FLYING FOR LIFE

WING DIMORPHISM IN CLOSELY RELATED SPECIES OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE)

Berend Aukema

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Promotor: Dr. J. C. van Lenteren
Hoogleraar in de Entomologie, in het bijzonder de oecologie der insekten

Co-promotor: Dr. P. J. den Boer
Universitair Hoofddocent Vakgroep Natuurbeheer

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Stellingen

1. De veronderstelling, dat voor geïsoleerde populaties van vleugeldimorfe loopkeversoorten het percentage langvleugelige kevers een "maat" is voor de ouderdom van de betreffende populaties, geldt niet voor die soorten, waarbij de vleugelontwikkeling genetisch bepaald is volgens een eenvoudige Mendelsplitsing met kortvleugelig dominant, maar waarbij de expressie van het langvleugelig genotype door omgevingsfaktoren wordt bepaald.

   (dit proefschrift; Lindroth, C. H., 1949. Die Fennoskandischen Carabiden 3: 1-911; 1979. In: Ball, G.E. & T.L. Whitehead (eds). *Carabid beetles, their evolution, natural history and classification*: 385-394; Den Boer, P. J., 1970. Oecologia 4: 1-28)

2. Vleugelontwikkeling (en vliegspierontwikkeling) vindt bij *Calathus melanocephalus* uitsluitend plaats onder "gunstige" milieuomstandigheden, zoals bijvoorbeeld de beschikbaarheid van voldoende voedsel en relatief hoge temperaturen, en vormt derhalve geen spontane reactie op "ongunstige" omstandigheden tijdens de larvale ontwikkeling.

   (dit proefschrift; Harrisson, R.G., 1980. *Annual Review of Ecology and Systematics* 11: 95-118; Van Schaick Zillesen, P. G. & A. M. H. Brunsting, 1984. *Entomologia Generalis* 9: 143-147)

3. Het ondubbelzinnig vaststellen van de taxonomische status van te bestuderen organismen dient bij elk onderzoek een eerste vereiste te zijn.

4. Ook zonder de veronderstelling, dat de dominante, kortvleugelige vorm van een vleugeldimorfe soort reproduktief in het voordeel is ten opzichte van de langvleugelige vorm, zijn de ontwikkeling en het voortbestaan van vleugeldimorfie in een heterogene omgeving te verklaren.

   (Roff, D. A., 1994. *The American Naturalist* 144: 772-798)

5. De fylogenie kan ons inzicht in evolutionaire gebeurtenissen, die in verband staan met de reductie van het vliegvermogen bij insekten, aanzienlijk verrijken.

   (Wagner, D. L. & J. K. Liebherr, 1992. *Tree* 7: 216-220)

6. Het door gemakzucht ingegeven voornemen om in de zoölogische nomenclatuur het tussen haakjes plaatsen van auteursnamen bij niet-originele combinaties van geslachts- en triviaalnaam af te schaffen, betekent een verarming van die nomenclatuur.

7. Bij het toepassen van biologische bestrijding van plaaginsekten dienen bij voorkeur inheemse parasieten en predatoren gebruikt te worden, omdat onze kennis met betrekking tot te verwachten neveneffecten van vestiging in de openlucht van niet-inheemse biologische bestrijders in het algemeen onvoldoende is.

8. Het privatiseren van diagnostiek verricht ten behoeve van de gewasbescherming staat op gespannen voet met de doelstellingen van het Meerjarenplan Gewasbescherming.

9. Natuurbescherming gebaseerd op zogenaamde "rode lijsten" van kwetsbare en bedreigde insekten mag niet leiden tot het uitsterven van "prikkebeen".

10. Natuurontwikkeling dient gericht te zijn op natuurlijke ontwikkeling, waarbij het opzettelijk (her)introduceren van planten en dieren zoveel mogelijk achterwege dient te blijven.

11. Sommige loopkevers doen het vliegend.

Stellingen behorende bij het proefschrift

"Flying for life. Wing dimorphism in closely related species of the genus *Calathus* (Coleoptera: Carabidae)"

Berend Aukema, Wageningen, 6 juni 1995

voor mijn vader
ter nagedachtenis aan mijn moeder

CONTENTS

I. INTRODUCTION

WING REDUCTION IN GROUND BEETLES (COLEOPTERA: CARABIDAE)

Flightlessness is a very common phenomenon in insects, also occurring in almost all pterygote orders (see Harrison (1980), Dingle (1986), Roff (1990) and Wagner & Liebherr (1992) for recent reviews). In the order Coleoptera, however, flightlessness is estimated to occur in less than ten percent of the known species, and in both males and females (Roff, 1990). Flightlessness in pterygote insects can be caused by either wing reduction, or the absence of functional flight muscles, or both. In Coleoptera both phenomenons occur, but hind wing reduction is the most obvious one. With regard to hind wing development species of the family Carabidae of this order can be classified as monomorphic, dimorphic, and polymorphic. In wing-monomorphic species all individuals show the same hind wing development: they are all short winged (brachypterous) or long winged (macropterous). In wing-dimorphic species individuals are either short winged, or long winged, whereas in wing-polymorphic species also intermediate wing-lengths occur. Short winged beetles are not able to fly, whereas long winged beetles may have flight capability, depending on relative wing size (Den Boer, 1977; Den Boer et al., 1980; Desender, 1989a), and the possession of fully developed wing muscles (Tietze, 1963; Van Huizen, 1979). Actual flight furthermore depends on weather conditions (Van Huizen, 1979).

In Coleoptera wing polymorphism has caught the attention since the times of Wollaston (1854; see also Roff, 1990), and Darwin (1859), both describing and discussing the high percentage of flightless beetles on the isles of the Madeira archipelago. Darwin was the first to recognize the evolutionary significance of the phenomenon of wing polymorphism in Coleoptera, by supposing that in the case of island populations flying specimens will be blown into the sea and thus be gradually eliminated by selection. In later years Darlington (1936, 1943, 1970, 1971) was struck by the frequent wing reduction observed in Carabidae from mountain tops and islands. He stated that in such isolated populations flightless morphs would be favoured because of a generally higher "viability". Palmén (1944) showed that only long winged specimens of wing-dimorphic species were washed ashore at the Northern coast of the Gulf of Finland after suitable weather conditions for flight.

Lindroth (1949, 1969) based his theory about the recolonization of Fennoscandia by carabid beetles after the last glaciation on the "postulate that long winged (macropterous) individuals are homozygotes and that populations entirely or very dominantly consisting of such individuals are pioneers (late colonizers)". This point was picked up by Den Boer (1970) in studying the differences in wing-morph frequencies between populations of carabid beetles in old and newly founded populations. Indeed, in general he found a considerable higher frequency of macropterous beetles among newly founded populations in the new polders, than in "old mainland" populations of the same species in the province of Drenthe. From these results Den Boer concluded that fully winged individuals "must have a much greater dispersal power than the flightless ones". Similar data were presented by Haeck (1971).

THE GENETIC BASIS OF WING DIMORPHISM

Two general models for the determination of wing-morph in insects (fig. 1) were presented by Roff (1986; see also Roff & Fairbairn, 1991; Fairbairn, 1994; Roff, 1994), based on a total of 29 cases of data of wing morph determination in Coleoptera (5 cases), Diptera (1), Hemiptera (6), Homoptera (5), Hymenoptera (2), Orthoptera (5), and Dermaptera (2). Two types of genetic determination were found: single locus systems, typically with the brachypterous condition dominant, and polygenic systems. In both cases the determination of wing-length is supposed to be subsumed under a single physiological mechanism based upon a threshold response to titres of juvenile hormone, wing production being suppressed if the titre of the juvenile hormone exceeds some threshold level at a particular stage of development. So, environmental control is supposed to act indirectly by influencing the physiology of immature stages in a susceptible stage.

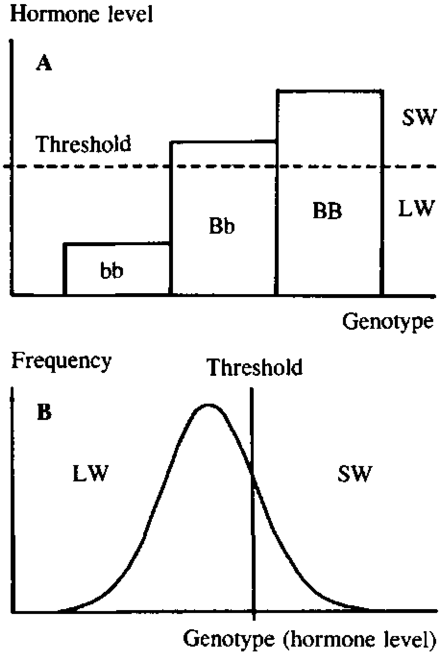

Fig. 1. Threshold models for determination of wing-morph. A, single locus, two-allele system with short winged dominant; B, polygenic system with additive effects of loci. SW: short winged; LW: long winged (source: Roff, 1986).

Lindroth (1946) was the first to start experimental work to unravel the determination of wing dimorphism in carabid beetles. He performed a limited cross-breeding experiment with the wing-dimorphic *Pterostichus anthracinus* (Illiger). He concluded that wing dimorphism in this species is inherited in a simple Mendelian fashion, i.e. a single locus, two-allele system, with the brachypterous condition dominant. The fact that Jackson (1928) got similar results with the weevil *Sitona hispidula* (Fabricius) tempted Lindroth (1946) to the statement, that "it therefore seems probable that the non-sexual wing dimorphism as a whole will prove to be of the same type". Indeed, Stein (1973) got comparable results with another weevil, *Apion virens* Herbst. However, concerning carabid beetles only a few efforts since have been made to confirm Lindroth's results. The data of Carter (1976) and Langor & Larson (1983) with *Agonum retractum* Leconte and *Bembidion lampros* (Herbst), respectively, do not allow unambiguous conclusions concerning the type of inheritance involved in this species. Desender (1989b) showed a high heritability of relative wing development in the wing-polymorphic *Pogonus chalceus* (Marsham).

Even less attention has been paid to the determination of flight muscle development in Carabidae. Van Schaick Zillesen (1984) and Nelemans (1987) showed that in both *Pterostichus oblongopunctatus* (Fabricius) and *Nebria brevicollis* (Fabricius), respectively, wing muscle development is at least under environmental control, but a similar genetic determination as in wing-morph cannot be excluded.

THE EVOLUTION OF WING DIMORPHISM

The evolutionary significance of wing polymorphism and dimorphism in Carabidae in relation to dispersal and habitat persistence was discussed by Den Boer (1970, 1971), and Den Boer et al. (1980). In general, their analysis of data on dispersal supported the hypothesis of Southwood (1962) that "within one taxon one should find a higher level of migratory movement in those species associated with temporary habitats than in those with more permanent ones", or in other words flightlessness will be favoured by habitat persistence. So, basically the evolution of flightlessness is supposed to be caused by disruptive selection induced by environmental heterogeneity. Similar results for Heteroptera (water striders), and Homoptera (plant-hoppers) have been listed by Roff (1990), and also his own analysis of Orthoptera of North America supports the hypothesis of Southwood.

Roff (1990) showed on the basis of mainly literature data that in Carabidae there is a significant trend for the incidence of flightlessness to increase with both altitude and latitude. Moreover, taking into account both altitude and latitude Roff (1990) found that oceanic islands in general do not have incidences of flightless insects higher than expected. Both altitudal and latitudal changes in the incidence of flightlessness may be a consequence of related changes in habitat persistence, or the inhibitory effects of low temperature favouring the evolution of flightlessness, but at present there are not sufficient data to test these hypotheses (Roff, 1990).

It is argued that since macropters are not necessarily migrants, the existence of short winged morphs implies a trade-off between flight capability and other fitness components (Roff & Fairbairn, 1991; Wagner & Liebherr, 1992), as for instance a decrease in the age of first reproduction and increased fecundity in the morph with reduced wings.

WING DIMORPHISM IN THE *CALATHUS MELANOCEPHALUS*-GROUP

The present study is aimed at the unravelling of the background of wing dimorphism in the closely related ground beetle species of the *Calathus melanocephalus*-group in relation to dispersal phenomena. The species of this group were selected for this study because the wing-dimorphic *Calathus melanocephalus* (Linnaeus) is one of the major species of the research program of the Biological Station at Wijster, focusing on population dynamics of carabid beetles in relation to dispersal (see e.g. Den Boer, 1990a, 1990b; Van Dijk, 1994; Van Dijk & Den Boer, 1992). From observations in the reclaimed IJsselmeerpolders (Den Boer, 1970; Haeck, 1971) it was shown that this species was able to found new populations with a high proportion of long winged beetles, despite the fact that normally the number of macropters in known populations was extremely low. Moreover, the sudden appearance of populations of '*melanocephalus*-like' beetles with an extremely high proportion of long winged beetles in the area of the field experiments of the Biological Station (Van Dijk, 1978) urged this study.

At first cross-breeding experiments and morphological studies were carried out to clarify the taxonomy of the taxa involved. The nomenclature of the species concerned was sorted out and data on their life-history and distribution were gathered (Chapter II, Appendix A-C). Single-pair crosses were carried out under different temperature and food conditions to establish the genetic background of wing dimorphism and the possible effect of temperature and food-supply on wing development (Chapter III). Differences in fecundity (egg production and oviposition period, Chapter IV) and development times and growth (Chapter V) were studied to detect possible differences in fitness between short and long winged beetles. Finally, flight muscle development and actual flight were studied (Chapter VI). The results were discussed in relation to current knowledge about the evolution and maintenance of wing dimorphism (Chapter VII).

REFERENCES

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera: Carabidae).- *Oecologia* 4: 1-28.

Boer, P. J. den, 1971. On the dispersal power of carabid beetles and its possible significance. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 8: 119-137.

Boer, P. J. den, 1977. Dispersal power and survival. Carabids in a cultivated countryside.- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J. den, 1990a. Density limits and survival of local populations in 64 carabid species with different powers of dispersal.- *Journal of Evolutionary Biology* 3: 19-48.

Boer, P. J. den, 1990b. The survival value of dispersal in terrestrial arthropods.- *Biological Conservation* 54: 175-192.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae).- *Entomologia Generalis* 6: 107-134.

Carter, A., 1976. Wing polymorphism in the insect species Agonum retractum Leconte (Coleoptera: Carabidae).- *Canadian Journal of Zoology* 54: 1375-1382.

Darlington, P. J., 1936. Variation and atrophy of flying wings of some carabid beetles.- *Annals of the Entomological Society of America* 49: 136-179.

Darlington, P. J., 1943. Carabidae on mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings.- *Ecological Monographs* 13: 39-61.

Darlington, P. J., 1970. Carabidae on tropical islands, especially the West Indies.- *Biotropica* 2: 7-15.

Darlington, P. J., 1971. The carabid beetles of New Guinea. Part IV. General considerations; analysis and history of fauna; taxonomic supplement.- *Bulletin of the Museum of Comparative Zoology* 142: 129-339.

Darwin, C., 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*: 1-389. Hazel, Watson & Viney, London.

Desender, K., 1989a. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Desender, K., 1989b. Heritability of wing development and body size in a carabid beetle, Pogonus chalceus Marsham, and its evolutionary significance.- *Oecologia* 78: 513-520.

Dijk, Th. S. van, 1978. Calathus mollis erythroderus Gemminger & Harold in Drenthe (Coleoptera, Carabidae).- *Entomologische Berichten, Amsterdam* 38: 151-153.

Dijk, Th. S. van, 1994. On the relationship between food, reproduction and survival of two carabid beetles: Calathus melanocephalus and Pterostichus versicolor.- *Ecological Entomology* 19: 263-270

Dijk, Th. S. van & P. J. den Boer, 1992. The life histories and population dynamics of two carabid species on a Dutch heathland. 1. Fecundity and the mortality of immature stages.- *Oecologia* 90: 340-352.

Dingle, H., 1986. Evolution and genetics of insect migration. In: *Insect flight, migration and survival* (W. Danthanarayana ed.): 11-26. Springer, Berlin.

Fairbairn, D. J., 1994. Wing dimorphism and the migratory syndrome: correlated traits for dispersal tendency in wing dimorphic insects.- *Proceedings of the Memorial and International Symposium on Dispersal Polymorphism of Insects, its Adaptation and Evolution, Okayama, Japan*: 143-152.

Haeck, J., 1971. The immigration and settlement of carabids in the new IJsselmeer-Polders. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 8: 33-52.

Harrison, R. G., 1980. Dispersal polymorphisms in insects.- *Annual Review of Ecology and Systematics* 11: 95-118.

Huizen, T. H. P. van, 1979. Individual and environmental factors determining flight in Carabid beetles. In: On the evolution of behaviour in carabid beetles (P.J. den Boer, H. U. Thiele & F. Weber, eds).- *Miscellaneous Papers of the Agricultural University Wageningen* 18: 199-211.

Jackson, D. J., 1928. The inheritance of long and short wings in the weevil, Sitona hispidula, with a discussion of wing reduction among beetles.- *Transactions of the Royal Society of Edinburgh* 55: 665-735.

Langor, D. W. & D. J. Larson, 1983. Alary polymorphism and life history of a colonizing ground beetle, Bembidion lampros Herbst (Coleoptera: Carabidae).- *The Coleopterists Bulletin* 37: 365-377.

Lindroth, C. H., 1946. Inheritance of wing dimorphism in Pterostichus anthracinus Ill.- *Hereditas* 32: 37-40.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae. 3. Allgemeiner Teil.- *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar* 6, Ser. B 4 (3): 1-911.

Lindroth, C. H., 1969. The theory of glacial refugia in Scandinavia. Comments on present opinions.- *Notulae Entomologicae* 49: 178-192.

Nelemans, M. N. E., 1987. Possibilities for flight in the carabid beetle Nebria brevicollis (F). The importance of food during adult larval growth.- *Oecologia* 72: 502-509.

Palmén, E., 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor.- *Annales Zoologici Societatis Zoologicae-Botanicae Fennicae, Vanamo* 10: 1-262.

Roff, D. A., 1986. The evolution of wing dimorphism in insects.- *Evolution* 40: 1009-1020.

Roff, D. A., 1990. The evolution of flightlessness in insects.- *Ecological Monographs* 60: 389-421.

Roff, D. A., 1994. Habitat persistence and the evolution of wing dimorphism in insects.- *The American Naturalist* 144: 772-798.

Roff, D. A. & D. J. Fairbairn, 1991. Wing dimorphism and the evolution of migratory polymorphisms among the insecta.- *American Zoologist* 31: 243-251.

Schaick Zillesen, P. G. van & A. M. H. Brunsting, 1984. The influence of food quantity and photoperiod during the pre-adult stages on flight muscle development in adult Philonthus decorus (Coleoptera: Staphilinidae) and Pterostichus oblongopunctatus

(Coleoptera: Carabidae).- *Entomologia Generalis* 9: 143-147.

Southwood, T. R. E., 1977. Habitat, the templet for ecological strategies?- *Journal of Animal Ecology* 46: 337-365.

Stein, W., 1973. Zur Vererbung des Flügeldimorphismus bei Apion virens Herbst (Col., Curculionidae).- *Zeitschrift für Angewandte Entomologie* 74: 62-63.

Tietze, F., 1963. Untersuchungen über die Beziehungen zwischen Flügelreduktion und Ausbildung des Metathorax bei Carabiden unter besonderer Berücksichtigung der Flugmuskulatur (Coleoptera, Carabidae).- *Beiträge zur Entomologie* 13: 88-167.

Wagner, D. L. & J. K. Liebherr, 1992. Flightlessness in insects.- *Tree* 7: 216-220.

Wollaston, T.V., 1854. *Insecta Madeirensia; being an account of the insects of the islands of the Madeiran group*: 1-xlii, 1-634, 13 plates. Van Voorst, London.

II. TAXONOMY, LIFE-HISTORY AND DISTRIBUTION OF THREE CLOSELY RELATED SPECIES OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE) *

ABSTRACT

After cross-breeding experiments between *Calathus melanocephalus*, *C. mollis mollis* and *C. mollis cinctus* and analysis of morphological data of these taxa, *Calathus cinctus* is established as a good species.
An identification key for the three species is given, main morphological differences are depicted and data on their biotope, life-history, distribution and time trends are provided and discussed.

Key words: Carabidae, *Calathus, cinctus, melanocephalus, mollis*, cross-breeding, identification key, life-history, distribution maps, time trends.

INTRODUCTION

In the past the status of *Calathus melanocephalus* (Linnaeus, 1758) and *C. mollis* (Marsham, 1802) as different species has been questioned many times, mainly because of the frequent occurrence of morphologically intermediate specimens. Schatzmayr (1937), Lindroth (1943) and Wiebes-Rijks (1949) treated them as distinct species, whereas Friederichs (1907) and Gersdorf (1937) could not find any distinguishing characters between both taxa at all. Furthermore the existence of a morphologically intermediate form *cinctus* Motschulsky, 1850 (= *erythroderus* Gemminger & Harold, 1868), established as a subspecies of *mollis* by Lindroth (1945), masks the status of these taxa.

This so-called *melanocephalus* group belongs to *Neocalathus*, established as a subgenus of the genus *Calathus* Bonelli by Ball & Negre (1972) with *Calathus melanocephalus* as the type species. For nomenclature in the *melanocephalus* group see Appendix (Aukema, 1990; Aukema & Luff, 1992; Opinion 1723/1993).

The discovery of populations of a *cinctus*-like *Calathus* on abandoned agricultural fields in the surroundings of the Biological Station of the Agricultural University, Wageningen, at Wijster (Van Dijk, 1978) offered a good opportunity for studying its taxonomic relationship with both *C. melanocephalus* and *C. mollis*, and its life-history.

Moreover, in the present study cross-breeding experiments between these three

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taxa were carried out to elucidate their taxonomic status. Morphological data (including biometrics) were used to support the resulting classification.

The taxonomic characters given in literature to distinguish *Calathus melanocephalus* and *C. mollis* from each other are:

1. The coloration of the pronotum in comparison to the head (and elytra): clear rufous, contrasting with the black head and elytra in *Calathus melanocephalus*, and piceous to brown and not or little contrasting in *C. mollis*. In the typical form of *C. melanocephalus* and in C. *mollis* all appendages are pale. However, a varying degree of melanism may occur in C. *melanocephalus*, in which the pronotum is more or less infuscated, from possessing only a faint cloud at the center to being black with only narrowly translucent margins (in that case also the appendages are melanistic, at least tarsi brown, often also the main part of legs and palps, as well as middle antennal segments (Jeannel, 1942; Lindroth, 1974, 1986; Vereshchagina, 1985).

2. The shape and size of the right paramere: widened at the tip and hooked at the extreme apex in *Calathus melanocephalus* and not widened and unarmed or with a very small hook at the apex in *C. mollis* (Lindroth, 1974, 1986; Freude, 1976; Vereshchagina, 1985). Differences in internal and external morphology of the vesica are indicated by Lindroth (1943) and Vereshchagina (1985).

3. The dimensions of the met-episterna: short in *Calathus melanocephalus* (ca. 1.6 times as long as wide in both brachypterous and macropterous specimens), and longer in macropterous specimens of *C. mollis* (ca. 1.8 times as long as wide) (Jeannel, 1942; Lindroth, 1974; Freude, 1976; Vereshchagina, 1985).

4. The shape of the pronotum: more slender, with the greatest width usually before the middle and clearly narrowed towards the base in *Calathus mollis*, and less slender, with the greatest width in or behind the middle and sides less convergent in the basal half in *C. melanocephalus* (Freude, 1976; Lindroth, 1986; Vereshchagina, 1985).

5. The shape of the elytra: longer oval (more stretched), with lateral margin curved and gradually tapering apically in *Calathus mollis*, and shorter oval, with sides almost parallel and broadly rounded apically in *C. melanocephalus* (Freude, 1976; Lindroth, 1986).

