Collemb.?	macr., flies only rarely
Leistus rufomarginatus Dfts.	late in autumn	13	winter (at the surface)	spring (aestivation)	only one year?	II-III	night	oligophagous : Collemb., mites	macr.(?), no flying ind. so far
Trichocellus placidus Gyll.	autumn, winter, spring	?	?	summer	?	I	day (and night?)	?	macr., flies frequently

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[1] see also: DEN BOER, this volume

[2] see also: BRANDMAYR, this volume

[3] see also: PAARMANN, this volume

[4] from VAN DIJK (this volume) it will be evident that the number of eggs in the ovaries does not give reliable information about the number of eggs laid; in each species this relation should be carefully investigated. These numbers are only given here to show that they do not indicate any trend, neither in favour, nor in contradiction of the theories of r-and K-selection, and we expect that better information would not give a significant difference between the species of Table 1 and those of Table 2 in this respect.

[5] size-classes:
I. < 5 mm
II. 5–$8\frac{1}{2}$ mm
III. 9–$12\frac{1}{2}$ mm
IV. $> 12\frac{1}{2}$ mm

[6] abbreviations: (macr. ?) = although the wings are larger than the elytra there is some doubt about the possibility of using them for flying (see also: VAN HUIZEN, this volume).

dim: 23% m. = wing dimorphic (or polymorphic) with 23% of the individuals studied with fully developed wings.

macr. = macropterous, i.e. wings always fully developed. brach. = brachypterous. i.e. no individuals with functional wings.

flies only rarely = in the course of 5–8 years sampling with window-traps only one or two specimens were caught during flying.

flies (very) regularly = each year a few (sometimes more) specimens are caught in window-traps.

flies (very) frequently = each year during the whole flight (migration?) period specimens (sometimes even many) are caught in window traps.

Table 2. Life tactics of carabid species that occur together at the surface of recently abandoned agricultural fields in Drenthe (unstable habitat).

Species	breeding season^3	mean number of eggs in ovaries^4	larvae in	young adults in^3	length of life of adults	size class adults^5	active during the	feeding habits	dispersal power^6
1	2	3	4	5	6	7	8	9	10
Amara plebeja Gyll.^{1}	spring	10	summer (in the soil)	August-Sept.	> 1 year	II	day	phytophagous	macr., all ind. fly 2x a year!
Amara aenea de Geer	spring	?	summer (in the soil)	autumn	> 1 year	II	day	mainly phytophagous	macr., flies very frequently
Amara familiaris Dfts.	spring	8	summer (in the soil)	late in summer	> 1 year	II	day	mainly phytophagous?	macr., flies very frequently
Amara lunicollis Schiödte	spring-summer	5	summer (in the soil)	summer-autumn	> 1 year	II	day	polyphagous	macr., flies regularly
Anisodactylus binotatus F.	spring	5	summer (in the soil)	late in summer	> 1 year	III	day + night?	polyphagous	macr., flies very regularly
Loricera pilicornis F.	spring	18	? (at the surface?)	autumn?	only 1 year?	II	day (+ night?)	oligophagous: Collemb., mites	macr., flies regularly
Pterostichus coerulescens L.	spring	12^2	summer (in the soil)	autumn	> 1 year till 3-4 y.	III	day	polyphagous	(macr.?) flies only rarely
Bembidion lampros Hbst.	spring	5^7	?	autumn	?	I	day	oligophagous: mainly eggs	dim: 17 % m. does not fly frequently
Carabus cancellatus Illig.	spring	?	summer (at the surface)	autumn	> 1 year	IV!	day	oligophagous: snails, worms	brach.
Harpalus aeneus F.^{8}	spring + summer	?	mainly summer (in the soil)	summer + autumn	> 1 year till 3-4 y.	III	day	phytophagous?	macr., flies regularly
Harpalus pubescens Müll.	late in summer	5	summer? (in the soil)	summer, also late in autumn	> 1 year	IV	night	very polyphagous	macr., flies very regularly