According to both Lindroth (1974, 1986) and Freude (1976) the subspecies *Calathus mollis cinctus* (at the time known as *C. mollis erythroderus)* can be distinguished from *C. mollis mollis* by the entirely rufous pronotum, contrasting with the piceous to brown head and elytra. Van Dijk (1978) furthermore mentions a difference in the colour of the sternites between *C. cinctus* and *C. melanocephalus*.

Material collected in the field was studied to evaluate the usefulness of these characters for identification.

Finally museum collections were revised in order to get an impression of their distributions in The Netherlands. Due to misidentification of much of the material in the past, existing distribution maps of the taxa concerned (Turin et al., 1977) have to be replaced.

The taxonomic status of the three taxa mentioned above is unravelled and the data presented lead to the conclusion that *Calathus cinctus* is a good species. Data on habitat, life-history and distribution of *C. cinctus*, C. *melanocephalus* and C. *mollis* are given.

MATERIAL AND METHODS

Cross-breeding experiments

Single-pair crosses between all possible combinations of the three taxa were carried out during 1978/1979 and 1979/1980 under approximately outside conditions in an outdoor insectary. In 1978/1979 selected pairs were kept either in glass jars in sieved peat litter (group 1) or in petri dishes in ground peat litter (group 2). In the first case newly emerged larvae were gathered from the peat litter as described by Van Dijk (1979a), whereas for the second group eggs were separated from the peat according the sieve-wash method of Mols et al. (1981). Eggs were incubated at a constant temperature of 19 °C. Larvae were moved to glass tubes in which they were reared individually in peat litter in the outdoor rearing facility. During the winter months (from the end of November until the end of March) the larvae were moved to a climate room at 5 °C under short day (LD 10/14) conditions. Single-pair crosses of males and females of the same taxon served as control groups. Crosses and origin of the beetles used are given in table 1.

Offspring of crosses performed by Van Dijk (1978) in 1977/1978 and specimens collected in the field before the start of the reproduction period (tenerals in the case of females; *Calathus cinctus* from Dwingeloo, C. *melanocephalus* from Kraloo, and *C. mollis* from Voorne) were used as starting material (table 1). Furthermore offspring of females inseminated in the field (*C. cinctus* from Nuil and Dwingeloo, and *C. melanocephalus* from Oost-Flevoland) were reared in order to get virgin females as starting material for the next crossing programme.

In 1979/1980 crosses were carried out comparable to those of group 2 of the preceding year. The food, however, was changed from pieces of mealworm to small

Table 1. Single-pair crosses between and within *Calathus cinctus*, *C. melanocephalus* and *C. mollis* (1978/1979). cin: *cinctus;* mel: *melanocephalus;* mol: *mollis;* LW: long winged; SW: short winged; N: number of crosses; NL: ibid., producing larvae; L: number of larvae; produced and reared; LR: number of larvae reared; B: number of beetles reared.

PARENTS							
Species/Wing-morph		Origin					
Males	Females	Males	Females	N	NL	L	B
Group 1							
mel SW	cin LW	Kraloo (28-6-78)	F_1 1978[1]	4	-	-	-
		Kraloo (28-6-78)	Dwingeloo (19-7-78, teneral)	1	-	-	-
mel SW	cin SW	Kraloo (28-6-78)	F_1 1978	5	-	-	-
cin LW	mel SW	F_1 1978	Kraloo (28-6-78, tenerals)	5	1	41	-
cin SW	mel SW	F_1 1978	Kraloo (28-6-78, tenerals)	5	1	32	-
Group 2							
cin LW	mel SW	Nuil (4-8-78)	F_1 1978	6	-	-	-
		F_1 1978	F_1 1978	6	-	-	-
cin SW	mel SW	Nuil (4-8-78)	F_1 1978	2	-	-	-
		F_1 1978	F_1 1978	7	-	-	-
mol LW	mel LW	Voorne (end July 1978)[2]	F_1 1978	1	-	-	-
mol LW	mel SW	Voorne (end July 1978)	F_1 1978	5	-	-	-
cin LW	mol LW	Voorne (end July 1978)	Voorne (end July 1978)	5	2	20	-
mel SW	mol LW	Kraloo (4-8-78)	Voorne (end July 1978)	5	2	27	-
Controls						LR	
cin LW	cin LW	Parents 1977[1]	F_1 1978	6	5	283	179
cin SW	cin LW	F_1 1978	Parents 1977	6	5	149	59
	cin LW	no males	Dwingeloo (23-8/22-9-78)	16	16	734	471
		no males	Nuil (23-8/22-9-78)	5	5	253	158
cin LW	cin SW	F_1 1978	Parents 1977	6	4	114	48
cin SW	cin SW	F_1 1978	F_1 1978	6	6	295	182
	cin SW	no males	Dwingeloo (7-9-78)	1	1	49	27
		no males	Nuil (23/31-8-78)	4	3	147	86
mel SW	mel SW	Kraloo (30-8-78)	Kraloo (30-8-78)	6	6	60	40
	mel LW	no males	O-Flevoland (20-9-78)	14	13	489	304
	mel SW	no males	O-Flevoland (27-9-78)	13	10	371	236

[1]: parents and offspring of crosses carried out by Th. S. van Dijk

[2]: material collected by A. van Tiggele

Fig. 2. Collecting sites of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in The Netherlands: 1, Drenthe (Dwingeloo, Kraloo, Nuil); 2, Ameland (Buren, Nes); 3, Texel ('t Horntje); 4, Oost-Flevoland (Ecological Reserve); 5, Amsterdam (Bijlmermeer); 6, Wassenaar (Meijendel); 7, Schouwen (Haamstede).

maggots. Again offspring of females inseminated in the field (*Calathus mollis* from the West Frisian Island of Ameland) were reared.

Information on these crosses is summarized in table 2. Collecting sites are depicted in fig. 2.

Morphology

Material collected in the field was studied to check the validity and usefulness of characters given in literature for identification of the species concerned. Samples of the following localities were used:

Calathus cinctus: Drenthe: Dwingeloo (Noordenveld), Ruinen (Nuil); Friesland:

Ameland (Buren, Nes); N-Holland: Texel ('t Horntje); Z-Holland: Wassenaar (Meijendel) and Zeeland: Schouwen (Haamstede).

Calathus melanocephalus: Friesland: Ameland (Buren, Nes); Drenthe: Dwingeloo (Noordenveld), Ruinen (Nuil, Kraloo); Flevoland: Oost-Flevoland (Oecologisch Reservaat); N-Holland: Texel ('t Horntje), Amsterdam (Bijlmermeer).

Calathus mollis: Friesland: Ameland (Buren, Nes); Z-Holland: Wassenaar (Meijendel) and Zeeland: Schouwen (Haamstede).

Table 2. Single-pair crosses between and within *Calathus cinctus, C. melanocephalus* and *C. mollis* (1979/1980). cin: *cinctus;* mel: *melanocephalus;* mol: *mollis;* LW: long winged; SW: short winged; N: number of crosses; E: number of eggs laid; NL: number of crosses producing larvae; L: number of larvae produced and reared; LR: number of larvae reared; B: number of reared beetles.

PARENTS								
Species/Wing-morph		Origin						
Males	Females	Males	Females	N	E	NL	L	B
mel LW	cin LW	O-Flevoland (11-10-78)	F_1 1979	4	422	3	68	-
mel SW	cin LW	F_1 1979 (O-Flevoland)	F_1 1979	4	591	-	-	-
mel SW	cin LW	F_1 1979 (Kraloo)	F_1 1979	4	320	-	-	-
mel LW	cin SW	O-Flevoland (11-10-78)	F_1 1979	4	91	-	-	-
mel SW	cin SW	F_1 1979 (O-Flevoland)	F_1 1979	4	219	-	-	-
mel SW	cin SW	F_1 1979 (Kraloo)	F_1 1979	4	201	-	-	-
mol LW	cin LW	Ameland (28-6-79)	F_1 1979	4	184	-	-	-
mol LW	cin SW	Ameland (28-6-79)	F_1 1979	4	254	-	-	-
cin LW	mel LW	F_1 1979	O-Flevoland (25-10-78)	2	59	-	-	-
cin LW	mel LW	Ameland (28-6-79)	O-Flevoland (25-10-78)	2	216	-	-	-
cin SW	mel LW	F_1 1979	O-Flevoland (25-10-78)	2	229	-	-	-
cin SW	mel LW	Ameland (28-6-79)	O-Flevoland (25-10-78)	2	418	1	173	-
cin LW	mel SW	F_1 1979	F_1 1979 (O-Flevoland)	2	23	-	-	-
cin LW	mel SW	Ameland (28-6-79)	F_1 1979 (O-Flevoland)	2	58	-	-	-
cin LW	mel SW	F_1 1979	F_1 1979 (Kraloo)	2	218	2	77	-
cin LW	mel SW	Ameland (28-6-79)	F_1 1979 (Kraloo)	2	14	-	-	-
cin SW	mel SW	F_1 1979	F_1 1979 (O-Flevoland)	2	15	-	-	-
cin SW	mel SW	Ameland (28-6-79)	F_1 1979 (O-Flevoland)	2	50	1	26	-
cin SW	mel SW	F_1 1979	F_1 1979 (Kraloo)	2	87	-	-	-
cin SW	mel SW	Ameland (28-6-79)	F_1 1979 (Kraloo)	2	4	-	-	-
mol LW	mel LW	Ameland (28-6-79)	O-Flevoland (25-10-78)	4	181	1	25	-
mol LW	mel SW	Ameland (28-6-79)	F_1 1979 (O-Flevoland)	4	57	-	-	-
mol LW	mel SW	Ameland (28-6-79)	F_1 1979 (Kraloo)	4	59	-	-	-

Tabel 2, continued

PARENTS								
Species/Wing-morph		Origin						
Males	Females	Males	Females	N	E	NL	L	B
Control groups							**LR**	
mel LW	mel LW	F_1 1979	F_1 1979	4	1173	4	238	85
mel SW	mel LW	F_1 1979 (O-Flevoland)	F_1 1979	4	1084	4	240	135
mel SW	mel LW	F_1 1979 (Kraloo)	F_1 1979	4	1279	4	217	139
mel LW	mel SW	F_1 1979	F_1 1979 (O-Flevoland)	4	1113	4	239	92
mel SW	mel SW	F_1 1979 (O-Flevoland)	F_1 1979 (O-Flevoland)	4	959	4	240	130
mel SW	mel SW	F_1 1979 (Kraloo)	F_1 1979 (O-Flevoland)	4	665	4	224	136
mel LW	mel SW	F_1 1979	F_1 1979 (Kraloo)	4	682	4	160	96
mel SW	mel SW	F_1 1979 (O-Flevoland)	F_1 1979 (Kraloo)	4	1079	4	240	132
mel SW	mel SW	F_1 1979 (Kraloo)	F_1 1979 (Kraloo)	4	920	4	240	112
cin LW	cin LW	F_1 1979	F_1 1979	2	468	2	120	43
cin LW	cin LW	Ameland (28-6-79)	F_1 1979	1	232	1	60	20
cin SW	cin LW	F_1 1979	F_1 1979	2	639	2	85	41
cin SW	cin LW	Ameland (28-6-79)	F_1 1979	1	509	1	60	13
cin LW	cin SW	F_1 1979	F_1 1979	2	496	2	116	68
cin LW	cin SW	Ameland (28-6-79)	F_1 1979	1	216	1	60	20
	mol LW	no males	Ameland (28-6-79)	28	573	9	309	194

Measurements were made with a Wild M5 stereo-microscope provided with a calibrated ocular-micrometer. The following measurements were taken (magnification between brackets):

- length and width of the body (12): length between tip of mandibles and apex of elytra and greatest width over elytra (fig. 3: BL and BW).
- length and width of the pronotum (25): median length and greatest width (fig 3: PL and PW).
- length and width of the (right) elytron (12): EL and EW in fig. 3. EW was calculated as half the greatest body-width (0.5*BW).
- length and width of the (right) wing (12): greatest length and greatest width (fig. 3: WL and WW).
- length and width of the (right) met-episternum (50) as shown in fig. 4 (length: ML1, ML2; width: MW1, MW2).
- length of the (right) hind tibia and of the (right) hind tarsus (25) (fig. 3: TIL and TAL).

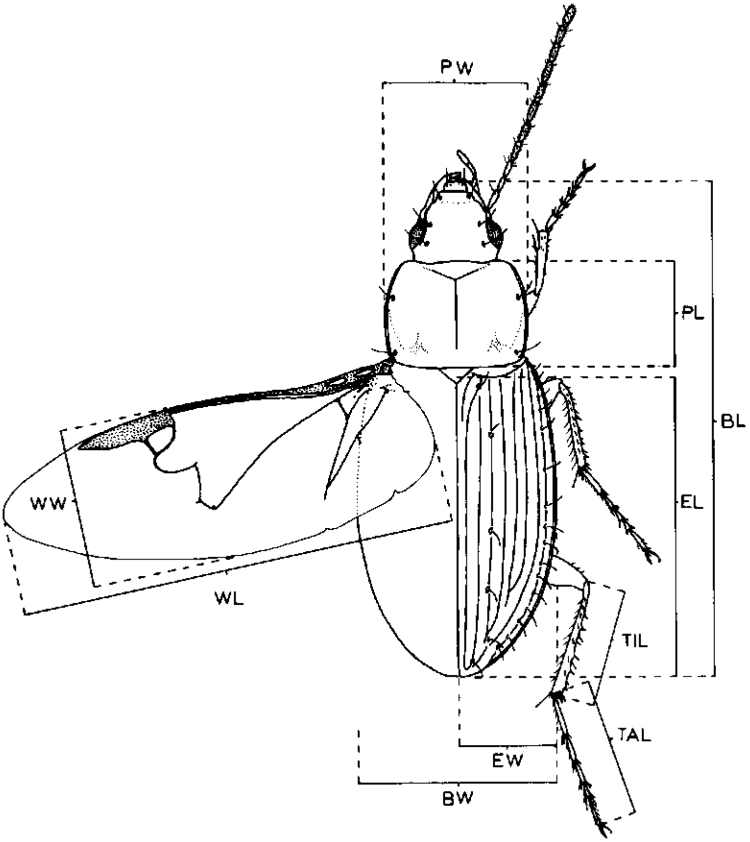


Fig. 3. Measurements. BL: body length, BW: body width, PL: length of pronotum, PW: greatest width of pronotum, EL: length of elytron, EW: greatest width of elytron, WL: greatest length of wing, WW: greatest width of wing, TIL: length of hind tibia, TAL: length of hind tarsus.

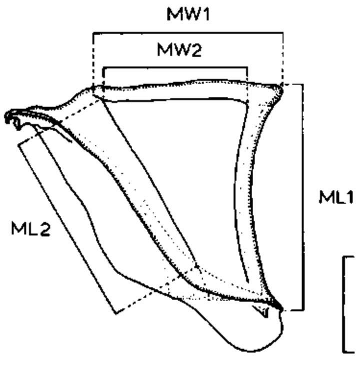


Fig. 4. Measurements of met-episternum. ML1, ML2: length; MW1, MW2: width (scale 0.5 mm).

Elytra, wings, met-episterna and hind-legs were removed from the body for proper measurement in a flat plane. Wings were put on a slide in alcohol and unfolded with a fine brush.

From these measurements ratios between length and width of the body (BL/BW), width and length of the pronotum (PW/PL), pronotum width and body width (PW/BW), length and width of the elytra (EL/EW), length of the elytra and body length (EL/BL), length and width of the wings (WL/WW), wing-length and length of the elytra (WL/EL), length and width of the met-episterna (ML2/MW2), and the ratio between the lengths of the hind tarsus and hind tibia (TAL/TIL) were estimated.

Special attention was paid to the colouration of the beetles, the size and shape of the right paramere and to the number of dorsal punctures in the third elytral interval.

Habitat and life-history

Details of the habitat and the life-history of the species were derived from the analysis of field data (mixed populations of *Calathus cinctus* and *C. melanocephalus* from Dwingeloo, Ruinen and the West Frisian Island of Texel and populations of *C. cinctus* and *C. mollis* from the West Frisian Island of Ameland), from literature (populations of *C. melanocephalus* studied by Vlijm & Van Dijk (1967), Vlijm et al. (1968) and Van Dijk (1972, 1973)) and from breeding experiments with the three species under outside conditions carried out in 1981/1982 and 1982/1983.

Distribution

Calathus-material of this group from Dutch collections was revised to be able to get an impression of the distribution of the species in The Netherlands. Material from the following collections is included:

Museums and Institutes: Zoölogisch Museum, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Vakgroep Entomologie, Landbouwuniversiteit, Wageningen; Biologisch Station, Landbouwuniversiteit, Wijster.

Private collections: K. den Bieman, Bennekom; E. H. M. Bouvy, Beek; H. T. Edzes, Nijmegen; T. van Gijzen, Arnhem; Th. Heijerman, Wageningen; S. van Heijnsbergen, Naarden; Y. Jongema, Wageningen and A. P. J. A. Teunissen, Vlijmen.

Additional material was supplied by K. Alders, Arnhem; M. A. Baars, De Koog, Texel (Loopkeverwerkgroep Texel); Th. S. van Dijk, Wijster; P. J. M. Mols, Heteren and H. Turin, Renkum.

Time trends in the occurrence of the species (i.e. numbers of occupied 10 x 10 km squares of the distribution maps per decade since 1870) were estimated according to the method of Turin & den Boer (1988).

RESULTS

Cross-breeding experiments

In total 123 single-pair crosses were carried out: 59 between *Calathus cinctus* and *C. melanocephalus*, 47 between C. *cinctus* and C. *mollis* and 17 between C. *melanocephalus* and C. *mollis* (tables 1 and 2). None of these crosses produced adult offspring although in 5 (8.5%), 3 (6.4%) and 3 (17.6%) cases respectively larvae were produced, which, however, never reached the third larval stage.

Of the control crosses (42 of *Calathus melanocephalus* and 30 of *C. cinctus*) all crosses which produced larvae (respectively 100% and 82% for both years together), also produced adult offspring (tables 1 and 2). In 1979/1980 all crosses of both species produced offspring (table 2). In the case of *C. mollis* sufficient material to carry out control crosses in the same way was not available. However, of 28 females collected in the field (Ameland, Buren, 28.vi.1979) and kept without males under the same conditions as single-pair crosses, 9 produced larvae and offspring (table 2: 194 beetles from 309 larvae). The other 19 females (10 of which were tenerals at the time of capture) produced no or only a few unfertilized eggs, and were considered not to have been inseminated at all. Nevertheless it is clear from these results that also in the case of *C. mollis* the failure of single-pair crosses with C. *cinctus* and C. *melanocephalus* cannot be attributed to the rearing conditions used.

In 1979/1980 egg production was also estimated and from the data in table 2 it is clear that although unfertilized females may produce a considerable number of eggs, the egg production of fertilized females generally is much higher.

From these breeding results it is concluded that *Calathus cinctus*, *C. melanocephalus* and C. *mollis* show mutual reproductive isolation, and, therefore, have to be considered as distinct species.

Morphology

Biometric data, especially the ratio length/width of the met-episterna, have been used in attempts to separate the taxa of this group of closely related species (Gersdorf, 1937; Wiebes-Rijks, 1949). The establishment of *Calathus cinctus* as a valid species as the result of the breeding programm necessitated a new attempt to find morphological differences between the three species. Concerning biometrics, however, two points have to be taken into account. Firstly, in these species there are general differences both between sexes (on average females are larger than males) and between wing-morphs (on average long winged specimens are larger than short winged specimens and differently shaped). Secondly, the way measurements are made should be described (and figured) in detail, which

Table 3. Measurements (in mm) of short winged males of *Calathus cinctus* and *C. melanocephalus* from Texel. N: number of measurements.

		cinctus			*melanocephalus*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	20	6.79	6.59-6.98	20	6.66	6.51-6.82
	Width (BW)	20	2.71	2.64-2.77	20	2.67	2.61-2.73
	BL/BW	20	2.51	2.47-2.55	20	2.50	2.45-2.55
Pronotum	Length (PL)	20	1.64	1.61-1.68	20	1.68	1.65-1.72
	Width (PW)	20	1.99	1.95-2.04	20	2.11	2.06-2.15
	PW/PL	20	1.21	1.20-1.23	20	1.25	1.23-1.27
	PW/BW	20	0.74	0.73-0.74	20	0.79	0.78-0.80
Elytron	Length (EL)	20	4.18	4.07-4.29	20	4.09	4.00-4.18
	Width (EW)	20	1.35	1.32-1.38	20	1.33	1.30-1.36
	EL/EW	20	3.09	3.05-3.12	20	3.07	3.03-3.11
	EL/BL	20	0.62	0.61-0.62	20	0.61	0.60-0.63
Wing	Length (WL)	20	1.93	1.85-2.01	20	1.93	1.86-2.00
	Width (WW)	20	0.48	0.45-0.51	20	0.51	0.47-0.54
	WL/WW	20	4.05	3.86-4.24	20	3.86	3.65-4.07
	WL/EL	20	0.46	0.45-0.47	20	0.47	0.46-0.49
Met-episternum	Length (ML2)[1]	20	0.76	0.74-0.78	20	0.70	0.68-0.73
	Width (MW2)[1]	20	0.57	0.55-0.59	20	0.57	0.55-0.58
	ML2/MW2 (ME2)	20	1.34	1.32-1.36	20	1.24	1.22-1.27
Hindleg	Length tarsus (TAL)	20	2.07	2.01-2.13	20	2.02	1.98-2.06
	Length tibia (TIL)	20	2.02	1.98-2.07	20	1.98	1.94-2.01
	TAL/TIL	20	1.02	1.01-1.03	20	1.02	1.01-1.04

[1]: see fig. 4.

seemingly is not normal practice. Lindroth (1974) and Freude (1976), for instance, use the ratio length/width of the met-episternawithout indicating how to measure it, and do not point out the differences between sexes and between wing-morphs in a proper way.

Tables 3-6 list measurements and ratio's of both males and females of short as well as long winged *Calathus cinctus* and *C. melanocephalus* collected on Texel by M. A. Baars and of long winged *C. mollis* collected in the coastal dunes near Haamstede (Province of Zeeland) by the author. From these data it became clear that although there are some differences between means (e. g. in the case of the ratio length/width of the metepisterna), these measurements (or ratios estimated from them)

Table 4. Measurements (in mm) of short winged females of *Calathus cinctus* and *C. melanocephalus* from Texel. N: number of measurements.

		cinctus			*melanocephalus*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	20	7.39	7.23-7.56	20	7.32	7.18-7.46
	Width (BW)	20	3.01	2.94-3.09	20	2.95	2.91-3.00
	BL/BW	20	2.46	2.42-2.50	20	2.48	2.44-2.52
Pronotum	Length (PL)	20	1.77	1.73-1.81	20	1.79	1.76-1.82
	Width (PW)	20	2.19	2.13-2.24	20	2.28	2.24-2.32
	PW/PL	20	1.23	1.22-1.25	20	1.27	1.26-1.28
	PW/BW	20	0.73	0.72-0.74	20	0.77	0.76-0.78
Elytron	Length (EL)	20	4.54	4.44-4.64	20	4.45	4.36-4.53
	Width (EW)	20	1.51	1.47-1.54	20	1.48	1.46-1.50
	EL/EW	20	3.02	2.98-3.05	20	3.01	2.97-3.04
	EL/BL	20	0.61	0.61-0.62	20	0.61	0.60-0.62
Wing	Length (WL)	20	2.14	2.08-2.20	20	2.06	1.99-2.13
	Width (WW)	20	0.60	0.57-0.62	20	0.60	0.55-0.64
	WL/WW	20	3.61	3.48-3.75	20	3.49	3.32-3.65
	WL/EL	20	0.47	0.46-0.48	20	0.46	0.45-0.48
Met-episternum	Length (ML2)	20	0.83	0.80-0.85	20	0.76	0.74-0.77
	Width (MW2)	20	0.64	0.62-0.65	20	0.62	0.61-0.64
	ML2/MW2 (ME2)	20	1.30	1.27-1.33	20	1.22	1.20-1.24
Hindleg	Length tarsus (TAL)	20	2.08	2.03-2.12	20	1.97	1.92-2.01
	Length tibia (TIL)	20	2.07	2.03-2.12	20	2.02	1.98-2.06
	TAL/TIL	20	1.00	0.99-1.02	20	0.97	0.96-0.98

do not allow unambiguous identification because of the great individual variation and the wide overlap in the ranges of measurements.

Table 7 summarizes length/width ratios (ME1: ML1/MW1 and ME2: ML2/MW2, see fig. 4) of long and short winged males and females of *Calathus cinctus* and *C. melanocephalus*, as well as of long winged males and females of *C. mollis* (all specimens collected or reared of the latter species turned out to be long winged) from localities mentioned above, as well as from a number of other localities too.

Although both ratios show a clear trend *melanocephalus* < *cinctus* < *mollis* for both males and females, the mutual overlap is so wide that identification on the basis of these ratios alone usually will not be possible. The observed differences between wing-morphs and sexes are smaller than those between species (table 7). In general differences between species, wing-morphs and sexes are better illustrated by ratio ME2 than by ratio ME1.

Table 5. Measurements (in mm) of long winged males of *Calathus cinctus* and *C. melanocephalus* from Texel and *C. mollis* from Haamstede. N: number of measurements.

		cinctus			*melanocephalus*			*mollis*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	11	6.78	6.52-7.03	7	7.19	6.93-7.46	20	7.34	7.18-7.50
	Width (BW)	11	2.64	2.55-2.73	7	2.85	2.77-2.94	20	2.79	2.73-2.85
	BL/BW	11	2.57	2.52-2.62	7	2.52	2.44-2.60	20	2.63	2.61-2.66
Pronotum	Length (PL)	11	1.60	1.54-1.65	7	1.77	1.70-1.83	20	1.65	1.61-1.69
	Width (PW)	11	1.92	1.85-1.99	7	2.24	2.17-2.31	20	2.05	2.00-2.09
	PW/PL	11	1.20	1.18-1.23	7	1.27	1.25-1.29	20	1.24	1.23-1.25
	PW/BW	11	0.73	0.72-0.74	7	0.79	0.78-0.79	20	0.73	0.73-0.74
Elytron	Length (EL)	11	4.12	3.98-4.25	7	4.32	4.19-4.45	20	4.38	4.27-4.49
	Width (EW)	11	1.32	1.27-1.36	7	1.43	1.38-1.47	20	1.39	1.36-1.42
	EL/EW	11	3.12	3.07-3.18	7	3.03	2.98-3.09	20	3.14	3.11-3.18
	EL/BL	11	0.61	0.59-0.63	7	0.60	0.58-0.62	20	0.60	0.59-0.60
Wing	Length (WL)	11	6.26	5.89-6.62	7	7.10	6.86-7.85	20	6.61	6.39-6.83
	Width (WW)	11	2.36	2.23-2.50	7	2.68	2.63-2.74	20	2.46	2.37-2.54
	WL/WW	11	2.65	2.53-2.77	7	2.65	2.58-2.72	20	2.69	2.66-2.73
	WL/EL	11	1.52	1.47-1.57	7	1.64	1.62-1.67	20	1.51	1.49-1.53
Met-episternum	Length (ML2)	11	0.77	0.74-0.79	7	0.77	0.73-0.81	20	0.82	0.80-0.84
	Width (MW2)	11	0.57	0.55-0.59	7	0.60	0.58-0.62	20	0.58	0.56-0.59
	ML2/MW2 (ME2)	11	1.35	1.31-1.39	7	1.28	1.21-1.35	20	1.43	1.40-1.45
Hindleg	Length tarsus (TAL)	11	2.01	1.93-2.09	6	2.18	2.11-2.24	20	2.19	2.14-2.25
	Length tibial (TIL)	11	1.96	1.90-2.03	6	2.13	2.04-2.22	20	2.09	2.04-2.15
	TAL/TIL	11	1.02	1.01-1.04	6	1.02	1.00-1.05	20	1.05	1.04-1.06

Table 8 illustrates the variation in the number of dorsal punctures in the third elytral interval of *Calathus cinctus* and *C. melanocephalus* from Texel and *C. mollis* from Haamstede. In both sexes and wing-morphs of *C. cinctus* considerable deviation (> 50 %) from the standard number of three punctures in the third elytral interval was found, whereas the deviation in *C. melanocephalus* and *C. mollis* was relatively low (< 40 %). Both the number and position of the punctures are also rather variable and certainly not of diagnostic value.

General coloration, shape of the elytra and shape of the right parameres are very constant and can be used to identify most specimens according to the key presented hereafter. Only a few long winged females of *Calathus cinctus* and C. *mollis* may give some problems in identification.

In all three species the females are less shining than the males, due to a denser microsculpture of usually isodiametric meshes, which is most obvious on the elytra.

Table 6. Measurements (in mm) of long winged females of *Calathus cinctus* and *C. melanocephalus* from Texel, and *C. mollis* from Haamstede. N: number of measurements.

		cinctus			*melanocephalus*			*mollis*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	11	7.04	6.78-7.30	20	7.85	7.72-7.97	20	8.03	7.86-8.19
	Width (BW)	11	2.87	2.74-3.00	20	3.15	3.12-3.18	20	3.18	3.10-3.25
	BL/BW	11	2.46	2.41-2.51	20	2.49	2.45-2.54	20	2.53	2.51-2.55
Pronotum	Length (PL)	11	1.67	1.60-1.74	20	1.89	1.86-1.92	20	1.77	1.74-1.81
	Width (PW)	11	2.09	1.99-2.20	20	2.43	2.40-2.47	20	2.28	2.22-2.34
	PW/PL	11	1.26	1.23-1.28	20	1.29	1.27-1.31	20	1.28	1.27-1.30
	PW/BW	11	0.73	0.72-0.74	20	0.77	0.76-0.78	20	0.72	0.71-0.72
Elytron	Length (EL)	11	4.34	4.18-4.50	20	4.80	4.72-4.88	20	4.81	4.71-4.92
	Width (EW)	11	1.43	1.37-1.50	20	1.57	1.56-1.59	20	1.59	1.55-1.62
	EL/EW	11	3.03	2.98-3.08	20	3.05	3.00-3.09	20	3.03	3.01-3.06
	EL/BL	11	0.62	0.61-0.63	20	0.61	0.60-0.62	20	0.60	0.60-0.60
Wing	Length (WL)	11	6.49	6.15-6.82	20	7.51	7.38-7.65	20	7.27	7.07-7.46
	Width (WW)	11	2.51	2.38-2.64	20	2.83	2.77-2.89	20	2.77	2.68-2.85
	WL/WW	11	2.58	2.52-2.64	20	2.65	2.62-2.69	20	2.63	2.60-2.65
	WL/EL	11	1.49	1.45-1.54	20	1.57	1.54-1.59	20	1.51	1.49-1.52
Met-episternum	Length (ML2)	11	0.82	0.77-0.88	20	0.83	0.81-0.84	20	0.92	0.88-0.94
	Width (MW2)	11	0.61	0.58-0.63	20	0.68	0.66-0.69	20	0.65	0.63-0.66
	ML2/MW2 (ME2)	11	1.36	1.31-1.41	20	1.22	1.21-1.24	20	1.42	1.39-1.45
Hindleg	Length tarsus (TAL)	11	2.00	1.89-2.06	20	2.09	2.06-2.11	20	2.21	2.16-2.25
	Length tibial (TIL)	11	1.97	1.92-2.08	20	2.18	2.15-2.22	20	2.19	2.15-2.23
	TAL/TIL	11	1.01	0.99-1.04	20	0.96	0.94-0.97	20	1.01	1.00-1.02

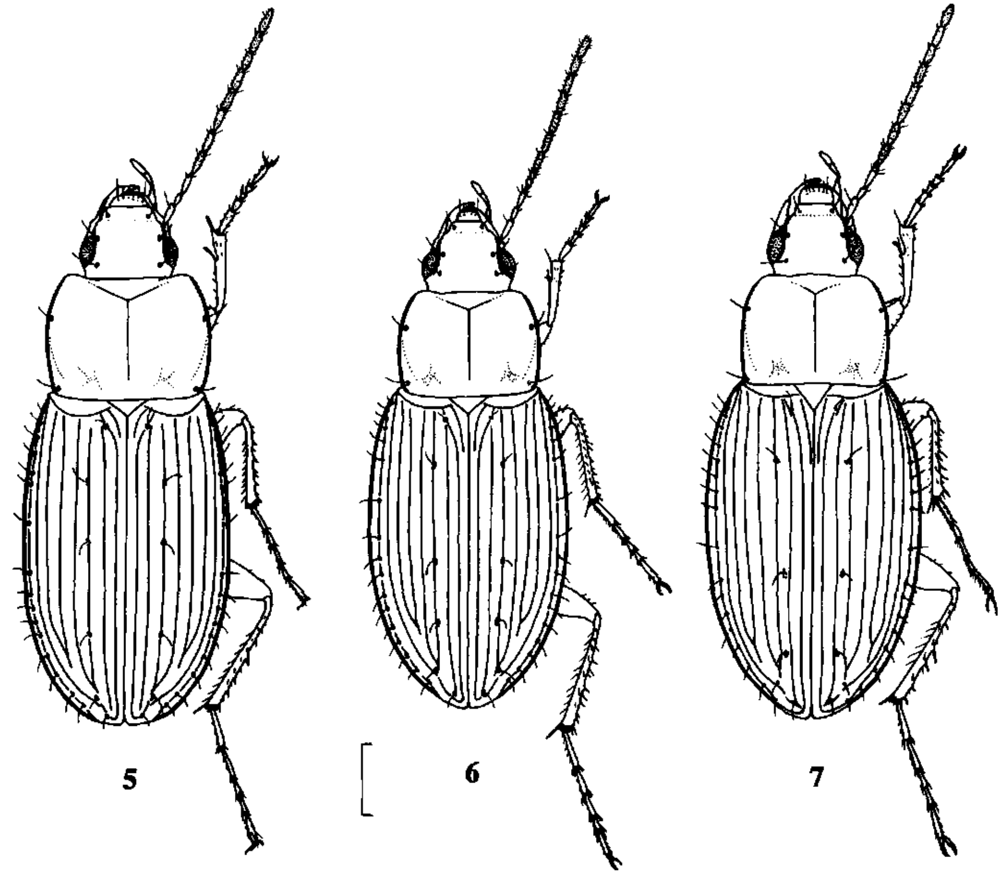
Table 7. Measurements of met-episterna: ratio length/width. ME1: ML1/MW1; ME2: ML2/MW2 (see fig. 4); SW: short winged; LW: long winged; N: Number of measurements.

				ME1			ME2		
Morph	Species	Locality	N	Range	Mean	95% c.l.	Range	Mean	95% c.l.
males									
SW	*cinctus*	Nuil	30	1.06-1.18	1.11	1.10-1.12	1.28-1.46	1.36	1.35-1.38
		Noordenveld 1)	27	1.03-1.22	1.11	1.09-1.13	1.19-1.47	1.34	1.31-1.37
		Texel	20	0.97-1.10	1.04	1.03-1.06	1.25-1.43	1.34	1.32-1.36
	melanocephalus	Oost-Flevoland	30	0.99-1.16	1.07	1.05-1.08	1.19-1.39	1.29	1.27-1.31
		Nuil	19	0.96-1.10	1.04	1.02-1.06	1.15-1.31	1.23	1.21-1.25
		Noordenveld 1)	30	0.94-1.10	1.03	1.02-1.05	1.10-1.39	1.25	1.23-1.28
		Kraloo	9	0.98-1.10	1.04	1.01-1.06	1.16-1.29	1.24	1.20-1.28
		Bijlmermeer	17	1.03-1.14	1.07	1.06-1.09	1.23-1.40	1.27	1.25-1.30
		Texel	20	0.95-1.07	1.02	1.00-1.03	1.15-1.32	1.24	1.22-1.27
LW	*cinctus*	Nuil	30	1.02-1.19	1.12	1.11-1.13	1.27-1.47	1.39	1.37-1.41
		Noordenveld 1)	30	1.04-1.26	1.14	1.12-1.16	1.18-1.57	1.37	1.33-1.40
		Texel	11	1.00-1.11	1.07	1.05-1.09	1.28-1.46	1.35	1.31-1.39
	melanocephalus	Oost-Flevoland	13	1.00-1.15	1.08	1.05-1.11	1.14-1.34	1.24	1.21-1.28
		Kraloo	2	1.09-1.12		1.39-1.45			
		Bijlmermeer	3	1.07-1.09		1.21-1.29			
		Texel	7	1.00-1.09	1.05	1.02-1.08	1.20-1.40	1.28	1.21-1.35
	mollis	Meijendel	14	1.15-1.25	1.19	1.18-1.21	1.33-1.52	1.43	1.40-1.47
		Haamstede	20	1.11-1.20	1.16	1.14-1.17	1.35-1.54	1.43	1.40-1.45
females									
SW	*cinctus*	Nuil	29	1.02-1.18	1.11	1.09-1.12	1.24-1.49	1.35	1.33-1.37
		Noordenveld 1)	29	1.00-1.20	1.08	1.07-1.10	1.17-1.44	1.30	1.28-1.33
		Texel	20	0.92-1.07	1.01	0.99-1.02	1.14-1.30	1.30	1.27-1.33
	melanocephalus	Oost-Flevoland	30	0.98-1.16	1.05	1.04-1.07	1.12-1.35	1.25	1.22-1.27
		Nuil	30	1.00-1.10	1.04	1.03-1.05	1.14-1.39	1.25	1.23-1.27
		Noordenveld 1)	30	0.98-1.22	1.06	1.04-1.09	1.16-1.39	1.27	1.24-1.29
		Kraloo	12	1.00-1.13	1.05	1.03-1.08	1.18-1.37	1.24	1.18-1.30
		Bijlmermeer	10	0.98-1.18	1.09	1.05-1.12	1.23-1.33	1.27	1.24-1.30
		Texel	20	0.92-1.07	1.01	0.99-1.02	1.14-1.30	1.22	1.20-1.24
LW	*cinctus*	Nuil	30	1.07-1.21	1.12	1.11-1.13	1.26-1.44	1.35	1.34-1.37
		Noordenveld 1)	29	0.98-1.30	1.13	1.11-1.16	1.24-1.58	1.36	1.33-1.39
		Texel	11	1.05-1.17	1.11	1.08-1.14	1.25-1.49	1.36	1.31-1.41
	melanocephalus	Oost-Flevoland	30	0.97-1.13	1.06	1.04-1.07	1.12-1.41	1.26	1.24-1.28
		Kraloo	18	0.98-1.18	1.08	1.05-1.11	1.17-1.48	1.30	1.25-1.34
		Bijlmermeer	7	1.03-1.12	1.08	1.05-1.12	1.25.1.43	1.31	1.26-1.37
		Texel	20	0.95-1.08	1.03	1.01-1.04	1.17-1.30	1.22	1.21-1.24
	mollis	Meijendel	17	1.13-1.28	1.19	1.17-1.21	1.33-1.54	1.43	1.40-1.46
		Haamstede	20	1.05-1.24	1.16	1.15-1.18	1.29-1.61	1.42	1.39-1.45

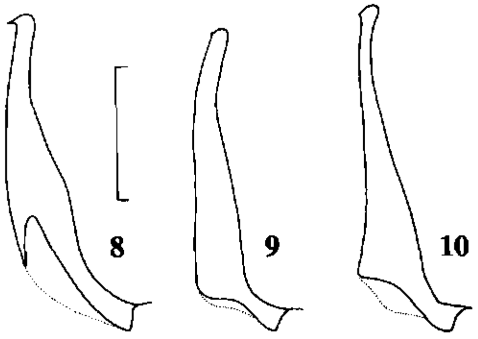
1): measurements M.G.J. Oude Wesselink

Tabel 8. Number of punctures in 3rd elytral striae. N: number of observations. D: deviation (%) from standard number of punctures (3/3) in 3rd striae; SW: short winged; LW: long winged.

				Punctures in 3rd elytral stria (right/left elytrum)											
Species	Sex	morph	N	2/2	2/3	2/4	3/2	3/3	3/4	4/3	4/4	4/5	5/3	5/4	D
cinctus	males	SW	20	-	1	-	-	9	5	2	3	-	-	-	55.0
		LW	11	-	-	-	-	5	3	2	1	-	-	-	54.5
	females	SW	20	-	2	-	-	2	5	5	5	-	1	1	90.0
		LW	11	-	-	-	-	4	2	1	3	-	1	-	63.6
melanocephalus	males	SW	20	-	-	-	-	13	1	4	2	-	-	-	35.0
		LW	7	-	-	-	-	5	2	-	-	-	-	-	28.6
	females	SW	20	-	-	-	-	13	3	3	1	-	-	-	35.0
		LW	20	-	-	-	-	14	3	2	1	-	-	-	30.0
mollis	males	LW	20	1	2	-	-	17	-	-	-	-	-	-	15.0
	females	LW	20	1	1	1	-	13	11	1	1	-	-	-	35.0



Figs 5-7. Habitus of females of *Calathus*. 5, *C. melanocephalus*; 6, *C. cinctus*; 7, *C. mollis* (scale 1 mm).



Figs 8-10. Right parameres of *Calathus*. 8, *C. melanocephalus*; 9, *C. cinctus*; 10, *C. mollis* (scale 0.5 mm).

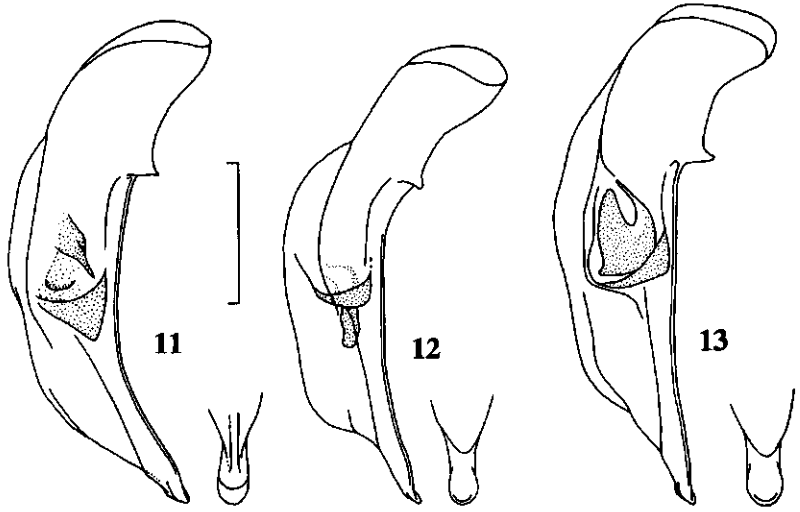
Key to the species

1. Elytra bicoloured, with epipleura, base and dorsal punctures clear rufous, contrasting with the black dorsal surface. Sides of elytra almost parallel and broadly rounded apically (fig. 5). Pronotum more or less rufous, clearly contrasting with the black head and with the elytral surface. Sternites dark, contrasting with the rufous meso- and metathoracical structures. Males: right paramere widened and hooked at the tip (fig. 8). Vesica: fig. 11. Wings reduced or fully developed (rarely specimens with only one fully developed wing are found) (body length 6-8 mm) . . . . *melanocephalus*

\- Elytra unicoloury rufous to piceous brown, with sides evenly rounded (figs 6-7). Little or no contrast in colour between pronotum and head and elytra, nor between sternites and meso- and metathorax. Males: right paramere not widened near the apex and unarmed or with a very small hook apically (figs 9-10) . . 2

2. Pronotum slightly contrasting with the darker head and the elytra. Males: right paramere hooked, tip unarmed or nearly so (fig. 9). Vesica: fig. 12. Wings either fully developed or strongly reduced (body length 6-8.5 mm) . . . . . . *cinctus*

\- Pronotum not contrasting with the head and the elytra. Males: right paramere almost straight with a very small hook apically (fig. 10). Vesica: fig. 13. Wings always full (body length 6.5-9 mm) . . . . *mollis*



Figs 11-13. Vesica of *Calathus*. 11, *C. melanocephalus*; 12, *C. cinctus*; 13, *C. mollis* (scale 0.5 mm).

Habitat and Life-history

Habitat

Calathus melanocephalus is mainly a species of open country, where it lives on different kinds of moderately dry soil with sparse vegetation, achieving its greatest abundance on sandy soils. It is a common inhabitant of dry meadows, grassland dunes and heaths; also on agricultural land and in thin forest, mainly of *Pinus* (Lindroth, 1986) or *Betula* (Den Boer, pers. comm.). Den Boer (1977) in his subdivision of carabids in habitat groups classified *C. melanocephalus* as an F-species, i.e. mainly a species of heath and peat moor.

Calathus cinctus is mainly found in mixed populations with the preceding and/or the following species in dry meadows, dune grassland, agricultural land and waste land. Van Dijk (1986) classified *cinctus* as an H-species sensu den Boer (1977), i.e. an eurytopic species, which in most cases prefer localities significantly influenced by human activities (arable fields, pastures, farm yards, gardens and roadside verges). In three cases a mixed population of *C. cinctus* and *C. melanocephalus* was observed during a period of several years: populations at Nuil and Dwingeloo (fields withdrawn from agricultural practice) and at the West Frisian Island of Texel (dune grassland) (table 9). In all three cases, however, *C. cinctus* disappeared or nearly disappeared after a number of years of coexistence with C. *melanocephalus*. These data might suggest that *C. cinctus* is adapted to changing, unstable habitats, whereas *C. melanocephalus* is less suited to that kind of change. At Nuil and Dwingeloo the impoverishing treatments most likely caused the decrease of *cinctus* (see also Van

Table 9. Numbers and ratio of *Calathus cinctus* (cin) and *C. melanocephalus* (mel) in mixed populations.

	Nuil			Schoongelegen			Texel		
	Species			Species			Species		
Year	cin	mel	%cin	cin	mel	%cin	cin	mel	%cin
1973	11	30	26.8	8	71	10.1			
1974	13	29	31.0	3	54	5.3			
1975	35	64	35.4	6	23	20.7			
1976	16	20	44.4	22	39	36.1			
1977	34	24	58.6	39	31	55.7			
1978	59	67	46.8	172	112	60.6			
1979	12	34	26.1	3	62	4.6			
1980	2	19	9.5	-	40	-			
1981	-	16	-	-	30	-			
1982	-	6		-	72	-			
1983	1	-		-	84	-			
1984	-	6		-	50	-	82	19	81.1
1985	-	4		-	91	-	264	265	49.9
1986	-	18		-	102	-	133	310	30.0
1987							32	176	15.3
1988							6	74	7.5
Total	183	337		253	861		517	844	

Dijk, 1986), whereas at the dune grassland at Texel a decrease of treading might be responsible for the same kind of shift.

Calathus mollis is strictly confined to dry sandy habitats in open country, occurring in sparse xerophilous vegetation, common on dune-sand along the coast, where it occurs in tufts of *Elymus* and *Ammophila* in company with *Demetrias monostigma* Samouelle and *Dromius linearis* (Olivier) (Lindroth, 1986; own observations), and only incidentally inland, e.g. on blown sands and other large sand deposits. In den Boer's subdivision (1977) *C. mollis* would be classified as an E-species (species of blown sands). In the coastal dune region as well as in inland blown sands mixed populations of *C. mollis* and *C. cinctus* and occasionally with both *C. cinctus* and *C. melanocephalus* occur.