Amara apricaria Payk.	late in summer	?	spring, winter (in the soil)	early in summer	> 1 year	II	night?	polyphagous	macr., flies very regularly
Calathus fuscipes Goeze	autumn	?	winter (in the soil?)	June	> 1 year	III	night	polyphagous	dim: 0.85 % m. no flying ind.
Pterostichus vulgaris L.	autumn	?	winter (in the soil)	late in summer	> 1 year	IV	night	polyphagous	dim: 2 % m. no flying ind. so far
Notiophilus aquaticus L.	during the whole year!	±4?	? (at the surface)	spring, summer + autumn	? > 1 year?	I-II	day	oligophagous? ; Collemb.?	dim: 1.2 % m. no flying ind. so far
Bradycellus harpalinus Payk.	autumn, winter, spring	5	?	late in summer	> 1 year	I	day (night?)	phytophagous	dim: 78 % m. flies in very high numbers (thousands)

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[1] see also: VAN HUIZEN (1977)
[2] see also: VAN DIJK (1979), and this volume
[3], [4], [5], [6] as Table 1
[7] from MITCHELL (1963)
[8] data from SCHJØTZ-CHRISTENSEN (1965)

exclusion', within a restricted area – like Drenthe – related species are more often than not coexisting; see e.g. WILLIAMS, 1964; for carabids, see also THIELE, 1977). A good example is given by NAGEL (this volume), who shows that Paussinae developed two quite different solutions to solve the problem 'How to live with ants?', the 'Trutztyp' and the 'Symphilentyp'. Therefore, it seems not very pobable that only special assemblages of traits will co-evolve, and will thus always be found together as 'optimal strategies', as is predicted in theories of r- and K-selection (compare e.g. BAUER, 1971, with BAUER, this volume). This latter approach, which has already been critized sufficiently by STEARNS (1976), is based on a number of biologically unrealistic assumptions, by which these ideas in fact cannot be tested. The only thing one can do with it, is–and this is rather in fashion at the moment–selecting examples that more or less seem to be 'r-strategists' or 'K-strategists' respectively. But one cannot make science by carefully selecting examples that seem to confirm some idea, as long as one does not also logically exclude the possibility of collecting counter-examples. To illustrate the latter point I wrote down what I know at the moment about the 'life tactics' (STEARNS, 1976) of the carabid beetles that generally live together in rather high numbers. Table 1 shows the species from the oak-birch forests of Drenthe (a stable habitat that should favour 'K-strategists'). Table 2 shows the species from very recently abandoned agricultural fields in Drenthe (an unstable habitat that should favour 'r-strategists).

Although much of the data in these tables (especially those in column 3) are only provisional, a comparison clearly suggests that among carabid species no special combination of traits has co-evolved to enable (or even 'maximize') survival in either a stable or an unstable habitat. All kinds of annual reproductive rhythms (compare PAARMANN, this volume) are apparently possible in both stable and unstable habitats. Actual differences between these two groups of carabid species are apparently not found among life-history traits (columns 2–6), but among other features: forest species are generally night-active, whereas most species from unstable habitats (but also of other open sites) are day-active (column 8); some carabid species from unstable habitats (only when these are associated with agricultural fields, or other man-made sites) are more or less phytophagous (column 9); most species from unstable habitats have high powers of dispersal, whereas the dispersal power of most forest species is low (column 10); (see also VAN HUIZEN, this volume). Only the latter trait is directly connected with the degree of stability of the habitat (see DEN BOER, 1977), but is – interestingly enough – not joined to a higher or lower reproductive power (column 3),* and/or a shorter or longer adult life (column 6), as predicted by theorists on r- and K-selection (STEARNS, 1976). It is also apparent in this respect that many 'solutions for the same problem' (survival in a certain kind of habitat) are possible.

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*Although these data cannot be trusted (see VAN DIJK, this volume), they at least indicate that a species such as *Agonum assimile* (Table 1) will not always lay low numbers of eggs, whereas species like *Anisodactylus binotatus*, *Bembidion lampros*, *Harpalus pubescens*, *Bradycellus harpalinus* (Table 2) will not lay very high numbers of eggs.