Life-history

Annual rhythms

All three species show a similar type of development. They belong to the group of autumn breeders with a thermic hibernation parapause in the larval stage and a

Table 10. Weekly catches of *Calathus cinctus* and *C. melanocephalus* at Nuil, Drenthe in 1976. N: number of beetles; ND: number of females dissected; MNE: mean number of eggs in the ovaries of dissected females.

	cinctus						*melanocephalus*					
	Males	Females					Males	Females				
Date	N	N	ND	Young	Old	MNE	N	N	ND	Young	Old	MNE
7 Jul							1	1	1	1	-	11.0
14 Jul							5	4	4	3	1	4.3
21 Jul	-	1	1	1	-	-	8	12	8	6	2	11.1
28 Jul	-	-	-	-	-	-	14	18	10	9	1	15.9
4 Aug	-	1	1	1	-	15.0	7	10	9	8	1	14.4
11 Aug	-	-	-	-	-	-	11	25	11	7	4	21.5
18 Aug	1	2	2	2	-	23.0	35	26	10	7	3	22.6
25 Aug	3	2	2	1	1	35.0	46	17	10	9	1	23.0
1 Sep	13	15	15	7	8	20.2	42	34	10	8	2	25.8
8 Sep	10	16	16	9	7	33.9	11	24	10	10	-	21.5
15 Sep	21	20	20	15	5	26.5	18	21	10	10	-	17.6
22 Sep	27	18	18	16	2	17.8	23	18	13	12	1	18.8
29 Sep	16	8	8	5	3	18.3	22	4	4	3	1	10.8
6 Oct	17	10	10	9	1	15.4	9	2	2	0	2	16.5
13 Oct	12	20	18	10	8	11.2	6	10	10	9	1	2.0
20 Oct	4	6	6	4	2	9.8	2	1	1	1	-	-
27 Oct	2	6	6	3	3	8.0	2	4	2	2	-	-
3 Nov	-	1	1	1	-	-	1	-	-			
10 Nov	2	3	1	1	-	-	3	1	-			
Total	128	129	125	85	40		262	231	125	105	20	

photoperiodic aestivation parapause in the adults (Thiele, 1977). As in most autumn breeders, adults of *Calathus melanocephalus* are almost strictly night active (Thiele, 1977). Larvae as well as a varying part of the adults overwinter (Lindroth, 1986). In northern and alpine areas, however, *C. melanocephalus* is a semivoltine spring breeder, instead of a univoltine autumn breeder, adapted to the shorter growing season of a cooler climate (Forsskåhl, 1972; DeZordo, 1979; Refseth, 1988). Under these circumstances larvae of *C. melanocephalus* need almost two years to develop.

Reproduction period and age-composition

Detailed information about the life-history of *Calathus melanocephalus* is given by Vlijm & Van Dijk (1967), Vlijm et al. (1968) and Van Dijk (1972, 1973). Young beetles emerge in June-July, reproduce from August onwards and a varying part of

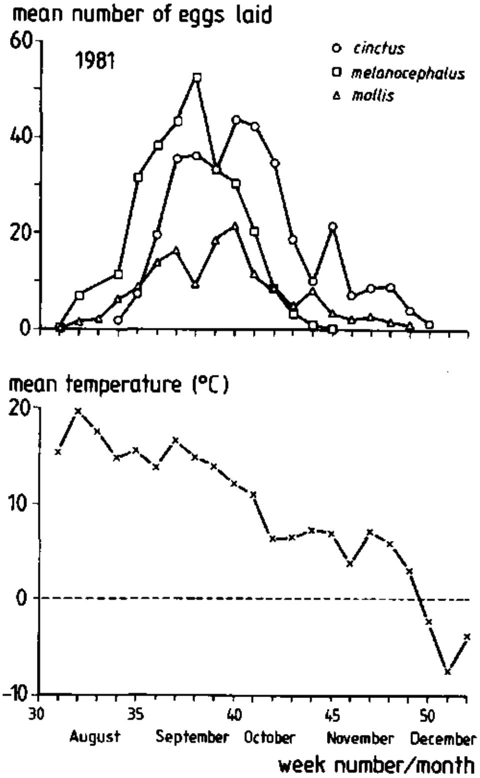


Fig. 14. Mean egg production of *Calathus cinctus* (29 females), *C. melanocephalus* (23 females) and *C. mollis* (16 females) and mean weekly temperature in 1981 under outside conditions.

these beetles hibernate to become active again in May-June, reproducing for thesecond time from July onwards. The total reproduction period covers the months July, August and September. Vlijm & Van Dijk (1967) and Vlijm et al. (1968) estimated the second year category as about one third of the adult population at Schiermonnikoog, but this figure may vary considerably from year to year and from place to place (Van Dijk, 1972; Baars & Van Dijk, 1984). Even three and four year old beetles were found by a mark-recapture experiment in a population of *C. melanocephalus* (Van Dijk, 1979b), representing 26.5 and 0.5% of the total catch during four years respectively.

Calathus cinctus was found to reproduce in Drenthe somewhat later than *C. melanocephalus* (August-November) (Van Dijk, 1978). From weekly samples of *C. cinctus* collected in 1976 at Nuil in pitfall traps, 165 females caught between 21 July and 17 November were dissected and checked for their ovarian development. The main reproductive period, defined here as the period in which the mean number of eggs in the ovaries is 10 or more, fell between the 1st week of August and the 3rd week of October (table 10). 40 Females (24.2%) were classified as old females, reproducing for the second year. Comparable data for *C. melanocephalus* collected at the same site were a main reproductive period between the 3rd week of July and the 1st week of October and 16% old females (table 10), of which only a single

Table 11. Reproduction period of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in outdoor breeding experiments. N: Number of females

			REPRODUCTION PERIOD					
Year	Species	N	Egg-laying Period			Mean number of eggs > 10		
1981	*cinctus*	29	12 Aug	- 9 Dec	(18 weeks)	26 Aug	- 21 Oct	(9 weeks)
	melanocephalus	36	31 Jul	- 6 Nov	(15 weeks)	7 Aug	- 9 Oct	(10 weeks)
	mollis	14	3 Aug	- 7 Dec	(19 weeks)	31 Aug	- 19 Oct	(8 weeks)
1982	*cinctus*	30	16 Aug	- 31 Jan	(25 weeks)	30 Aug	- 22 Nov	(13 weeks)
	melanocephalus	8	30 Jul	- 22 Oct	(13 weeks)	13 Aug	- 15 Oct	(10 weeks)
	mollis	17	6 Aug	- 3 Jan	(23 weeks)	20 Aug	- 5 Nov	(12 weeks)

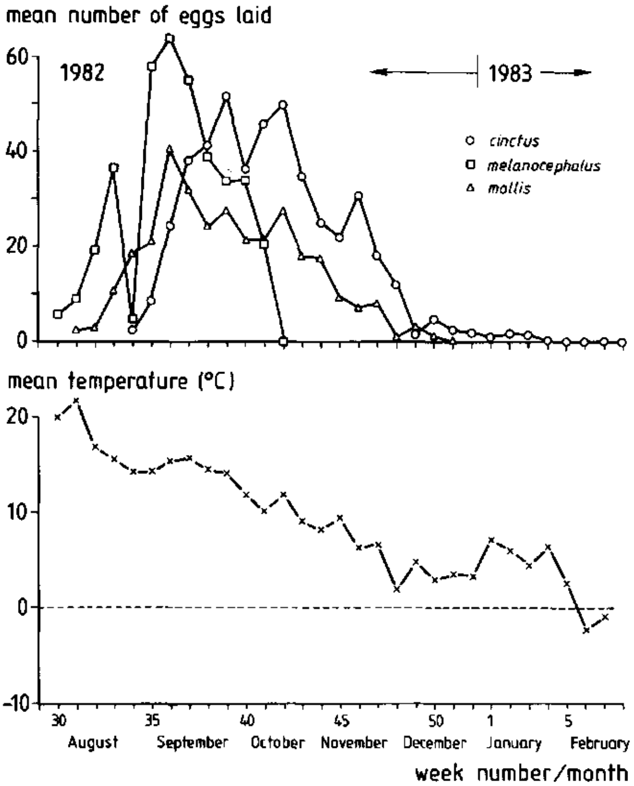


Fig. 15. Mean egg production of *Calathus cinctus* (30 females), *C. melanocephalus* (4 females) and *C. mollis* (17 females) and mean weekly temperatures in 1982/1983 under outside conditions

female caught on 13 October was not or no longer reproductive.

Calathus mollis was not studied in detail in this respect but hand catches on the West Frisian Island of Ameland on 27 May 1981 comprised old beetles only (29), whereas on 28 June 1979 about 12% of the 248 beetles collected at the same site were just emerged tenerals. These data suggest a similar type of age composition of populations of this species.

Table 12. Egg production of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* during the day at a constant temperature of 19° C and approximately natural daylength (light period: 6.30-19.00 hours). D: dark period (■); L: light period (□).

			cinctus								*melanocephalus*								*mollis*								
Date	Time	D/L	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	Total
14 Sep 1981	18.30	□																									
(start)		■																									
15 Sep 1981	8.30	□			3		2			2	7	7		6	1	6	13	2	1			3		1			54
		□																									0
	10.30	□					5								9	1											15
	12.30	□															1										1
	14.30	□																									0
	16.30	□																									0
	18.30	□																									0
	20.30	■					1										2	1				2					6
	22.30	■					4							2			6	6				1					19
16 Sep 1981	00.30	■					2				3					1	3	1				3			2	3	18
	02.30	■	5				1											6						1		8	21
	04.30	■	13				2							2											4	2	23
	06.30	■					1									1				3						1	6
	08.30	□																		1			1				2
	10.30	□																					1				1
	12.30	□																									0
		□																									
	18.30	□																									0
		■																									
17 Sep 1981	10.30	□				4	4				14	2		22	13	6	17								4	7	93
		□																									
	18.30	□					3					1										2					6
		■																									
Total			18	0	3	4	25	0	0	2	24	10	0	32	23	15	42	16	1	4	0	11	2	2	10	21	265

Table 13. Emergence of adult beetles in outdoor breeding experiments. N: number of beetles.

		Species					
		cinctus		*melanocephalus*		*mollis*	
Year	Decade	N		N		N	
1982	1-10 June	3	(1.8 %)	113	(43.3 %)	158	(98.7 %)
	11-20 June	136	(80.5 %)	101	(38.7 %)	2	(1.2 %)
	21-30 June	29	(17.2 %)	40	(15.3 %)	-	-
	1-10 July	1	(0.6 %)	7	(2.7 %)	-	-
1983	1-10 June	-	-	-	-	-	-
	11-20 June	69	(53.9 %)	12	(34.3 %)	32	(68.1 %)
	21-30 June	58	(45.3 %)	23	(65.7 %)	15	(31.9 %)
	1-10 July	1	(0.8 %)	-	-	-	-

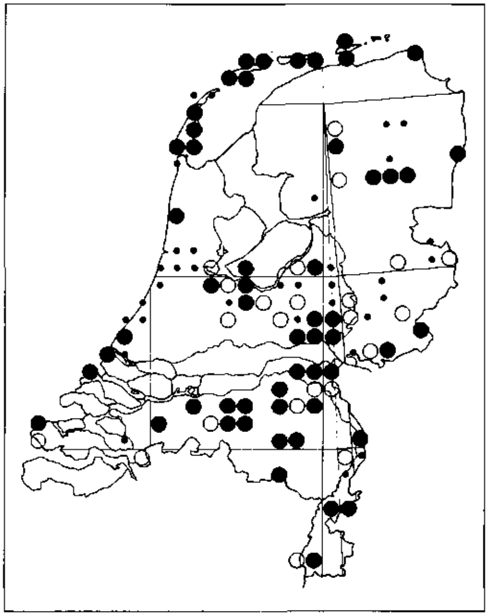
In the laboratory a small part of the females of all three species kept individually even survived a second hibernation period and laid eggs during a 3rd year. Outdoor breeding experiments carried out in 1981 and 1982 also gave an impression of the reproductive period of the three species (table 11). In these experiments too *Calathus melanocephalus* showed an earlier start and finish of the egg-laying period than both *C. cinctus* and *C. mollis*. Differences between the results for the two years are largely due to different temperature conditions. In 1981, for instance, all females stopped egg production in the first third of December because of a sudden frost period (fig. 14). Due to the later start, *C. cinctus* and *C. mollis* suffered more from this event than *C. melanocephalus*. But even under the more favourable weather conditions of 1982/1983 *C. melanocephalus* showed about the same length of the reproduction period, whereas both *C. cinctus* and *C. mollis* are able to prolong their reproduction periods substantially under these conditions (fig. 15).

Data on egg production and larval development of the three species in relation to wing development, temperature and availability of food will be published elsewhere.

Daily rhythms

Information about the daily activity of the species was derived from a small experiment in which the egg production was estimated every two hours under fixed temperature and daylength conditions. On 14 September 1981 eight reproductive females of *Calathus cinctus*, *C. melanocephalus* and *C. mollis*, collected at Ameland on 14 July, were transferred from the outdoor breeding house to an incubator adjusted at 19 °C and a daylength of 14.75 hours (6.15-19.00 hrs). They were kept there with males in single pairs for three days. In all three species egg production took place

Fig. 16. Dutch distribution of *Calathus cinctus*. Symbols on this and the following maps: open cirkels: recorded before 1930 only; small dots: recorded between 1930 and 1960; large dots: recorded since 1960.



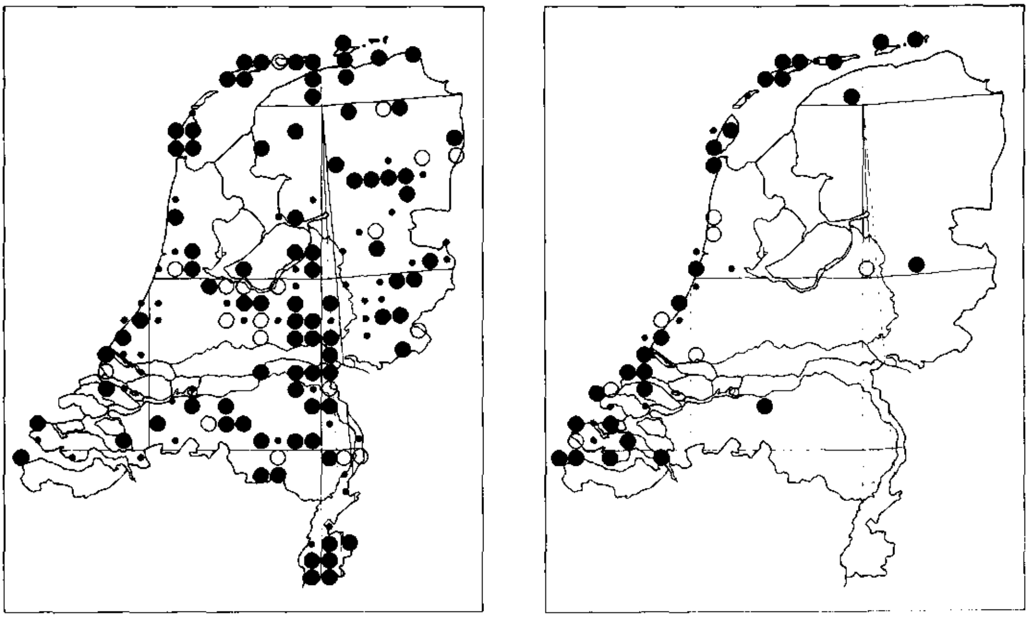
mainly during the dark hours (18.30-6.30 hrs); a very few eggs were also laid during the early morning hours (table 12).

Emergence of young beetles

The outdoor breeding experiments also gave an impression of the time of emergence of young beetles (table 13). In 1982 almost all beetles of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* emerged in the first two thirds of June, whereas in 1983 this occurred in the latter half of the same month. Van Dijk (1973) trapped teneral females of *C. melanocephalus* in the field as well as in enclosure experiments during a short period from 15 June onwards. Samples of *C. cinctus* and *C. mollis* collected on 28 June 1979 at the West Frisian Island of Ameland consisted of 75% (102 of 138 specimens) and 11.7% (26 of 248 specimens) tenerals respectively.

Feeding

Feeding behaviour and prey spectrum of *Calathus melanocephalus* were studied by Hengeveld (1980) by identifying food remains in the gut contents of beetles trapped in the field and killed instantly. From the diet components found, it appeared that *C. melanocephalus* is a polyphagous species, but not exclusively carnivorous (see also Melber 1983). Similar results were found by Smit (1957), Skuhravy (1959) and



Figs 17-18. Dutch distribution of *Calathus*. 17, *C. melanocephalus*; 18, *C. mollis*.

Hengeveld (1980) for the closely related *Calathus ambiguus* (Paykull), *C. erratus* Sahlberg and *C. fuscipes* (Goeze).

Dispersal

Den Boer (1977) developed criteria to classify carabid beetles in three dispersal groups using data on wing development, wing-morph frequencies and actual flight (catches of flying beetles in window traps). A-species are those with a relatively low power of dispersal (monomorph brachypterous or wing-polymorphic species with a very low frequency (< 1%) of macropterous beetles). B-species have a relatively high power of dispersal due to their capability of flight (macropterous and wing-polymorphic species caught in window traps, see also Van Huizen, 1980), whereas C-species are the remaining species (macropterous or wing-polymorphic with a high frequency of macropterous beetles, but never or rarely caught flying) with uncertain dispersal power.

The wing-dimorphic *Calathus cinctus* was caught in window-traps (Van Huizen, 1980; Den Boer et al., 1980) and consequently belongs to the group of B-species (Van Dijk, 1986).

The wing-dimorphic *Calathus melanocephalus* and the monomorph macropterous *C. mollis* were never caught flying, but laboratory-bred beetles of both species developed flight muscles and flew frequently in a laboratory test (the results of this test will be treated in chapter VI). For the time being both species therefore have to

Table 14. Number of 10 X 10 km squares occupied per decade by *Calathus cinctus*, *C. melanocephalus* and *C. mollis*. TO: total number of squares occupied by all carabid species per decade; F: correction factor calculated from the total number of squares covering The Netherlands (F=448/TO); O: actual number of occupied squares; OF: corrected number of occupied squares (OF=O*F).

				Species					
Decade				*cinctus*		*melanocephalus*		*mollis*	
Nr	Years	TO	F	O	OF	O	OF	O	OF
1	1870-1879	72	6.22	2	12	0	0	2	12
2	1880-1889	81	5.53	1	6	1	6	3	17
3	1890-1899	108	4.15	5	21	7	29	5	21
4	1900-1909	150	3.03	16	48	18	55	6	18
5	1910-1919	192	2.35	26	61	24	56	11	26
6	1920-1929	214	2.10	22	46	28	59	9	19
7	1930-1939	213	2.10	18	38	29	61	15	32
8	1940-1949	246	1.82	12	22	26	47	7	13
9	1950-1959	264	1.70	16	27	35	59	13	22
10	1960-1969	312	1.44	9	13	20	29	10	14
11	1970-1979	336	1.33	23	31	35	47	12	16
12	1980-1989	350[1]	1.28	21	27	33	42	9	11

[1] Estimated value. Up till now 14.714 records from 321 squares were recorded, but many have to be added (H. Turin, personal communication)

be considered C-species. Den Boer (1977) and Van Dijk (1986) treated *C. melanocephalus* as A-species, based on the extremely low frequency of macropterous beetles in populations investigated in the Dutch province of Drenthe (0.23%). Populations in the recently reclaimed Flevopolders, however, showed a considerable higher frequency of macropterous beetles (25-40%: Den Boer, 1970; Aukema, 1986). During breeding the flight muscles are autolysed in these species and flight only occurs before breeding. Data on the development of flight muscles and the occurrence of actual flight from the field and from breeding experiments in relation to temperature and availability of food will be treated elsewhere. Den Boer et al. (1980) already published some preliminary data for *C. cinctus*.

Distribution

The Netherlands

Available data were used to prepare distribution maps on the UTM 10x10 square km scale as used by the European Invertebrate Survey (figs 16-18).

Calathus cinctus (fig. 16) and *C. melanocephalus* (fig. 17) are widely distributed over the whole country, whereas *C. mollis* (fig. 18) is almost restricted to the coastal

Table 15. Spearman rank correlation coefficients between the corrected number of squares occupied and the decade rank.

Species	All decades	20th Century [1]
cinctus	+0.21	-0.74*
melanocephalus	+0.72*	-0.54
mollis	-0.20	-0.60

* 0.02 < p < 0.05

[1]) decades 4-12 of table 14

dune region, with only a few inland populations on blown sands or other large sand deposits. Desender (1985, 1986) and Moncel (1972) published comparable maps and data for Belgium and France respectively.

A closer examination of the data of *Calathus cinctus* (fig. 16) shows that this species has been caught regularly in The Netherlands since 1864 (Overveen, vi, 1♀, leg. J. Kinker, coll. Zoölogisch Museum, Amsterdam). For *C. melanocephalus* and *C. mollis* respectively the first records are Overveen, x.1864, J. Kinker, 1♂ (coll. Zoölogisch Museum, Amsterdam) and Driehuizen, 23.vii.1882, 1♂ (coll. Zoölogisch Museum, Amsterdam).

Time-trends in the number of 10 x 10 km squares occupied per decade by the three species were estimated according to the method of Turin & den Boer (1988). Fig. 19 shows the time-trends after correction of the number of occupied squares for differences in collecting intensity between the decades (table 14). *Calathus melanocephalus* shows a significantly increasing time-trend, whereas both *C. cinctus* and *C. mollis* show rather indifferent time trends (table 15). When considering the 20th century only (table 14: decades 4-12) all three species show negative correlation coefficients, but only in the case of *C. cinctus* was this significant, largely due to the high number of squares occupied in the years 1910-1930.

Ranges

Concerning their general distribution, revision of material on a larger scale is necessary to get a reliable picture (the data in Turin (1981) are only based on a survey of the literature). In the Dutch collections mentioned and/or in the collection of the British Museum (Natural History), London, the collection of the Zoologisches Museum, Berlin, the collection of the Zoologische Staatssammlung, München, or the collection of M. Baehr, München, I saw material from the following localities:

Calathus cinctus: South-England (south of the line River Seven - The Wash), Wales, Ireland, The Netherlands, Belgium, Germany, Poland, the Baltic States (Estonia), Russia, France, Spain, Sardinia, Corsica, Italy, Sicily, Malta, Yugoslavia, Austria, Hungary, Romania, Bulgaria, Albania, Greece, Cyprus, Turkey, Crimea,

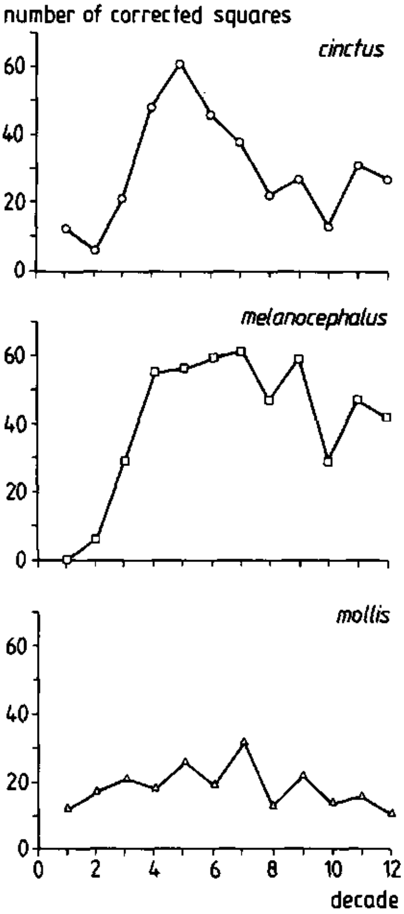


Fig. 19. Plots of the corrected time trends of *Calathus cinctus*, *C, melanocephalus* and *C. mollis*; decades: 1870-1879 (1), 1880-1889 (2), 1890-1899 (3), etc.

Ukraine, the Caucasus, Iran, Syria, Israel and Morocco;

Calathus melanocephalus: Finland, Sweden, Norway, Denmark, Iceland, England, Scotland, Whales, Ireland, The Netherlands, Belgium, Luxembourg, Germany, Poland, the Baltic States (Estonia), France, Spain, Sardinia, Corsica, Italy, Sicily, Yugoslavia, Switzerland, Austria, Hungary, Romania, Albania, Greece, Turkey, Ukraine and the Caucasus;

Calathus mollis: Denmark, England, Wales, Scotland, Ireland, The Netherlands, Belgium, Germany (the East Frisian Islands), France, Portugal, Spain, Mallorca, Italy, Sicily, Yugoslavia, Greece, Turkey, Gibraltar, Malta, Algeria and Morocco.

Lindroth (1986) indicated the occurrence of *Calathus cinctus* in South-Sweden and Denmark (see also Bangsholt, 1983) and of *C. mollis* in Norway. Since Lindroth listed the right combination of characters for both taxa, his findings, although not confirmed, are considered reliable. Anderson (1987, in litt. 1990) furthermore found *C. cinctus* to be sporadically distributed around the Irish coast south of the line from the Shannon Estuary to Dublin.

Calathus melanocephalus obviously has a European distribution, ranging from Iceland and Scandinavia in the North to the Mediterranean in the South. It is the only species of this group also occurring at higher altitudes in mountain areas. The subspecies *C. melanocephalus alpinus* Dejean is restricted to the eastern Alps (Koch, 1989). Ball & Negre (1972) list a probably introduced specimen of *C. melanocephalus* from North America.

Calathus cinctus does not occur as far north as *C. melanocephalus*, but in the Mediterranean it reaches further south, occurring as far as Morocco and Algeria in the west and Syria and Iran in the east.

Calathus mollis seemingly is restricted to the Atlantic and Mediterranean coastal areas.

DISCUSSION

The establishment of *Calathus* (*Neocalathus*) *cinctus* as a good species has solved a major identification problem in the genus *Calathus*, although even now long winged females of *C. cinctus* sometimes are difficult to distinguish from those of *C. mollis*. On the other hand a new problem arises in the interpretation of existing literature on the species of the *melanocephalus*-group. It is quite clear from the data presented here that *C. cinctus*, although in literature still considered to be mainly distributed in Eastern Europe (southeast and east of the river Weser) (Lienemann, 1981; Koch, 1989), is a very common species in Western Europe too. For instance in England *C. cinctus* was already present at the time of Stephens, because in his collection, bought in 1853 by the British Museum (Natural History), London, and kept in its original state (Hammond, 1972) 4 out of the 13 specimens in the box of *C. melanocephalus* belong to *C. cinctus* (1 male and 3 females, all short winged). Furthermore Jeannel (1942) already indicated the occurrence of *C. cinctus* in western France (Vendée).

Lindroth (1949) used data on wing development in *Calathus mollis* as one of the main illustrations for his theory of postglacial recolonization of Fennoscandia. Although Lindroth indicated in the same publication that there were two taxa involved, his data were never revised.

Furthermore data from, for instance, the following studies will have to be reconsidered concerning species identity for: larval taxonomy (Kůrka, 1971: description of larval stages of *Calathus melanocephalus* and *C. mollis*), diagnostics of eggs (Luff, 1981: characteristics of the eggs of *C. melanocephalus* and *C. mollis*), chromosome numbers (Serrano, 1981: chromosome numbers of *C. melanocephalus* ($n=37$) and *mollis* ($n=39$)), population dynamics (Gilbert, 1956: population dynamics of *C. melanocephalus* and *C. mollis* in the coastal dunes of the Isle of Anglesey where, as we know now, all three species occur), the occurrence in agricultural fields

(Luff, 1987: only references for the occurrence of *C. melanocephalus*), flight observations (Palmén, 1944: long winged *C. melanocephalus* washed ashore on the southwestern coast of Finland; Honek & Pulpán, 1983: *C. melanocephalus* caught in a light trap), and bionomics and breeding (Kůrka, 1972: *C. melanocephalus* and *C. mollis*).

CONCLUSIONS

1. *Calathus* (*Neocalathus*) *cinctus* Motschulsky is a good species, reproductively isolated from both the closely related *C.* (*N.*) *melanocephalus* (Linnaeus) and *C.* (*N.*) *mollis* (Marsham).
2. The species of this so-called *melanocephalus* group can be distinguished from each other reliably only on the basis of the shape of the elytra, coloration characters and the shape of the right parameres.
3. Morphological measurements and ratios are not useful in identifying these species.
4. Both *Calathus cinctus* and *C. melanocephalus* are wing-dimorphic with either fully developed wings (of about 1.5 times the length of the elytra) or reduced wings (of about 0.5 times the length of the elytra), whereas Dutch *C. mollis* always are macropterous.
5. According to the subdivision in habitat groups of Den Boer (1977) *Calathus cinctus* is classified as H-species (species preferring localities significantly influenced by human activities), *C. melanocephalus* as mainly a species of heath and peatmoor (F-species) and *C. mollis* as E-species (species of blown sands and sand dunes).
6. The species are night-active autumn breeders. *Calathus melanocephalus* reproduces earlier and during a shorter period in the season than *C. cinctus* and *C. mollis*.
7. Age-composition of populations of *Calathus cinctus* and *C. mollis* resembles those of *C. melanocephalus* (not only larvae, but also a varying part of the adult beetles overwinters and reproduces for a second time).
8. Concerning dispersal power *Calathus cinctus* is classified as a good disperser (B-species sensu Den Boer, 1977), whereas *C. melanocephalus* and *C. mollis* are considered C-species (species with uncertain dispersal power) by lack of information on actual flight.
9. All three species are common in The Netherlands and were so during the 20th century. Both *Calathus cinctus* and *C. melanocephalus* are well distributed all over the country, whereas *C. mollis* is limited to coastal dunes and a few inland blown sands or other large sand deposits.
10. All three species are mainly European in distribution, with *Calathus*

melanocephalus reaching further north and occurring also at higher altitudes in mountain areas, *C. cinctus* reaching further south and *C. mollis* limited to coastal areas in the Atlantic and Mediterranean area.

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REFERENCES

Anderson, R., 1987. Some uncommon Carabidae (Coleoptera) from South Dublin/Wicklow.- *Irish Naturalist Journal* 22: 259-260.

Aukema, B., 1986. Winglength determination in relation to dispersal by flight in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae). In: *Carabid beetles. Their adaptations and dynamics* (P. J. den Boer, M. L. Luff, D. Mossakowski and F. Weber eds): 91-99. Fischer, New York.

Aukema, B., 1990. The nomenclature of the melanocephalus group of the genus Calathus (Coleoptera: Carabidae).- *Entomologische Berichten, Amsterdam* 50: 143-145.

Aukema, B. & M. L. Luff, 1992. Carabus mollis Marsham, 1802 (currently Calathus mollis; Insecta, Coleoptera): proposed conservation of the specific name.- *Bulletin of Zoological Nomenclature* 49: 28-29.

Baars, M. A. & Th. S. van Dijk, 1984. Population dynamics of two carabid beetles at a Dutch Heathland II. Egg production and survival in relation to density.- *Journal of Animal Ecology* 53: 389-400.

Ball, G. E. & J. Negre, 1972. The taxonomy of the Nearctic species of the genus Calathus Bonelli (Coleoptera, Carabidae).- *Transactions of the American Entomological Society* 98: 413-533.

Bangsholt, F., 1983. Sandspringernes og lobebillernes udbredelse og forekomst i Danmark ca. 1830-1981 (Coleoptera: Cicindelidae and Carabidae).- *Dansk Faunistik Bibliotek* 4: 1-271.

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae).- *Oecologia* 4: 1-28.

Boer, P. J. den, 1977. Dispersal power and survival. Carabids in a cultivated countryside.- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae).- *Entomologia Generalis* 6: 107-134.

Desender, K., 1985. Carabid beetles new for the Belgian Fauna.- *Bulletin et Annales de la Société (Royale) Entomologique de Belgique* 121: 69-74.

Desender, K., 1986. Distribution and ecology of carabid beetles in Belgium (Coleoptera, Carabidae). 4. Species 153-217.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 30: 1-23.

DeZordo, I., 1979. Phänologie von Carabiden im Hochgebirge Tirols (Obergurgl, Österreich) (Insecta: Coleoptera).- *Bericht Naturwissenschaftlich-Medizinischen Vereins Innsbruck* 66: 73-83.

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

Dijk, Th. S. van, 1973. The age-composition of populations of Calathus melanocephalus L. analysed by studying marked individuals kept in fenced sites.- *Oecologia* 12: 213-240.

Dijk, Th. S. van, 1978. Calathus mollis erythroderus Gemminger & Harold in Drenthe (Coleoptera, Carabidae).- *Entomologische Berichten, Amsterdam* 38: 151-153.

Dijk, Th. S. van, 1979a. On the relationship between reproduction, age and survival in two carabid beetles: Calathus melanocephalus L. and Pterostichus coerulescens L. (Coleoptera, Carabidae).- *Oecologia* 40: 63-80.

Dijk, Th. S. van, 1979b. Reproduction of young and old females in two carabid beetles and the relationship between the number of eggs in the ovaries and the number of eggs laid. In: On the evolution of behaviour in Carabid beetles (P. J. den Boer, H.-U. Thiele & F. Weber eds).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 18: 167-183.

Dijk, Th. S. van, 1986. Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments.- *Netherlands Journal of Zoology* 36: 413-437.

Forsskåhl, B., 1972. The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland. 9. Carabidae, with special notes on ecology and breeding biology.- *Acta Societas pro Fauna et Flora Fennica* 80: 99-119.

Friederichs, K., 1907. Über Verbreitung und Lebensweise einiger Käfer.- *Archiv Freunde Naturgeschichte Mecklenburg* 61: 48-60.

Freude, H., 1976. Adephaga I.- *Die Käfer Mitteleuropas* 2: 1-302.

Gersdorf, E., 1937. Ökologisch-faunistische Untersuchungen über Carabiden der mecklenburgische Landschaft.- *Zoologische Jahrbücher für Systematik, Geographie und Biologie der Tiere* 70: 17-86.

Gilbert, O., 1956. The natural histories of four species of Calathus (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales.- *Oikos* 7: 22-46.

Hammond, P. M., 1972. On the type material of Staphylinidae (Col.) described by T.

Marsham and J. F. Stephens.- *Entomologist's Gazette* 23: 129-135.

Hengeveld, R., 1980. Polyphagy, oliphagy and food specialization in ground beetles (Coleoptera, Carabidae).- *Netherlands Journal of Zoology* 30: 564-584.

Honek A. & J. Pulpán, 1983. The flight of Carabidae (Coleoptera) to light trap.- *Vestník Československé Společnosti Zoologické* 47: 13-26.

Huizen, T. H. P. van, 1980. Species of Carabidae in which the occurrence of dispersal by flight of individuals has been shown.- *Entomologische Berichten, Amsterdam* 40: 167-168.

Jeannel, R., 1942. Coléoptères Carabiques.- *Faune de France* 40: 572-1173.

Koch, K., 1989. Ökologie. I.- *Die Käfer Mitteleuropas*: 1-440.

Kůrka, A., 1971. Larvae of the Czechoslovak species of the genus Calathus Bonelli (Coleoptera, Carabidae).- *Acta Entomologica Bohemoslovaca* 68: 233-262.

Kůrka, A., 1972. Bionomy of the Czechoslovak species of the genus Calathus Bon., with notes on their rearing (Coleoptera: Carabidae).- *Vestník Československé Společnosti Zoologické* 36: 101-114.

Lienemann, K., 1981. Calathus erythroderus Gemminger et Harold 1868 (Coleoptera, Carabidae) neu im Rheinland.- *Decheniana* 134: 176.

Lindroth, C. H., 1943. Zur Systematik Fennoskandischer Carabiden.- *Entomologisk Tidskrift* 64: 1-68.

Lindroth, C. H., 1945. Die Fennoskandischen Carabidae. Eine tiergeografische Studie. 1. Spezieler Teil.- *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar* 6, Ser. B 4 (1): 1-709.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae. 3. Allgemeiner Teil.- *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar* 6, Ser. B 4 (3): 1-911.

Lindroth, C. H., 1974. Coleoptera, Carabidae.- *Handbooks for the Identification of British Insects* 4(2): 1-148.

Lindroth, C. H., 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark.- *Fauna Entomologica Scandinavica* 15(2): 233-497.

Luff, M. L., 1981. Diagnostic characters of the eggs of some Carabidae (Coleoptera).- *Entomologica Scandinavica*, Supplement 15: 317-327.

Luff, M. L., 1987. Biology of polyphagous ground beetles in agriculture.- *Agricultural Zoology Reviews* 2: 237-278.

Melber, A., 1983. Calluna-Samen als Nahrungsquelle für Laufkäfer in einer nordwestdeutschen Sandheide (Col.: Carabidae).- *Zoologische Jahrbücher für Systematik* 110: 87-95.

Mols, P. J. M., Th. S. van Dijk & Y. Jongema, 1981. Two laboratory techniques to separate eggs of carabids from a substrate.- *Pedobiologia* 21: 500-501.

Moncel, J., 1972. A propos de Calathus mollis (Col. Carabidae) et de sa variété erythroderus.- *l'Entomologiste* 28: 26-30.

Opinion 1723, 1993. Carabus mollis Marsham, 1802 (currently Calathus mollis; Insecta, Coleoptera): specific name conserved.- *Bulletin of Zoological Nomenclature* 50: 166

Palmén, E., 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor.- *Annales Zoologici Societas Zoologicae-Botanicae Fennicae, Vanamo* 10: 1-262.

Refseth, D., 1988. Annual pattern of activity, reproduction and development in some Norwegian Carabidae (Col.).- *Fauna Norvegiae* Ser. B 35: 21-30.

Schatzmayr, A., 1937. I Calathus d'Europa.- *Publicazioni del Museo Entomologico "Pietro Rossi" Duino* 2: 1-50.

Serrano, J., 1981. Chromosome numbers and karyotypic evolution of Caraboidea.- *Genetica* 55: 51-60.

Skuhravy, V., 1959. Die Nahrung der Feldcarabiden.- *Acta Societas Entomologicae Ceskoslovenské* 56: 1-18.

Smit, H., 1957. Onderzoek naar het voedsel van Calathus erratus Sahlb. en Calathus ambiguus Payk. aan de hand van hun maaginhouden.- *Entomologische Berichten, Amsterdam* 17: 199-209.

Thiele, H.-U., 1977. *Carabid beetles in their environments.* A study on habitat selection by adaptations in physiology and behaviour: i-xvii, 1-369. Springer, Berlin, Heidelberg, New York.

Turin, H., J. Haeck & R. Hengeveld, 1977. Atlas of the carabid beetles of The Netherlands.- *Verhandelingen der Koninklijke Nederlandse Academie van Wetenschappen, Afdeling Natuurkunde* (2) 68: 1-228, Amsterdam.

Turin, H., 1981. Provisional checklist of the European groundbeetles (Coleoptera: Cicindelidae & Carabidae).- *Monografieën Nederlandse Entomologische Vereniging* 9: 1-249.

Turin, H. & P. J. den Boer, 1988. Changes in the distribution of carabid beetles in The Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae).- *Biological Conservation* 44: 179-200.

Vereshchagina, T. N., 1985. The genus Calathus Bon. (Coleoptera, Carabidae) in the USSR.- *Entomological Review* 63: 75-94.

Vlijm, L. & Th. S. van Dijk, 1967. Ecological studies on carabid beetles. II. General pattern of population structure in Calathus melanocephalus (Linn.) at Schiermonnikoog.- *Zeitschrift für Morphologie und Ökologie der Tiere* 58: 396-404.

Vlijm, L., Th. S. van Dijk & S. Y. Wijmans, 1968. Ecological studies on carabid beetles. III. Winter mortality in adult Calathus melanocephalus (Linn.). Egg production and locomotory activity of the populations which has hibernated.- *Oecologia* 1: 304-314.

Wiebes-Rijks, A. A., 1959. Het onderscheid tussen Calathus melanocephalus L. en Calathus mollis Marsh. (Coleoptera, Carabidae).- *Entomologische Berichten, Amsterdam* 19: 248-253.

III. WING LENGTH DETERMINATION IN TWO WING-DIMORPHIC *CALATHUS* SPECIES (COLEOPTERA: CARABIDAE) *

ABSTRACT

Wing dimorphism in the carabid beetles *Calathus cinctus* and *C. melanocephalus* was studied by rearing offspring of single-pair crosses. In both species wing dimorphism was found to be determined genetically according to a single-locus model with brachyptery dominant to macroptery. In *C. melanocephalus*, however, the expression of the long winged genotype is modified by environmental factors such as temperature and food supply, whereas in *C. cinctus* winglength is independent of these factors. Moreover in *C. melanocephalus* the expression of the long winged genotype was found to be favoured by relatively better environmental conditions (higher temperatures and abundant food) and to be more frequent in females than in males, both in the field and in laboratory experiments.

It is argued that the resulting differences in phenotypic plasticity of the long winged genotype (none in *C. cinctus* and a varying amount in *C. melanocephalus*) contribute to temporal and spatial differences in dispersal abilities between the two species. The adaptive significance of the two types of inheritance is discussed.

Key words: Carabidae, *Calathus*, *cinctus*, *melanocephalus*, Wing dimorphism, Asymmetric wing development, Inheritance, Environmental control, Dispersal Potential.

INTRODUCTION

Wing polymorphism is a very common phenomenon in insects, occurring in many groups (see Harrison (1980) and Dingle (1986) for recent reviews). In carabid beetles it has caught the attention of zoologists since the times of Darwin (1859: flightless morphs on Madeira) and Darlington (1936; 1943: wing development in relation to mountain tops and islands), but little experimental work has been done to unravel the background of wing development in this group. Lindroth (1949, 1969) based his theory about the recolonization of Fennoscandia by Carabidae after the last glaciation on 'the postulate that long winged (macropterous) individuals are

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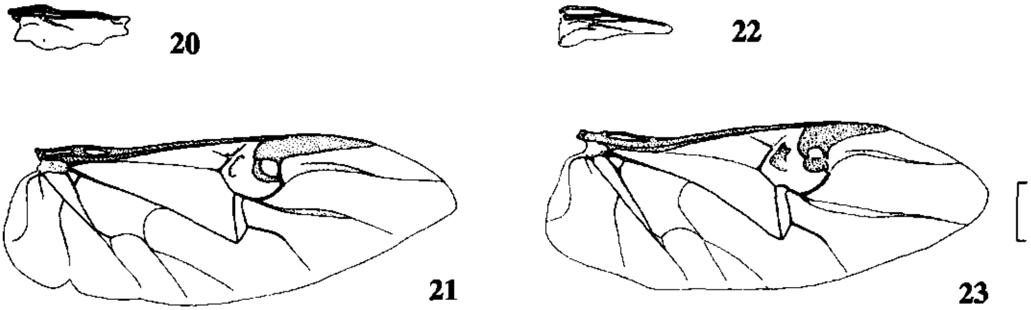
homozygotes and that populations entirely or very dominantly consisting of such individuals are pioneers (late colonizers)' (Lindroth, 1969: 181). This postulate was mainly based on his limited but thus far unique breeding experience (a progeny of 52 beetles of 7 parental females) with the wing-dimorphic *Pterostichus anthracinus* (Illiger) (Lindroth, 1946), which lead him to the conclusion that wing dimorphism in this species is inherited in a simple Mendelian fashion with the brachypterous condition dominant. The fact that Jackson (1928) had already got similar results with the weevil *Sitonia hispidula* (Fabricius) tempted Lindroth (1946) to the statement that 'it therefore seems probable that the non-sexual wing dimorphism in the order of Coleoptera as a whole will prove to be of the same type'. Stein (1973) indeed got comparable results for another weevil, *Apion virens* Herbst.

Concerning carabid beetles, since then very few efforts have been made to confirm Lindroth's postulate. Breeding results with the wing-polymorphic *Agonum retractum* LeConte (Carter, 1976) and with *Bembidion lampros* (Herbst) (Langor & Larson, 1983) do not allow unambiguous conclusions concerning the type of inheritance involved in these species. Desender (1989a) showed a high heritability of relative wing development in the wing-polymorphic *Pogonus chalceus* (Marsham). Den Boer et al. (1980) used some preliminary data of *Calathus cinctus* from the study presented here to illustrate their theory on the evolution of wing dimorphism in carabids.

The aim of the work presented here was to study the inheritance of wing dimorphism in two closely related species of the genus *Calathus* Bonelli: *Calathus* (*Neocalathus*) *cinctus* Motschulsky (= *erythroderus* Gemminger & Harold) and *Calathus* (*Neocalathus*) *melanocephalus* (Linnaeus) and thus test Lindroth's postulate of a single-locus model with dominance of the short winged condition for these two species. A third species under investigation, the closely related *Calathus* (*Neocalathus*) *ochropterus* (Duftschmid), appeared to be monomorph macropterous in field samples, collection material as well as in breeding experiments (Aukema, 1990).

Offspring of single-pair crosses between all possible combinations of wing-morphs of both species were reared under approximately outside conditions in an outdoor insectary as well as under fixed temperature conditions in incubators in the laboratory. In the case of *Calathus melanocephalus* also the effect of the quantity of available food during larval development on wing development was established. Some preliminary data have already been published (Aukema, 1986).



Figs 20-23. Wing-morphs in *Calathus*: 20, *C. cinctus* (short winged); 21, ibid., long winged; 22, *C. melanocephalus* (short winged); 23, ibid., long winged (scale 2 mm).

MATERIAL AND METHODS

Species

Calathus cinctus and *C. melanocephalus* are both wing-dimorphic with either strongly reduced short wings (about half the length of the elytra) or fully developed long wings (about 1.5 times the length of the elytra) (figs 20-23; table 16).

Detailed information on biology of the species is given by Aukema (1990). Parents and offspring of crosses carried out by Van Dijk (1978) were used as starting material for a first crossing programme. Assumed parental genotypes were derived from phenotypes of parents and their offspring. Long winged phenotypes were considered to represent the recessive homozygote, whereas short winged offspring of long winged females were supposed to be heterozygous. The short winged homozygotes could not be established with certainty, but fully short winged offspring of short winged females from localities with a low to very low percentage of long winged individuals were used as such.

All three assumed genotypes of *Calathus cinctus* were obtained from offspring of females caught at Nuil and Dwingeloo in the surroundings of the Biological Station.

Table 16. Measurements (in mm) of winglength and elytronlength of *Calathus cinctus* (cin), *C. melanocephalus* (mel), and *C. mollis* (mol). RWL: relative winglength = winglength/elytronlength). Measurements were made according to Aukema (1990). N: number of measurements; sw: short winged; lw: long winged.