This does not mean, however, that we do not sometimes meet with examples that seem to confirm the ideas behind r- and K-selection. A good example is found in PAARMANN (1966): *P. angustatus* (living in unstable habitats, see above) on average produces about twice as many eggs as *P. oblongopunctatus* (living in stable habitats, see above); see also THIELE (1977, p. 132). I am quite sure, however, that it will be possible to find counter-examples (see above). This example only tells us that *P. angustatus* produces more eggs than *P. oblongopunctatus*, but not that *P. angustatus* necessarily has been 'r-selected', i.e. the work of PAARMANN (1966) is important independent of these – untestable – theories.

Each of us in his own field of study has already discovered that it is impossible to evade the hard work of rigorous empiricism (compare e.g. MOLS, this volume). There is especially no easy way to develop general insights about the diversity of nature. From the foregoing it will be evident that even the construction of general mathematical models in most cases will not bring us closer to that goal. This does not imply that such models cannot be very useful to order and test our thoughts, or the thoughts of others, concerning nature. To test nature itself however, we will have to study, compare and manipulate populations (see e.g. THIELE, this volume; LEYK, this volume). Populations are composed of individuals (see DEN BOER, this volume), we will therefore have to know the properties of these individuals, and to study how they use this equipment to react to the environment, in an attempt to begin to understand population processes. On this reason autecologists, who study the same kind of animals from different aspects, need each other. To be able to quantify these processes we will also have to take into account the variability of these properties and reactions within populations (see e.g. VAN DIJK, this volume), and here population biologists will have to invoke the help of autecologists and biomathematiciens.

We therefore hope that this symposium will be the start of the kind of cooperation that will help us more than the construction of simple 'optimality models' to understand the processes that govern the diversity of at least one group of organisms. The review by THIELE (1977) made it evident that for this purpose carabid beetles are very suitable material.

REFERENCES

BAUER, TH.: Zur Biologie von *Asaphidion flavipes* L. (Col., Carabidae). Ent. Z. **81**: 154–164 (1971).

DEN BOER, P. J.: Fluctuations in morph frequency in catches of the ground beetle *Pterostichus oblongopunctatus* F. and its ecological significance (1962). Can be obtained from the library of the Biol. Station, Wijster.

DEN BOER, P. J.: Spreading of risk and stabilization of animal numbers. Act. Biotheor. (Leiden) **18**: 165–194 (1968).

DEN BOER, P. J.: On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). Oecologia (Berl.) **4**: 1–28 (1970).

DEN BOER, P. J.: Dispersal power and survival. Carabids in a cultivated countryside. Miscell. Papers, Landb. Hogeschool, Wageningen **14** Veenman & Zn. (1977).

FORD, E. B.: Ecological genetics. Methuen & Co. Ltd. London, 1964.

HAECK, J.: The immigration and settlement of carabids in the new IJsselmeerpolders. Miscell. Papers, Landb. Hogeschool Wageningen **8**: 33–52. Veenman & Zn., (1971).

MITCHELL, B.: Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). 1. Life cycles and feeding behaviour. J. An. Ecol., **32**: 289–299 (1963).

PAARMANN, W.: Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*Pterostichus angustatus* Dfts, und *Pterostichus oblongopunctatus* F.) an ihre verschiedenen Lebensräume. Z. wiss. Zool. **174**: 83–176 (1966).

SCHARLOO, W., F. R. VAN DIJKEN, A. J. W. HOORN, G. DE JONG & G. E. W. THÖRIG: Functional aspects of genetic variation. In F.B. CHRISTIANSEN & T. FENCHEL (eds.): Measuring selection in natural populations. Springer Verlag, Heidelberg, 1977.

SCHJØTZ-CHRISTENSEN, B.: Piology and population studies of Carabidae of the Corynephoretum. Natura Jutlandica **11**: 1–173 (1965).

STEARNS, C.: Life-history tactics: a review of the ideas. Quart. Review Biol. **51**: 3–47 (1976).

THIELE, H. U.: Carabid beetles in their environments. Springer Verlag, Heidelberg, 1977.

VAN DIJK, TH, S.: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. (Coleoptera, Carabidae). Oecologia (Berl.) **40**: 63–80 (1979).

VAN HUIZEN, T. H. P.: The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). Oecologia (Berl.) **29**: 27–41 (1977).

WILLIAMS, C. B.: Patterns in the balance of nature. Academic Press London, 1964.