				Wing-length		Elytron-length		RWL	
Morph	Species	Locality	N	Mean	95% c.l.	Mean	95% c.l.	Mean	95% c.l.
males									
sw	cin	Nuil	25	1.98	1.95-2.03	4.48	4.42-4.54	0.44	0.44-0.45
		Texel	20	1.93	1.85-2.01	4.17	4.07-4.29	0.46	0.45-0.47
	mel	Texel	20	1.93	1.86-2.00	4.09	4.00-4.18	0.47	0.46-0.49
lw	cin	Dwingeloo 1)	30	7.18	7.02-7.35	4.65	4.59-4.72	1.54	1.52-1.57
		Texel	11	6.26	5.89-6.62	4.12	3.98-4.25	1.52	1.47-1.57
	mel	O-Flevoland 2)	25	7.34	7.17-7.51	4.69	4.60-4.78	1.57	1.53-1.60
		Texel	7	7.10	6.86-7.35	4.32	4.19-4.32	1.64	1.62-1.67
females									
sw	cin	Nuil	25	2.16	2.11-2.20	4.82	4.73-4.90	0.45	0.44-0.45
		Texel	20	2.14	2.08-2.20	4.54	4.44-4.64	0.47	0.46-0.48
	mel	Texel	20	2.06	1.99-2.13	4.45	4.36-4.53	0.46	0.45-0.48
lw	cin	Dwingeloo 1)	30	7.77	7.63-7.91	5.03	4.96-5.11	1.54	1.53-1.56
		Texel	11	6.49	6.15-6.82	4.34	4.18-4.50	1.49	1.45-1.54
	mel	O-Flevoland 2)	29	7.60	7.47-7.62	5.02	4.96-5.08	1.51	1.49-1.54
		Texel	20	7.51	7.38-7.65	4.80	4.72-4.88	1.57	1.54-1.59

1): measurements M. G. J. Oudewesselink
2): measurements A. Spee

Supposed long winged homozygotes and short winged heterozygotes of *C. melanocephalus* were reared from females collected in the in 1957 reclamed polder of Oost-Flevoland from a population with a relatively high percentage of long winged beetles (23% in 1978). Short winged offspring of females collected at the heath of Kraloo (a population with a very low percentage of macropterous beetles - estimated as 0.23% by Den Boer (1977) - were used as short winged homozygotes. In *C. melanocephalus* males and females with asymmetric wing development (a fully developed wing on the left or the right site and a short wing on the opposite site) occur in both field populations and in laboratory bred offspring (see also Desender, 1989b). In this study those specimens are considered to represent long winged genotypes.

Table 17. Winglenth determination in *Calathus cinctus* (cin) and *C. melanocephalus* (mel): crossing program. LW: long winged; SW: short winged; N: number of crosses; NL: number of crosses, producing larvae; L: number of larvae reared; B: number of beetles reared; DW: Dwingeloo; OF: Oost-Flevoland;

	PARENTS				CROSSES			
	Morph		Origin					
Species	Males	Females	Males	Females	N	NL	L	B
1978								
cin	LW	LW	Parents 1977 1)	F_1 1978 1)	6	5	283	179
	LW	SW	F_1 1978	Parents 1977	6	4	114	48
	SW	LW	F_1 1978	Parents 1977	6	5	149	59
	SW	SW	F_1 1978	F_1 1978	6	6	295	182
	SW	SW	F_1 1978	Parents 1977	1	1	59	25
	-	LW	no males	DW (23-8/22-9-78)	16	16	734	471
	-	LW	no males	Nuil (23-8/22-9-78)	5	5	253	158
	-	SW	no males	DW (7-9-1978)	1	1	49	27
	-	SW	no males	Nuil (23/31-8-78)	4	3	147	86
mel	LW	SW	OF (20/27-9-1978)	F_1 1978	4	4	188	113
	SW	SW	Kraloo (30-8-1978)	Kraloo (30-8-1978)	6	6	60	40
	SW	SW	Kraloo (30-8-1978)	F_1 1978	2	2	90	51
	-	LW	no males	OF (20-9-1978)	14	13	489	304
	-	SW	no males	OF (27-9-1978)	13	10	371	236
1979								
cin	LW	LW	F_1 1979	F_1 1979	2	2	120	43
	LW	LW	Ameland (28-6-1979)	F_1 1979	1	1	60	20
	SW	LW	F_1 1979	F_1 1979	2	2	85	41
	SW	LW	Ameland (28-6-1979)	F_1 1979	1	1	60	13
	LW	SW	F_1 1979	F_1 1979	2	2	116	68
	LW	SW	Ameland (28-6-1979)	F_1 1979	1	1	60	20
mel	LW	LW	F_1 1979	F_1 1979	4	4	238	85
	SW	LW	F_1 1979 (OF)	F_1 1979	4	4	240	135
	SW	LW	F_1 1979 (Kraloo)	F_1 1979	4	4	217	139
	LW	SW	F_1 1979	F_1 1979 (OF)	4	4	239	92
	W	SW	F_1 1979 (OF)	F_1 1979 (OF)	4	4	240	130
	SW	SW	F_1 1979 (Kraloo)	F_1 1979 (OF)	4	4	224	136
	LW	SW	F_1 1979	F_1 1979 (Kraloo)	4	4	160	96
	SW	SW	F_1 1979 (OF)	F_1 1979 (Kraloo)	4	4	240	132
	SW	SW	F_1 1979 (Kraloo)	F_1 1979 (Kraloo)	4	4	240	112

1) crosses carried out by Th. S. van Dijk

Cross-breeding

For both *Calathus cinctus* and *C. melanocephalus* single-pair crosses between all combinations of wing-morphs were carried out during the years 1978/1979 and 1979/1980 under approximately outside conditions in an outdoor insectary. Selected pairs were kept in petri dishes in ground peat litter. Eggs were separated from the peat with the sieve-wash technique of Mols et al. (1981) and further incubated at a constant temperature of 19 °C. Larvae were transferred to glass tubes in which they were reared individually in sieved peat litter in the outdoor insectary. During the winter months (from the end of November until the end of March) the larvae were moved to a climate room at 5 °C under short-day (SD 10/14) conditions. Crosses and origin of the beetles used are given in table 17.

Offspring of crosses performed by Van Dijk (1979) (F1 1978 in table 17) and specimens collected in the field before the start of the reproduction period (tenerals in the case of females) were used as starting material (table 17). Furthermore offspring of females inseminated in the field (*Calathus cinctus* from Nuil and Dwingeloo and *C. melanocephalus* from Oost-Flevoland) was reared in order to get virgin females as starting material for the next crossing experiments.

In 1979/1980 crosses were carried out in the same way as in the preceding year. The larvae, however, were kept in small petri dishes and the food was changed from pieces of mealworm to small maggots. Information on these crosses is also summarized in table 17.

The effect of temperature on wing development in both *Calathus cinctus* and *C. melanocephalus* was studied in 1981/1982 by rearing larvae of different groups of single pairs of long winged parents collected in the field at three constant temperatures (8.5, 12 and 15.5 °C) and natural daylength in incubators in the laboratory as well as under outside conditions in the outdoor insectary. Parental material of *C. cinctus* and *C. melanocephalus* was collected on the West Frisian Island of Ameland and in Oost-Flevoland respectively.

During the winter months the larvae of the outside-group were kept in a wooden box sunk in the ground, where they stayed from the third week of December until the last week of April.

The effect of the amount of available food on wing development in *Calathus melanocephalus* was studied in 1982/1983 and 1983/1984 by rearing groups of larvae at two different levels of food supply under different temperature conditions.

In 1982/1983 offspring of different groups of long winged parents collected in Oost-Flevoland was reared at three different constant temperatures as well as under outside conditions (the same temperature conditions as in the 1981/1982 programme).

To avoid maternal effects of using different groups of parental females at different temperatures, which might have affected the preceding experiments, in

Table 18. Offspring of females of *Calathus cinctus* and *C. melanocephalus* inseminated in the field (1978/1979, outside conditions/5 °C, SD10). N: number of parental females; n: number of offspring; LW: long winged; SW: short winged.

	PARENTS			OFFSPRING			
	Female			Observed phenotype (♂/♀)			
Species	Phenotype	Origin	N	n	SW	LW	%LW
cinctus	LW	Dwingeloo	16	471	38/ 26	198/209	83.9/88.9
		Nuil	5	158	7/ 6	75/ 70	91.5/92.1
	SW	Dwingeloo	1	27	3/ 10	5/ 9	62.5/47.4
		Nuil	3	86	43/ 27	8/ 8	15.7/22.9
melanocephalus	LW	Oost-Flevoland	13	304	120/131	14/ 39	10.4/22.9
	SW	Oost-Flevoland	10	236	100/ 92	16/ 28	13.8/23.3

Table 19. Wing-morph frequencies in pitfall samples of field populations of *Calathus cinctus* and *C. melanocephalus*. n: number of beetles trapped; LW: long winged; SW: short winged.

			Observed phenotypes (males/females)			
Species	Locality	Year	n	SW	LW	%LW
cinctus	Dwingeloo	1978	180	21/ 25	63/ 71	75.0/74.0
	Nuil	1978	33	1/ 4	13/ 25	92.9/86.2
melanocephalus	Oost-Flevoland	1978	982	389/365	91/137	19.0/27.3

1983/1984 newly hatched larvae of the same eight pairs of long winged F1-parents were distributed as equally as possible over six different rearing conditions: four constant temperatures (8.5, 12, 12.5 and 19 °C) with natural daylength (adjusted once a week), one alternating temperature (12 hours light at 15.5 °C and 12 hours dark at 8.5 °C), and approximately outside conditions (comparable to the experiment carried out in 1981/1982).

In both years larvae of the high food-supply group were fed twice a week with about their own weight in small maggots, whereas larvae of the low food-supply group only got two milligrams of maggots twice a week during their whole development. Larvae were weighed twice a week during the entire developmental period.

Table 20. F_1-beetles from single-pair crosses of *Calathus cinctus* with assumed genotypes (1978/1979, outside conditions/5 °C, SD10). B: short winged allele; b: long winged allele; LW: long winged; SW: short winged; N: number of crosses; n: number of offspring; SD10, see table 18.

PARENTS				OFFSPRING					
Phenotype		Genotype		Phenotype (males/females)					
		Assumed		Observed					Expected
Male	Female	Male	Female	N	n	SW	LW	%LW	%LW
LW	LW	bb	bb	5	179	- / -	93/86	100/100	100
LW	SW	bb	Bb	4	48	9/11	12/16	57.1/59.3	50
SW	LW	Bb	bb	5	59	14/22	13/10	48.1/31.2	50
SW	SW	Bb	Bb	6	182	23/25	69/65	25.0/27.8	25
SW	SW	BB	BB	1	25	10/15	- / -	- / -	0

Table 21. F_2-beetles from single-pair crosses of *Calathus cinctus* with assumed genotypes (1979/1980, outside conditions/5 °C, SD10). Symbols, see table 20.

PARENTS				OFFSPRING					
Phenotype		Genotype		Phenotype (males/females)					
		Assumed		Observed					Expected
Male	Female	Male	Female	N	n	SW	LW	%LW	%LW
LW	LW	bb	bb	3	63	- / -	27/36	100/100	100
SW	LW	Bb	bb	2	41	12/10	5/14	29.4/58.3	50
SW	LW	BB	bb	1	13	5/ 8	- / -	- / -	0
LW	SW	bb	Bb	2	88	18/27	25/18	58.1/40.0	50

RESULTS

Calathus cinctus

Wing-morph frequencies among offspring reared from females inseminated in the field are given in table 18 and data on wing-morph frequencies in the parental field populations are summarized in table 19. Long winged females produced significantly more long winged offspring than short winged ones ($\chi^2=208.6$, df=1, $p << 0.001$) and for both groups of females there are no significant differences in the frequencies of long winged offspring between males and females

Table 22. F_1-beetles from single-pair crosses of long winged *Calathus cinctus* from Ameland reared at different temperatures (1981/1982, natural daylength). Symbols, see table 20.

			OFFSPRING		
			Observed phenotypes (males/females)		
Temperature	N	n	SW	LW	%LW
8.5 °C	7	118	-/-	59/59	100/100
12 °C	7	120	-/-	61/59	100/100
15.5 °C	5	68	-/-	29/39	100/100
outside	2	50	-/-	26/24	100/100

(long winged females: $\chi^2=1.8$, df=1, $0.5<p<0.1$; short winged females: $\chi^2=0.8$, df=1, $0.5<p<0.1$). Nine out of the 21 long winged females (43%) used in this experiment only produced long winged offspring (137 males and 135 females, representing 43% of the entire offspring). Rearing mortality, calculated from table 17, varied between 35 and 45%.

These preliminary data already suggest a genetic determination of wing development in this species.

Wing-morph frequencies of both the F_1- and the F_2-generation of *Calathus cinctus* (tables 20-21) reared in 1978/1979 and 1979/1980 respectively, are in accordance with the expectations from the assumed single-locus model: fully long winged offspring from long winged parents, 50% long winged offspring from long winged and assumed heterozygous parents, 25% long winged offspring from heterozygous parents and no long winged offspring from crosses with one or both parents short winged homozygote.

Heterogeneity between different crosses of the same group, taken together in tables 20 and 21, was considerable, but never significant. The six crosses between heterozygous short winged beetles (table 20), expected to segregate 3 short winged: 1 long winged, show a pooled chi-square of 0,183 (df=1, ns, $0.5<P<0.9$), a summed chi-square of 6.606 (df=6, ns, $0.1<P<0.5$) and a heterogeneity chi-square of 5.423 (df=5, ns, $0.1<P<0.5$).

Furthermore offspring of single-pair crosses of *Calathus cinctus* collected on Ameland and reared at constant temperatures of 8.5, 12 and 15.5 °C and natural daylength as well as under outside conditions was entirely long winged in all cases (table 22).

From these data it is concluded that in *Calathus cinctus* wing dimorphism is

Table 23. F$_1$-beetles from single-pair crosses of *Calathus melanocephalus* with assumed genotypes (1979/1980, outside conditions/5 °C, SD 10). Symbols, see table 20.

PARENTS				OFFSPRING					
Phenotype		Genotype		Phenotype (males/females)					
		Assumed		Observed					Expected
Male	Female	Male	Female	N	n	SW	LW	%LW	%LW
LW	LW	bb	bb	4	85	38/34	7/ 6	15.6/15.0	100
SW	LW	Bb	bb	4	135	67/58	4/ 6	5.6/ 9.4	50
SW	LW	BB	bb	4	139	66/73	-/ -	- / -	0
LW	SW	bb	Bb	4	92	38/50	1/ 3	2.6/ 5.7	50
SW	SW	Bb	Bb	4	130	55/68	-/ 7	- / 9.3	25
SW	SW	BB	Bb	4	136	75/61	-/ -	- / -	0
LW	SW	bb	BB	4	96	47/49	-/ -	- / -	0
SW	SW	Bb	BB	4	132	75/56	1/ -	0.8/ -	0
SW	SW	BB	BB	4	112	66/46	-/ -	- / -	0

Table 24. F$_2$-beetles from single-pair crosses of *Calathus melanocephalus* with assumed genotypes (1981/1982, 12 °C, natural daylength). Symbols, see table 20

PARENTS				OFFSPRING					
Phenotype		Genotype		Phenotype (males/females)					
		Assumed		Observed					Expected
Male	Female	Male	Female	N	n	SW	LW	%LW	%LW
SW	SW	bb	bb	3	49	11/ 2	12/24	52.2/92.3	?
SW	SW	Bb	bb	1	4	2/ -	1/ 1	-	?
SW	SW	Bb	Bb	8	75	26/13	11/25	29.7/65.7	25
LW	SW	bb	BB	2	40	19/11	3/ 7	13.6/38.9	0
SW	SW	BB	BB	4	57	27/27	-/ 3	- /10.0	0

inherited in a simple Mendelian fashion with brachyptery dominant to macroptery.

Asymmetric wing development was not observed in this species, neither in the field nor in breeding experiments.

Under the assumptions of the Hardy-Weinberg Equilibrium (genetically static, randomly breeding populations, see Goodenough, 1978), it is possible to calculate the frequency of alleles and the frequency of genotypes for populations of *Calathus*

Table 25. F_1-beetles from single-pair crosses of long winged *Calathus melanocephalus* from Oost-Flevoland reared at different temperatures (1981/1982, natural daylength). Symbols, see table 20.

		OFFSPRING			
		Observed phenotypes (males/females)			
Temperature	N	n	SW	LW	%LW
8.5 °C	9	128	54/57	4/13	6.9/18.6
12 °C	10	121	34/19	38/30	52.8/61.2
15.5 °C	10	151	62/43	21/25	25.3/36.8
outside	9	129	54/47	12/16	18.2/25.4

Table 26. F_1-beetles from single-pair crosses of short winged *Calathus melanocephalus* from Ameland reared at different temperatures (1981/1982, natural daylength). N: number of crosses (between brackets: number of crosses with long winged offspring). Symbols, see table 20.

		OFFSPRING			
		Observed phenotypes (males/females)			
Temperature	N	n	SW	LW	%LW
8.5 °C	10 (2)	125	73/50	- / 2	- / 3.8
12 °C	9 (2)	132	65/60	- / 7	- /10.4
15.5 °C	10 (5)	111	55/47	2/ 7	3.5/12.9
outside	10 (5)	129	69/55	1/ 4	1.4/ 6.8

cinctus (table 19). The frequencies of the b allele of populations of Dwingeloo and Nuil are 0.862 and 0.940 respectively and the populations contain 1.9 and 0.4% homozygous short winged genotypes and 23.6 and 21.2% heterozygous short winged genotypes respectively. The (isolated) island population on the West Frisian island of Ameland on the other hand contained in 1979 only 13% (29/223) long winged beetles, i.e a much lower frequency of the b allele (0.360), 40.9% homozygous short winged genotypes and 46.1% heterozygous short winged beetles.

Calathus melanocephalus

Calathus melanocephalus, collected in Oost-Flevoland, did not show differences between the proportion of long winged offspring reared from long and short winged females respectively (table 18; $\chi^2=0.06$, df=1, $p<0.1$). For both long and short winged females the proportion of long winged offspring is higher in females, but this difference is only significant for long winged females (long winged females: $\chi^2= 7.28$, df= 1, $p>0.01$; short winged females: $\chi^2=2.94$, df=1, $0.1<p<0.05$). Six crosses between short winged males and females, collected at the heath of Kraloo, as well as two crosses between such males and F1-offspring of similar crosses carried out in 1977 by Th. S. van Dijk (table 17) only produced short winged offspring. Four crosses between long winged males collected in Oost-Flevoland and (short winged) offspring of short winged males and females collected at Kraloo (table 17), however, produced not only the expected short winged offspring (110 beetles), but three out of the four crosses each produced a long winged female as well.

These preliminary data strongly contrast with those of *Calathus cinctus* and suggest at least another type of wing-morph determination in *C. melanocephalus* than the simple genetic one found in *C. cinctus*.

Wing-morph frequencies among the F1-generation of *Calathus melanocephalus* reared in 1979/1980 indeed deviated from the expectations of the single-locus model in that crosses which are expected to produce a certain proportion of long winged offspring produced much lower ones (table 23). Crosses which are expected to produce only short winged offspring did so indeed, with only one exception: a long winged male reared from one of the crosses between assumed heterozygous males and homozygous short winged females (table 23).

Additional crosses between F1-individuals carried out at a constant temperature of 12 °C. under natural daylength in a temperature room in 1981/1982, on the other hand, resulted in rather high frequencies of long winged offspring, which is difficult to explain (table 24). Seemingly all combinations involved are able to produce at least some long winged offspring under certain conditions, even crosses between supposed short winged homozygotes (three out of four of such crosses each produced one long winged female!). The highest proportion of long winged offspring, however, was produced by crosses between short winged beetles resulting from crosses between long winged parents (table 24).

In all types of crosses females showed a higher frequency of long winged beetles than males (table 24).

Offspring of single pairs of long winged *Calathus melanocephalus*, collected in Oost-Flevoland, and reared at three different constant temperatures as well as under outside conditions, showed clear temperature dependent wing-morph frequencies (table 25) with the highest proportion of long winged beetles at 12 °C

(56.2%) and the lowest proportion at 8.5 °C (13.3%). Again females were more frequently long winged than males (table 25), both for separate temperatures as well as for the combined set of temperatures, though not significantly so ($\chi^2=8.7$, df=4, $0.05<p<0.10$). Even single-pair crosses between short winged *C. melanocephalus*, collected at the West Frisian Island of Ameland from an entirely short winged population (all 421 specimens (212 males and 209 females) collected there in 1979, 1981 and 1984 were short winged), gave similar results (table 26).

In 1982/1983 a preliminary experiment to establish the effect of the amount of available food on the phenotypic expression of the assumed long winged genotype was performed. Table 27 gives the phenotypes of the offspring of single pairs of long winged *Calathus melanocephalus*, collected in Oost-Flevoland, and reared at constant temperatures of 8.5 and 15.5 °C and natural daylength as well as under outside conditions. Since from this preliminary data it is clear that not only temperature but also food supply affects the expression of the assumed long winged genotype, a larger experiment (more temperature conditions tested and more larvae reared) was carried out the next year. In that experiment possible maternal effects were excluded by using about equal numbers of larvae from the same eight single pairs in each group.

Again, the results of this experiment (table 28) show a strong temperature-dependent expression of the long winged genotype in the high food-supply group. The highest expression was found at a constant temperature of 15.5 °C (66.7%), lower proportions of long winged offspring were found at 19 and 12 °C (40.6 and 30.0% respectively), whereas the lowest expression was found at 8.5 °C. The results at the alternating temperature condition (36.2% long winged) and under outside conditions closely resembles those at 12 °C. Mortality in the high-food supply group was only significant at 19 °C (table 28). The difference in expression of the long winged genotype between the high and the low food-supply group in this experiment turned out to be extremely large, since none of the 259 beetles reared with a low food supply was of the long winged phenotype. Only a single male of the group reared at 15.5 °C possessed a fully developed wing on the right side only. In general the mortality was substantially higher in the low food-supply groups than in the corresponding groups with a high food supply.

In this experiment too under all tested temperature conditions the frequencies of long winged offspring were higher in females than in males. However, these differences only were significant at 12 °C ($\chi^2=4.00$, df=1, $p<0.05$) and under outside conditions ($\chi^2=5.08$, df=1, $p<0.05$), whereas for the combination of all six temperature conditions the difference was insignificant ($\chi^2=12.55$, df=6, $0.05<p<0.10$).

Analysis of year-samples of *Calathus melanocephalus* collected in Oost-Flevoland (table 29) showed that also in the field the proportion of long winged beetles was

Table 27. F_1-phenotypes from single-pair crosses of long winged *Calathus melanocephalus* from Oost-Flevoland reared under three different temperatures at two food-supply levels (1982/1983, natural daylength). NL: number of larvae used. Symbols, see table 20.

				OFFSPRING			
				Observed phenotypes (males/females)			
Food-supply	Temperature	N	NL	n	SW	LW	%LW
low	8.5 °C	7	35	24	11/13	- / -	- / -
	15.5 °C	6	37	20	7/ 8	2/ 3	22.2/27.3
	outside	4	30	23	8/12	1/ 2	11.1/14.3
high	8.5 °C	4	15	14	6/ 5	- / 3	- /37.5
	15.5 °C	4	31	17	1/ 1	8/ 7	88.9/87.5
	outside	4	43	37	15/17	- / 3	- /15.0

Table 28. F_2-phenotypes of *Calathus melanocephalus* reared from the same parental long winged single-pair crosses at different temperature conditions at two food-supply levels (1983/1984, natural daylength). NL: number of larvae used. Symbols, see table 20.

			OFFSPRING			
			Observed phenotypes (males/females)			
Food-supply	Temperature	NL	n	SW	LW	%LW
low	8.5 °C	65	50	25/25	- / -	- / -
	12 °C	64	37	20/17	- / -	- / -
	15.5 °C	62	44	20/23	1/ -	4.8/ - *)
	19 °C	65	36	27/ 9	- / -	- / -
	15.5/8.5 °C	63	44	25/19	- / -	- / -
	outside	58	48	20/28	- / -	- / -
high	8.5 °C	66	64	29/31	1/ 3	3.3/ 8.8
	12 °C	63	60	28/14	7/11	20.0/44.0
	15.5 °C	58	54	10/ 8	17/19	63.0/70.4
	19 °C	64	32	10/ 9	6/ 7	37.5/43.7
	15.5/8.5 °C	61	58	16/21	5/16	23.8/43.2
	outside	63	57	24/14	6/13	20.0/48.1

*) one fully developed wing on the right side only

higher in females than in males. The difference is significant for all years, with the exception of 1983 (the year with the lowest catch).

Asymmetric wing development in *Calathus melanocephalus* was observed in a low

Table 29. Phenotypes of *Calathus melanocephalus* in pitfall-samples from the Ecological Nature Reserve, Oost-Flevoland. Symbols, see table 20.

	Phenotypes (males/females)			
Sampling period	n	SW	LW	%LW
19-8/29- 9-1975 *)	968	195/446	75/252	27.8/36.1
28-6/21- 9-1976 *)	857	188/361	83/225	30.6/38.4
28-9/25-10-1978	982	391/365	89/137	18.5/27.3
5-8/30-10-1981	428	156/105	81/ 86	34.2/45.0
18-5/28-10-1982	311	120/113	30/ 48	20.0/29.8
26-5/10-11-1983	58	18/ 21	7/ 12	28.0/36.4
21-6/29-11-1984	1005	332/409	86/178	20.6/30.3

*) unpublished data of R. Hengeveld & J. Haeck, Institute for Ecological Research, Heteren.

frequency both in the field and in breeding experiments. For instance, among long winged beetles reared in experiments at different temperatures and with different food supplies (tables 25-28) for instance 1 of 130 males (0.7%) and 11 of 191 females (5.8%) showed asymmetric wing development.

From these data it is concluded that although in *Calathus melanocephalus* wing dimorphism basically might be inherited according to a single-locus model too, at least the expression of the long winged genotype is under environmental control in threshold response. During this study, however, also a small number of long winged *C. melanocephalus* was reared from crosses which according to the above mentioned single-locus model should have produced short winged offspring only (tables 23-24, 26).

DISCUSSION

Harrison (1980) in his review of dispersal polymorphism in insects recognises two ways in which flight polymorphism might be controlled: by genes and/or by the environment. Concerning genetic determination Harrison states that 'Only in the weevil *Sitonia hispidula* is there unambiguous evidence that wing length is determined by a single gene (or cluster of tightly linked genes)..... In other insect species, crossing experiments indicate that wing determination has a genetic compound but is not a simple Mendelian trait'. In the first case he refers to the work of Jackson (1928) and as instances of the latter type of inheritance he refers to studies on field crickets (Orthoptera) (Harrison, 1979; McFarlane, 1964), on

Heteroptera (Honek, 1976) and on Homoptera (Rose, 1972). Harrison argues that 'since it has been demonstrated that environmental factors directly influence wing and flight muscle development, much of the genetic data can be interpreted (or reinterpreted) in terms of individual variation in threshold response'.

From a literature review Roff (1986) concluded that the presence or absence of wings may be controlled by a single-locus, two-allele genetic system or by a polygenic system, and that both types of inheritance can be subsumed within a general threshold model. He suggests that suppression of wing development results when some hormone, perhaps juvenile hormone, exceeds a threshold value during a critical stage of development. In his view evolution towards wing dimorphism requires an increase in the rate of the wing suppressing hormone and a change in the threshold level at which wing development is suppressed. Consequently, due to net gene-migration selection in stable habitats will act against the long winged morph, because beetles with a low production of wing-suppressing hormone and/or a low threshold level will tend to leave the population. The kind of reasoning used by Roff is basically the same as Den Boer et al. (1980) developed to construct a possible pathway for the evolution of the genetic dominance of brachyptery.

Returning to our species we found both types of inheritance: genetic determination according to a single-locus model in *Calathus cinctus* and a combination of both genetic determination and environmental control of the long winged genotype in threshold response in *C. melanocephalus*.

The few deviating crossing results with assumed short winged homozygotes, collected at the Heath of Kraloo or reared from short winged parents collected there (tables 23-24), can be explained in terms of the 'threshold theory'. In this stable habitat net gene-migration has led to both a low frequency of long winged genotypes and a relatively high threshold for the wing-suppressing hormone of the remaining long winged genotypes. Although a considerable part of the population still might consist of heterozygous short winged beetles, the long winged genotype wil be expressed only incidentally in offspring of crosses with this beetles. For the isolated island population at Ameland similar results (table 26) can be explained in the same way.

These findings are in accordance with the other available data on wing-length determination in Carabidae and contrast with the polygenic control found in species of other taxonomic groups (especially Orthoptera, Heteroptera and Homoptera, see Roff (1986) for a review). In two other families of Coleoptera (Ptiliidae and Bruchidae) indications of polygenic control are found for respectively *Ptinella apterae* Guérin and *Callosobrochus maculatus* (Fabricius) (Taylor, 1981; Utida, 1972), but in both cases no single-pair crosses were carried out. Different taxonomic groups apparently may exhibit different types of control of wing development (cf Zera et al., 1983; Desender, 1989; Zera, 1989).

Since also in carabids environmental factors may play an important role in wing-morph determination, the interpretation of data on wing-morph frequencies in natural populations (Lindroth, 1949; 1969) consequently should be done with care. Pearson (1965), for instance, examined the distribution of wing-morph frequencies in *Bembidion grapei* Gyllenhal in relation to isotherms of maximum summer temperature. Note, that this is one of the most important species Lindroth used to illustrate his theory of postglacial recolonization of Fennoscandia (Lindroth, 1949; 1969; Darlington, 1971; Thiele, 1977). Pearson showed that wing dimorphism might be controlled by temperature, with the short winged morph more cold-resistant than the long winged one!

Observed differences in frequency of long winged beetles between males and females (the latter more frequently long winged) may result from differences in threshold or from differences in sensitivity between the two sexes. Although this difference in most cases was not significant in our breeding experiments, we believe it to exist because of the highly convincing field data (table 28). Moreover it must be realized that sample sizes required for detecting such a difference with 80 % certainty at the 5 % level of significance are much larger than those that could be realized in our breeding program (Sokal & Rohlf, 1969). For instance, in theory at least 504 individuals, instead of the 151 individuals actually reared, are needed to detect the difference between 25.3 and 36.8 % at 15.5 °C (table 25). Similar differences were observed by Carter (1976) in *Agonum retractum* and Bengtson & Erikstad (1984) in *Amara quenseli* (Schönherr).

The adaptive significance of a higher frequency of long winged beetles in females may only be understood if actual flight is preceded by insemination, while otherwise the chance of founding new populations will diminish due to the lower chance of a sufficient number of males arriving through the air at the right sites.

Concerning the resident population the relatively high amount of net migration of long winged genes caused by the departure of females is at least partly balanced by the lesser amount in males.

Asymmetric wing development apparently is a rare phenomenon in carabids: from literature and from own observations Desender (1989b) lists only five species in which it has been found: *Agonum obscurum* (Herbst), *A. retractum*, *Bradycellus harpalinus* (Serville), *Calathus melanocephalus* and *Carabus clathratus* Linnaeus. If asymmetric wing development is linked to environmental control of the expression of long winged genotypes as found in *C. melanocephalus*, this kind of wing-length determination consequently should be equally rare among carabids.

In general dispersal activities (production of dispersal morphs included) are generally thought to be associated with adverse conditions, i.e. with detoriating environments (Harrison, 1980). In the case of wing-morph determination in *Calathus melanocephalus* the opposite was found, the dispersal morph being more frequently produced under relatively favourable conditions (i.e high temperatures and abundant food during larval development). Concerning carabids there is still very little and contradicting information on this point. Nelemans (1987) found that flight muscle development in the autumn breeder *Nebria brevicollis* (Fabricius) depends on favourable environmental conditions (temperature and food supply) during the development of the larvae, whereas Van Schaick Zillesen & Brunsting (1984) presented the opposite in the spring breeder *Pterostichus oblongopunctatus* (Fabricius).

Perhaps these differences might have to do with a more general difference in effect of environmental factors between quickly developing summer larvae (*Pterostichus oblongopunctatus*) and slowly developing and overwintering winter larvae (*Calathus melanocephalus* and *Nebria brevicollis*). In the first case a direct response to the quality of the environment could be more advantageous than in the second case, in which the higher unpredictability of environmental conditions during future adult life could favour a more opportunist 'strategy'.

Furthermore it should be realized that both the development of both wings and flight muscles will cost additional energy, which generally is not likely to be available under conditions in which food is scarce.

The differences in wing-morph determination between *Calathus cinctus* and *C. melanocephalus* result in different dispersal 'strategies'. In *C. cinctus* the dispersal potential is genetically fixed, which means that independent of environmental conditions the genetic potential of possible dispersers is always realized. In *C. melanocephalus*, however, the dispersal potential is under environmental control, allowing a more dynamic production of possible dispersers depending on environmental quality. Under relatively favourable conditions during larval development (such as a high amount of available food and/or relatively high temperatures) a high proportion of the potentially long winged genotypes will actually develop long wings, whereas in the opposite situation only a few beetles will do so.

Actual flight in both species, however, furthermore depends on the development of functional flight muscles and on appropriate weather conditions in the short period that functional flight muscles are present. In accordance with the oogenesis-flight syndrome (Johnson, 1969) both species are only able to fly during a short period just before the start of reproduction. Moreover, during this period flight only occurs under special weather conditions: a minimum temperature of about 18 °C, no rain and preferable no or little wind (Van Huizen, 1979). Details on wing-muscle development and actual flight of *C. cinctus* and *C. melanocephalus* will be treated in chapter VI.

Under comparable stable conditions entirely genetic determination (referred to as the 'fixed system') will lead to a more rapid decrease of dispersal potential than a combination of genetic determination and environmental control (the 'dynamic system'), since in the first case relatively more of this potential will be lost by flying activities. Thus wing dimorphism will be maintained better with the 'dynamic system', but, on the other hand, the chance of establishing new populations on short terms will be greater with the 'fixed system'. Therefore, the 'fixed system' can be considered an opportunistic short-term 'between sites strategy', and the 'dynamic system' a flexible, more assuring long- term 'within-sites strategy'.

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REFERENCES

Aukema, B., 1986. Wing length determination in relation to dispersal by flight in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae). In: *Carabid beetles, their adaptations, dynamics and evolution* (P. J. den Boer, M. L. Luff, D. Mossakowski & F. Weber eds): 91-99. Fischer, Stuttgart.

Aukema, B., 1990. Taxonomy, life-history and distribution of three closely related species of the genus Calathus (Coleoptera, Carabidae).- *Tijdschrift voor Entomologie* 133: 121-141.

Bengtson, S.-A. & K. E. Erikstad, 1984. Wing polymorphism in Amara quenseli (Schönherr) (Coleoptera: Carabidae) in Iceland.- *Entomologica Scandinavica* 15: 179-183

Boer, P. J. den, 1977. Dispersal power and survival (carabids in a cultivated landscape).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process.- *Entomologia Generalis* 6: 107-134.

Carter, A., 1976. Wing polymorphism in the insect species Agonum retractum Leconte (Coleoptera, Carabidae).- *Canadian Journal of Zoology* 54: 1375-1382.

Darlington, P. J., 1936. Variation and atrophy of flying wings of some carabid beetles.- *Annals of the Entomological Society of America* 49: 136-179.

Darlington, P. J., 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings.- *Ecological Monographs* 13: 39-61.

Darlington, P. J., 1971. Modern Taxonomy: reality and usefulness.- *Systematic Zoolology* 20: 341-365.

Darwin, C., 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*: 1-389. Hazell, Watson & Viney, London.

Desender, K., 1989a. Heritability of wing development and body size in a carabid beetle, Pogonus chalceus Marsham, and its evolutionary significance.- *Oecologia* 78: 513-520.

Desender, K., 1989b. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Dingle, H., 1986. Evolution and genetics of insect migration. In: *Insect Flight. Dispersal and migration* (W. Danthanarayana ed.): 11-26. Springer, Berlin, Heidelberg, New York.

Dijk. Th. S. van, 1978. Calathus mollis erythroderus Gemminger & Harold in Drenthe (Coleoptera, Carabidae).- *Entomologische Berichten, Amsterdam* 38: 151-153.

Goodenough, U., 1978. *Genetics*. 2nd ed.: i-xvii, 1-840. Holt, Rinehart & Winsten, New York.

Harrison, R. G., 1979. Flight polymorphism in the field cricket, Gryllus pennsylvanicus.- *Oecologia* 40: 125-132.

Harrison, R. G., 1980. Dispersal polymorphism in insects.- *Annual Review of Ecology and Systematics* 11: 95-118.

Honek, A., 1976. Factors influencing the wing polymorphism in Pyrrhocoris apterus (Heteroptera, Pyrrhocoridae).- *Zoologische Jahrbücher für Systematik* 103: 547-570.

Huizen, T. H. P. van, 1979. Individual and environmental factors determining flight in carabid beetles. In: On the evolution of behaviour in carabid beetles (P. J. den Boer, H.-U. Thiele & F. Weber eds.).- *Miscellaneous Papers Landbouwhogeschol Wageningen* 18: 199-211.

Johnson, C. G., 1969. *Migration and dispersal of insects by flight*: 1-763. Methuen, London.

Langor, D. W. & D. J. Larson, 1983. Alary polymorphism and life history of a colonizing ground beetle, Bembidion lampros Herbst (Coleoptera, Carabidae).- *Coleopterists' Bulletin* 37: 365-377.

Lindroth, C. H., 1946. Inheritance of wing dimorphism in Pterostichus anthracinus Ill.- *Hereditas* 32: 37-40.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae. 3. Allgemeiner Teil.- *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar* 6, Ser. B 4 (3): 1-911.

Lindroth, C. H., 1969. The theory of glacial refugia in Scandinavia. Comments on present opinions.- *Notulae Entomologicae* 49: 178-192.

Nelemans, M. N. E., 1987. Possibilities for flight in the carabid beetle Nebria brevicollis (F.). The importance of food during larval growth.- *Oecologia* 72: 502-509.

Mols, P. J. M., Th. S. van Dijk & Y. Jongema, 1981. Two laboratory techniques to separate eggs of carabids from a substrate.- *Pedobiologia* 21: 500-501.

Pearson, R., 1965. Alary polymorphism in Bembidion grapei Gyll. (Col., Carabidae).- *Entomologist's Monthly Magazine* 100: 152-153.

Roff, D. E., 1986. The evolution of wing dimorphism in insects.- *Evolution* 40: 1009-1020.

Rose, D. J. W., 1972. Dispersal and quality in populations of Cicadulina species (Cicadellidae).- *Journal of Animal Ecology* 41: 589-609.

Schaick Zillesen, P. G. & A. H. M. Brunsting, 1984. The influence of food quality and photoperiod during the pre-adult stages on flight muscle development in adult Philonthus decorus (Coleoptera: Staphylinidae) and Pterostichus oblongopunctatus (Coleoptera: Carabidae).- *Entomologia Generalis* 9: 143-147.

Stein, W., 1973. Zur Vererbung des Flügeldimorphismus bei Apion virens Herbst (Col., Curculionidae).- *Zeitschrift für Angewandte Entomologie* 74: 62-63.

Sokal R. R. & F. J. Rohlf, 1969. *Biometry*: 1-609. Freeman, San Francisco.

Taylor, V. A., 1981. The adaptive and evolutionary significance of wing polymorphism and parthenogenesis in Ptinella Motschulsky (Coleoptera: Ptillidae).- *Ecological Entomology* 6: 89-98.

Thiele, H.-U., 1977. *Carabid beetles in their environments.* A study on habitat selection by adaptations in physiology and behaviour: i-xvii, 1-369. Springer, Berlin, Heidelberg, New York.

Utida, S., 1972. Density dependent polymorphism in the adult of Callosobruchus maculatus (Col., Bruchidae).- *Journal of Stored Products Research* 8: 111-126.

Zera, A. J., D. J. Innes & M. E. Saks, 1983. Genetic and environmental determinants of wing polymorphism in the waterstrider Limnoporus canaliculatus.- *Evolution* 37: 513-522.

Zera, A. J. & M. A. Rankin, 1989. Wing dimorphism in Gryllus rubens: genetic basis of morph determination and fertility differences between morphs.- *Oecologia* 80: 249-255.

IV. FECUNDITY IN RELATION TO WING-MORPH OF THREE CLOSELY RELATED SPECIES OF THE *MELANOCEPHALUS* GROUP OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE) *

ABSTRACT

During two successive years the fecundity of the carabid beetles *Calathus* (*Neocalathus*) *cinctus*, *C.* (*N.*) *melanocephalus* and *C.* (*N.*) *mollis* was studied in relation to wing-morph and temperature. Specific differences were found between the three species in both egg production and timing and length of the oviposition period. In all species the fecundity of laboratory bred beetles was significantly higher than that of females collected in the field.

Long winged females of both *Calathus cinctus* and *C. melanocephalus* showed a significantly higher egg production than short winged females, and they also tended to produce eggs during a longer period. In *C. mollis* the fecundity of only the long winged morph could be established.

The observed lower relative fitness of the short winged morph in both *Calathus cinctus* and *C. melanocephalus* contradicts the supposed increase of the frequency of this morph in ageing, more or less isolated, populations of these species. The loss of long winged genotypes, resulting from flight activities, is considered the most plausible cause of the increase of short winged beetles in ageing populations.

The higher fecundity of macropterous females makes them especially suited for (re)establishing populations.

Key words: Carabidae, *Calathus*, *cinctus*, *melanocephalus*, *mollis*, Wing dimorphism, Wing-morph, Fecundity, Oviposition period

INTRODUCTION

Populations of wing-dimorphic carabid beetles show considerable variation in the frequency of long winged beetles (Lindroth, 1949; Den Boer, 1970; Haeck, 1971; Den Boer et al., 1980; Honek, 1981; Desender, 1989b). In a number of species this proportion was found to be remarkably high in newly founded populations

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in the recently reclaimed polder Oost-Flevoland, in comparison with settled populations of the same species at the Dutch mainland. It was therefore suggested that this proportion tends to decrease in ageing populations (Den Boer, 1970; Haeck, 1971). These data were in accordance with the assumption of Lindroth (1946) that wing dimorphism in carabid beetles is inherited in a simple Mendelian fashion with brachyptery dominant to macroptery. This implies that a net emigration of long winged genotypes will result in a decrease of the proportion of long winged beetles in the resident population. Especially in isolated populations (at islands, for instance) the decrease is assumed to progress rapidly.

This shift towards brachyptery, however, could result not only from the frequent emigration of the long winged morph by flight, but might also be partly due to a higher relative Darwinian fitness of the short winged morph (cf Roff, 1986). Differences between the morphs in development time, adult longevity, preovipostional period (or oviposition period) and fecundity all could influence the proportion of long winged beetles in populations of the species involved.

A comparative study of fecundity and oviposition period forms the theme of this paper.

The carabids *Calathus* (*Neocalathus*) *cinctus* Motschulsky (= *erythroderus* Gemminger & Harold) and *C.* (*N.*) *melanocephalus* (Linnaeus) are both wing-dimorphic with either fully developed wings or strongly reduced wings (Aukema, 1990, 1991). In both species wing dimorphism was found to be determined genetically according to a single-locus model with brachyptery dominant to macroptery (Aukema, 1991). In *C. melanocephalus*, however, environmental factors modify the expression of the long winged genotype, whereas in *C. cinctus* no such 'phenotypic plasticity' is found (Aukema, 1991).

Both egg production and oviposition period of short and long winged females were compared for two successive years (1981/1982 and 1982/1983) to discover possible differences in fitness between the two wing-morphs. Since egg production in carabids is highly temperature-dependent both features were established in relation to temperature. Furthermore, comparable data for the long winged morph of a third species, *Calathus* (*Neocalathus*) *mollis* (Marsham), are included. Preliminary data on the fecundity of *C. cinctus* have already been published (Aukema, 1987).

MATERIAL AND METHODS

Species

All three species of the *melanocephalus* group of the genus *Calathus* used in this study are nocturnal autumn-breeders, reproducing from August onwards. Details

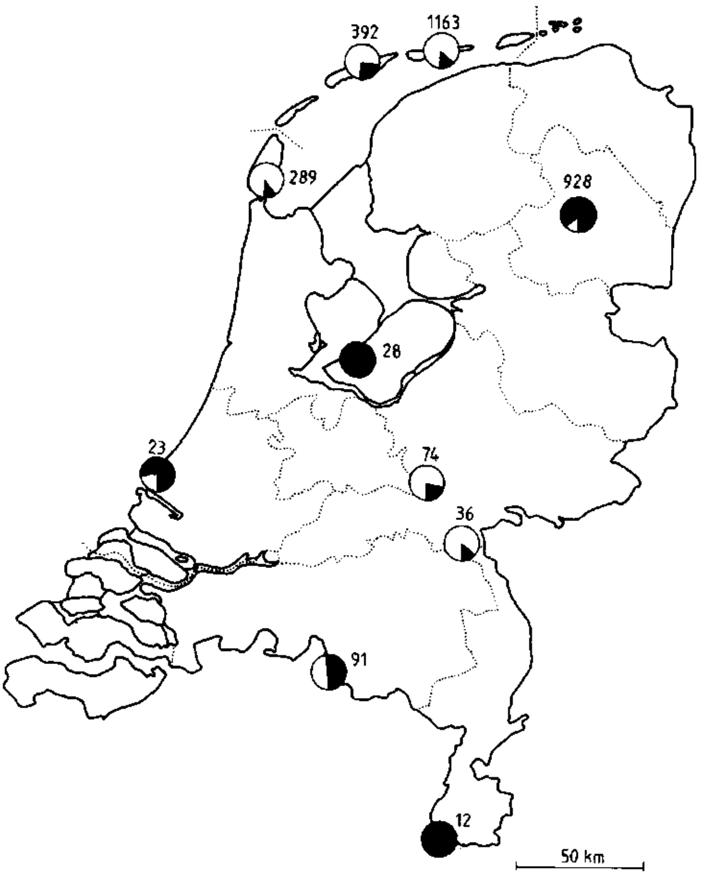

Fig. 24. *Calathus cinctus.* Frequencies of long winged beetles (black segments) in various Dutch populations (number of specimens examined are indicated).

on habitat and life-history are given by Aukema (1990).

Calathus cinctus

Some data on wing dimorphism in Dutch populations of *Calathus cinctus* are summarised in fig. 24. Note the low percentages of long winged beetles on the Dutch West Frisian Islands of Texel (8.6%), Ameland (13.5%) and Terschelling (22.7%), and the absence of short winged beetles among specimens caught in the recently reclaimed polder of Zuid-Flevoland, which ran dry in 1968. Actual flight was observed in the field (Van Huizen, 1980) as well as in the laboratory.

Experiments were started with young females collected by hand on the West Frisian Island of Ameland on 27 May 1981, and in 1982/1983 with offspring of these females. After collecting, males and females, both short and long winged were kept separately in peat litter under outside conditions with plenty of food until

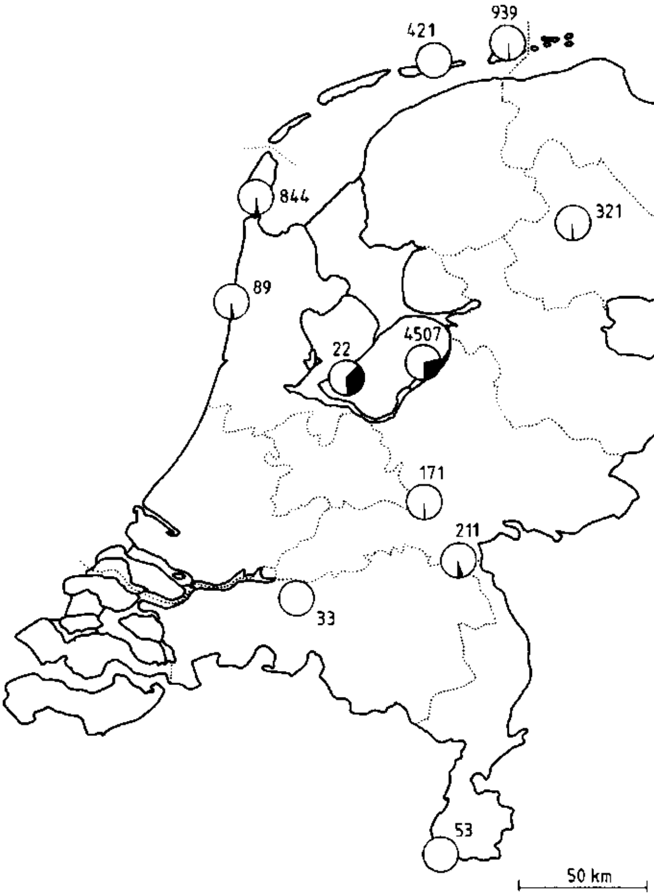

Fig. 25. *Calathus melanocephalus*. Frequencies of long winged beetles (black segments) in various Dutch populations (number of specimens examined are indicated).

two weeks before the start of the reproduction period (approximately the last week of August).

In 1981 each short winged group consisted of 30 females, whereas long winged groups were smaller because of a shortage of specimens (12 females at both 8.5 and 12 °C, and 5 females at both 15.5 °C and under outside conditions). In 1982 group size was 20 and 18 for short and long winged females respectively.

Calathus melanocephalus

Usually, long winged beetles of *Calathus melanocephalus* are very rare. Den Boer (1977) lists a percentage of 0.23% (70 out of 30,887 beetles) for populations in the surroundings of Wijster, province of Drenthe, and Desender (1989b) found only 1.6% long winged beetles in samples from a number of Belgian localities.

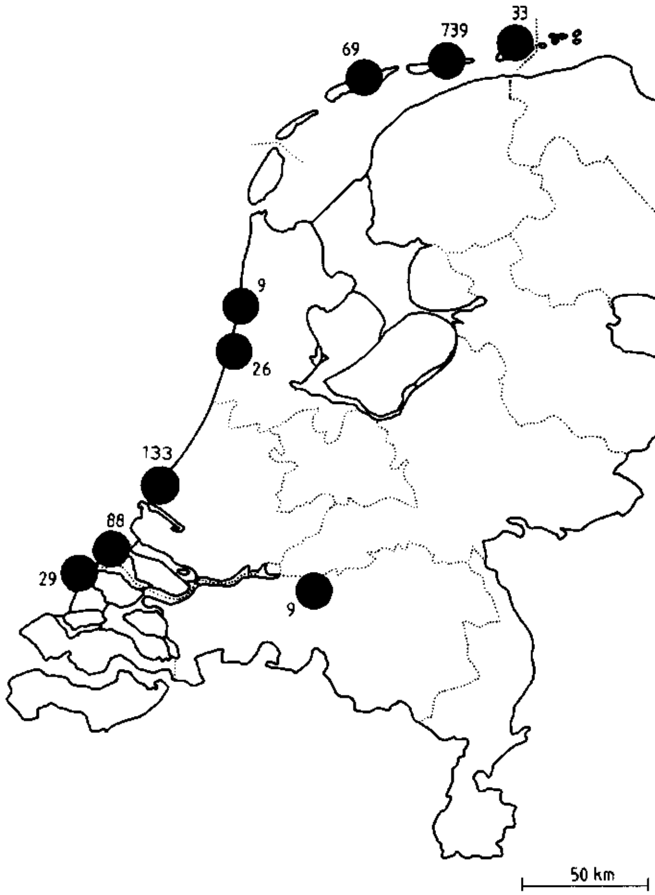

Fig. 26. *Calathus mollis*. Frequencies of long winged beetles (black segments) in various Dutch populations (number of specimens examined are indicated).

Fig. 24 shows data on wing-morph frequencies for some Dutch populations. Substantially higher percentages of long winged beetles were found only in populations in the recently reclaimed polders of Oost- and Zuid-Flevoland (Den Boer, 1970; Haeck, 1971; Aukema, 1991). These polders ran dry in 1957 and 1968 respectively. In 1981 39% of the 428 beetles caught that year in pitfall traps at the Ecological Nature Reserve in Oost-Flevoland were long winged (Aukema, 1991). Actual flight was only observed in the laboratory. Data from literature, as for instance in Palmén (1944: 18 long winged individuals drifted ashore at the southern coast of Finland), and in Honek & Pulpán (1983: catches in light traps), are not reliable because of possible confusion with *C. cinctus* (Aukema, 1990).

Since it was difficult to get sufficient starting material of the long winged morph of *Calathus melanocephalus*, fecundity experiments were carried out in two different ways.

In the first experiment egg production was measured weekly during the whole oviposition period. In 1981 long winged females were collected in pitfall traps at the Ecological Nature Reserve (Oost-Flevoland) just before the start of egg production. Their long winged offspring were used in 1982/1983. The short winged females used in 1981/1982 were collected at the heath of Kraloo, Drenthe. Group size was 20 in the case of short winged females (1981/1982) and 8 for long winged females (1981/1982 and 1982/19-83).

In the second experiment in 1981 short and long winged females collected once a week in pitfall traps at the Ecological Nature Reserve (Oost-Flevoland) between the 28th of August and the 4th of September, and short winged females collected during the same period at the heath of Kraloo, Drenthe, were divided each week equally over four temperature conditions. After one week of acclimatization egg production was estimated during five successive weeks. The three groups consisted of ten females each.

Calathus mollis

Although also a wing-dimorphic species, so far only long winged specimens of *Calathus mollis* have been collected (fig. 26) and reared from Dutch populations (Aukema, 1990). Flight was only observed in the laboratory. Young long winged females collected at Ameland in 1981 as well as their offspring were used to establish egg production and oviposition period of this species. Group size was 20 in both years.

Experiments

Egg production and oviposition period of short and long winged females of *Calathus cinctus* and *C. melanocephalus* and of long winged females of *C. mollis* were estimated during two successive years (1981/1982 and 1982/1983) at constant temperatures of 8.5, 12 and 15.5 °C and natural daylength (adjusted once a week) in incubators, as well as under approximately natural conditions in an outdoor insectary. Temperatures were chosen representative for the range of temperatures of the oviposition seasons during the preceding thirty years (1951-1980) at the meteorological station of the KNMI at Eelde (about 35 km north of Wijster): mean temperature during the period between the last third of August and the last third of November was 10.1 ± 3.9 °C.

Single pairs were kept in petri dishes in ground peat litter and fed twice a week with plenty of small maggots. Eggs were separated once a week from the peat according to the sieve-wash method of Mols et al. (1981) and counted. Females that ceased laying eggs for two successive weeks were removed from the experiments. Experiments were ended when the last female stopped laying eggs. Egg counts from females that either died during the experiments or did not

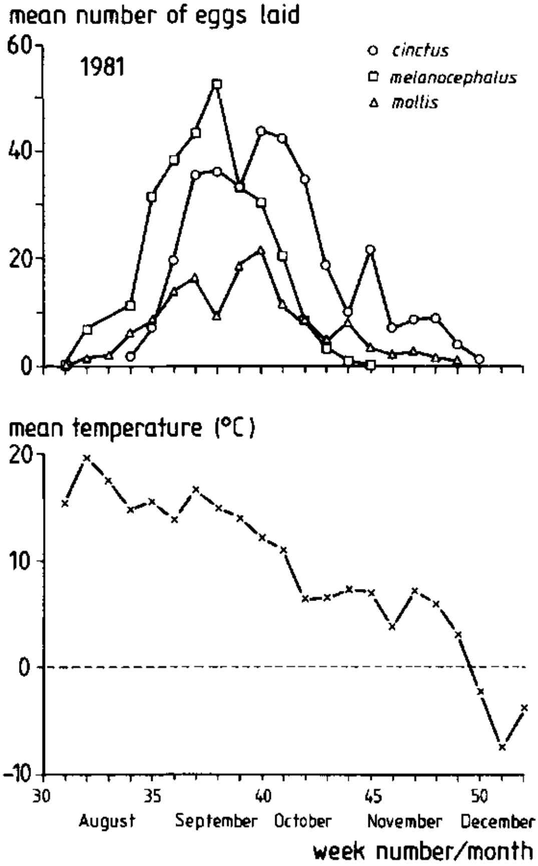

Fig. 27. Mean egg production of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in 1981 in an outdoor insectary cumulated over weeks, and mean weekly temperature measured at Eelde. Closed symbols: long winged females; open symbols: short winged females.

produce eggs during at least eight successive weeks were discarded.

Data on egg production and oviposition period were analysed with GENSTAT by means of regression analysis based on a generalized linear model (GLM) with a Poisson distribution (McCullagh & Nelder, 1989).

RESULTS

General

The mean egg production of the three species in the outdoor insectary in 1981/1982 and 1982/1983 cumulated over weeks is depicted in figs 27 and 28, together with data on the mean weekly temperature, measured at the meteoro-

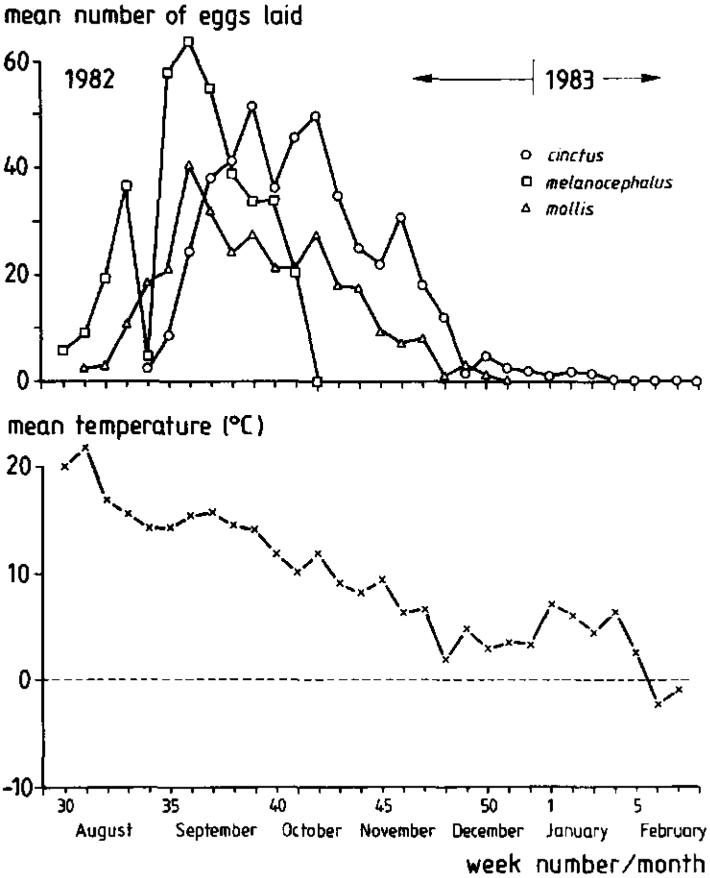

Fig. 28. Mean egg production in 1982/1983, see fig. 27.

logical station of the KNMI at Eelde. *Calathus melanocephalus* started and ended egg production earlier than *C. cinctus*, whereas *C. mollis* occupied an intermediate position in this respect (an early start and a relatively long oviposition period). Egg production under these circumstances was highest in *C. cinctus*, lowest in *C. mollis* and intermediate in *C. melanocephalus*.

The mean reproductive effort (fecundity x egg weight), however, differed less between the three species then egg production, because the eggs of *Calathus mollis* weigh twice as much (0.31 ± 0.063 mg, n=18) as those of *C. cinctus* (0.14 ± 0.014 mg, n=30) and of *C. melanocephalus* (0.16 ± 0.025 mg, n=18). Eggs were weighed within 24 hours after oviposition.

Differences between the two years were due both to differences in temperature between the years (figs 27-28) and to differences in fecundity between field collected beetles (1981/1982) and laboratory bred beetles (1982/1983) (see discussion). In 1981 egg production of both *Calathus cinctus* and *C. mollis* was ended in the third week of December by a sudden frost period (fig. 27), whereas

Table 30. Oviposition period (weeks) of *Calathus cinctus* (short and long winged females from Ameland), *C. melanocephalus* (short winged females from Kraloo, Drenthe and long winged females from Oost-Flevoland) and *C. mollis* (long winged females from Ameland) at four temperatures in 1981/1982 and from their offspring in 1982/1983. N: number of females.

			Species					
			cinctus		*melanocephalus*		*mollis*	
Morph	Year	Temp	N	Mean (± s.e.)	N	Mean (± s.e.)	N	Mean (± s.e.)
SW	1981/82	8.5 °C	28	7.4 (± 0.39)	15	7.1 (± 0.28)	14	10.9 (± 0.56)
		12 °C	25	18.3 (± 1.36)	15	8.4 (± 0.33)		
		15.5 °C	24	25.4 (± 1.55)	15	11.6 (± 0.51)		
		outside	27	14.3 (± 0.39)	14	11.0 (± 0.32)		
	1982/83	8.5 °C	15	12.4 (± 0.79)				
		12 °C	14	19.8 (± 1.43)				
		15.5 °C	14	20.3 (± 1.30)				
		outside	16	17.4 (± 0.75)				
LW	1981/82	8.5 °C	10	8.1 (± 0.31)	7	8.3 (± 0.41)	14	10.9 (± 0.56)
		12 °C	10	21.7 (± 2.65)	7	8.9 (± 0.41)	15	11.7 (± 0.98)
		15.5 °C	5	26.0 (± 1.40)	6	11.3 (± 0.35)	14	24.2 (± 1.72)
		outside	2	(17.0)	4	10.5 (± 0.66)	12	13.7 (± 0.68)
	1982/83	8.5 °C	17	13.6 (± 0.94)	5	9.0 (± 0.83)		
		12 °C	14	21.5 (± 1.07)	7	11.4 (± 0.74)		
		15.5 °C	12	21.6 (± 1.30)	6	13.7 (± 0.58)	17	25.5 (± 1.79)
		outside	12	18.1 (± 1.05)	4	10.5 (± 0.88)	17	15.3 (± 0.71)

in 1982/1983 the more favourable temperature conditions (fig. 28) enabled both *C. cinctus* and *C. mollis* to prolong their egg production considerably (6-9 and 4 weeks respectively). In both years *C. melanocephalus*, however, showed about the same oviposition period (12-14 weeks). The data on the latter species closely resemble similar figures published by Van Dijk (1982, 1983).

Calathus cinctus

Data on the length of the oviposition period and the weekly egg production of *Calathus cinctus* in relation to temperature are summarised in table 30 and fig. 29. Analysis of the data on the length of the oviposition period (table 31) showed a significant difference between wing-morphs in this respect for both years, i.e. a longer oviposition period in long winged females (table 30). Differences between both years and significant interactions between temperature and wing-morph and

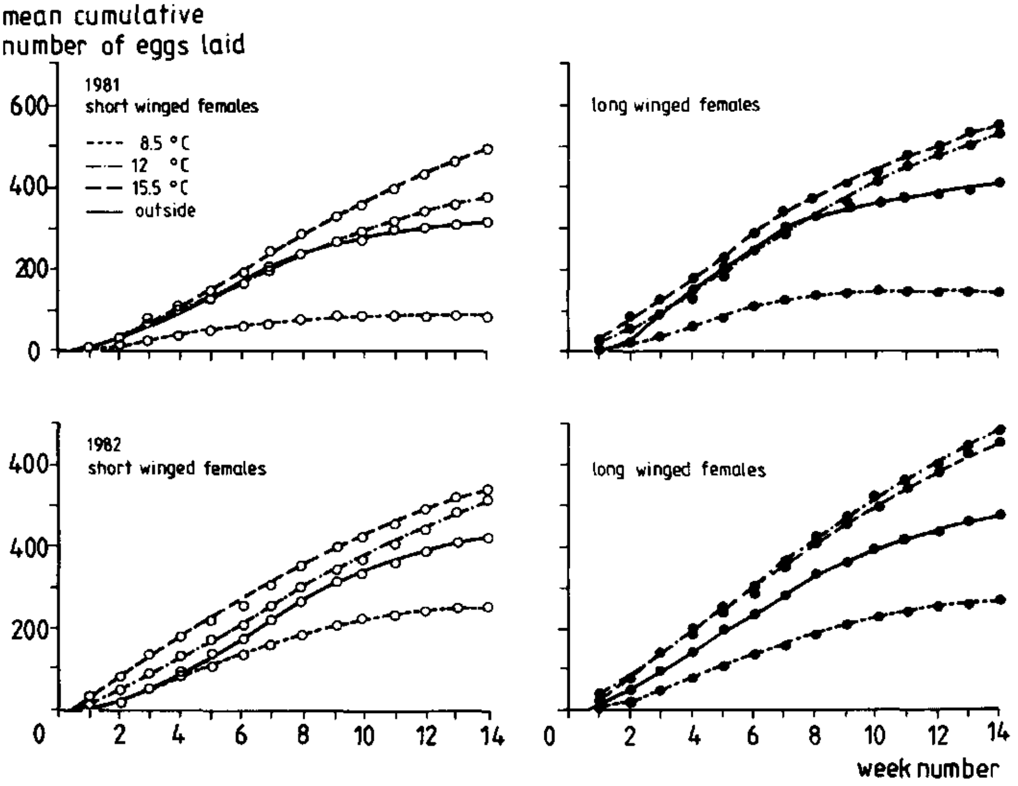

Fig. 29. *Calathus cinctus.* Mean egg production at four temperatures conditions cumulated over weeks in the main oviposition period in 1981 (19 August - 24 November) and 1982 (23 August - 28 November). For numbers of females used, see table 30.

between year and wing-morph, however, obscure this result. Since a highly significant effect of temperature on the length of the oviposition period of both short and long winged females was found (table 31), egg production can be compared appropriately only during the same, fixed period. The period used, further indicated as the main oviposition period, is derived from the data on weekly egg production under outside conditions, representing the period in which at least 50 % of the females laid eggs (14 weeks in the case of *C. cinctus*).

Fig. 26 illustrates that, on a weekly scale, no substantial differences in the start of egg production were found between short and long winged females.

Regression analysis of the data on egg production during the main oviposition period (table 31) showed:

1. a highly significant difference in egg production between wing-morphs for both years, long winged females producing more eggs;

Table 31. Testing results of regression analysis of data on oviposition period and egg production of short and long winged *Calathus cinctus* (cin) and *C. melanocephalus* (mel) and long winged *C. mollis* (mol) at four temperatures in two years. n.s.=not significant, ***: $P<0.001$, **: $P<0.01$, *: $P<0.05$.

	Oviposition period			Egg production		
	Species			Species		
Source of variation	cin	mel	mol	cin	mel	mol
year	***	***	n.s.	***	***	***
temperature	***	***	***	***	***	***
wing-morph	*	n.s.	-	***	***	-
temperature x wing-morph	*	*	-	*	n.s.	-
year x temperature	***	*	n.s.	n.s.	**	n.s.
year x wing-morph	n.s.	-	-	n.s.	-	-

2. a highly significant effect of temperature on egg production for both years, i.e. a higher egg production at higher temperatures;
3. a highly significant difference in egg production between the two years for both wing-morphs, i. e. a higher egg production in 1982 than in 1981;
4. a significant difference in response to temperature between wing-morphs between the two years, caused by the relatively high egg production of long winged females at 12 °C in 1982 (in both years there were only slight differences in egg production between long winged females at 12 and at 15.5 °C).

Egg production under approximately outside conditions (mean temperatures of 10.4 ± 4.5 and 11.6 ± 3.7 °C in 1981 and 1982 respectively) was consistent with the results at constant temperatures (fig. 29).

Calathus melanocephalus

EXPERIMENT 1

Data on the oviposition period and the weekly egg production of *Calathus melanocephalus* are summarised in table 30 and fig. 30. Analysis of data on the length of the oviposition period (table 31) showed that in *C. melanocephalus* there was no difference between short and long winged females in this respect. Furthermore, as in *C. cinctus*, the oviposition periods were significantly longer in 1982 than in 1981 and again a highly significant effect of temperature on the length of the oviposition period was found. The main oviposition period of 11 weeks,

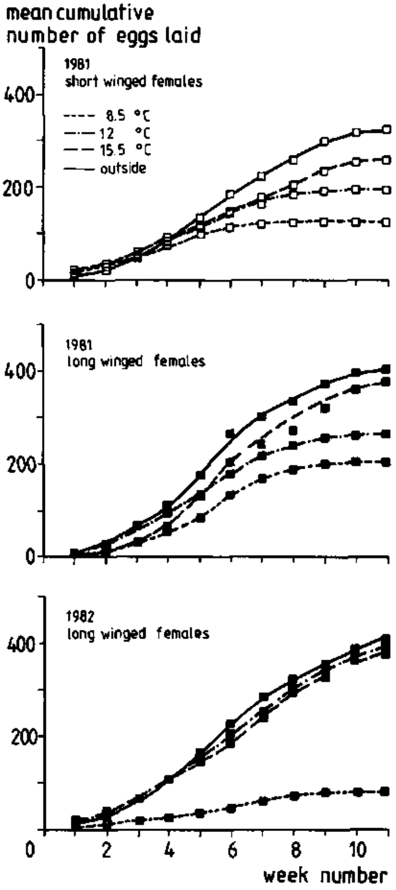

Fig. 30. *Calathus melanocephalus*. Mean egg production at four temperatures cumulated over weeks in the main oviposition period in 1981 (31 July - 14 October) and 1982 (30 July - 14 October). Experiment 1; for numbers of females used, see table 30.

however, was much shorter than in *cinctus*.

The cumulative mean egg production is shown in fig. 30. Again the start of egg production was quite similar for both short and long winged females. Note that in *Calathus melanocephalus* the highest egg production occurred under outside conditions, whereas in *C. cinctus* (fig. 29) the egg production was higher at both 12 and 15.5 °C than under outside conditions.

Regression analysis of data on egg production during the main oviposition period (table 31) showed:

1. a highly significant difference in egg production between wing-morphs, long winged females producing more eggs in 1981 and 1982 than short winged ones in 1981;

2. a highly significant effect of temperature on egg production in both wing-morphs, i.e. a higher egg production at higher temperatures;
3. a highly significant difference in egg production between the two years, i.e. a higher egg production in 1982;
4. a significant difference in response to temperature of long winged females between the two years (see fig. 30).

Egg production under approximately outside conditions (mean temperatures of 14.3 ± 3.4 and 15.4 ± 3.3 °C in 1981 and 1982 respectively) was higher than found at 15.5 ° C, the highest constant temperature used (fig. 30).

EXPERIMENT 2

Data on weekly egg production during five weeks of short winged females from Oost-Flevoland and Kraloo and of long winged females from Oost-Flevoland are summarised in table 32. Regression analysis of data on egg production during these five weeks showed:

1. a significant difference in egg production between short and long winged females, i.e. a higher egg production of long winged females ($P<0.01$);
2. a highly significant effect of temperature on the egg production of both wing-morphs, i.e. a higher egg production at higher temperatures ($P<0.001$);
3. a significant difference in egg production between females from Oost-Flevoland and those from Kraloo, i.e. a higher egg production of females collected at Oost-Flevoland ($P<0.05$).

When restricting the analysis, however, to data from females collected in Oost-Flevoland no significant difference in egg production between short and long winged females was found.

Analysis of the data of experiment 1 (fig. 30) divided into two periods (period 1: week 1-5; period 2: week 6-11) showed a highly significant difference ($P<0.001$) in egg production between the two periods both for years, temperatures and wing-morphs as well. The difference between short and long winged females was especially due to a higher egg production of long winged females during the second period (fig. 31).

Calathus mollis

Data on oviposition period and egg production of *Calathus mollis* are presented in table 30 and fig. 32. Regression analysis of these data again showed the highly significant effect of temperature on the length of the oviposition period (table 31). The length of the main oviposition period was similar to that of *C. cinctus* (14 weeks). Egg production during this period (fig. 32) was clearly temperature-

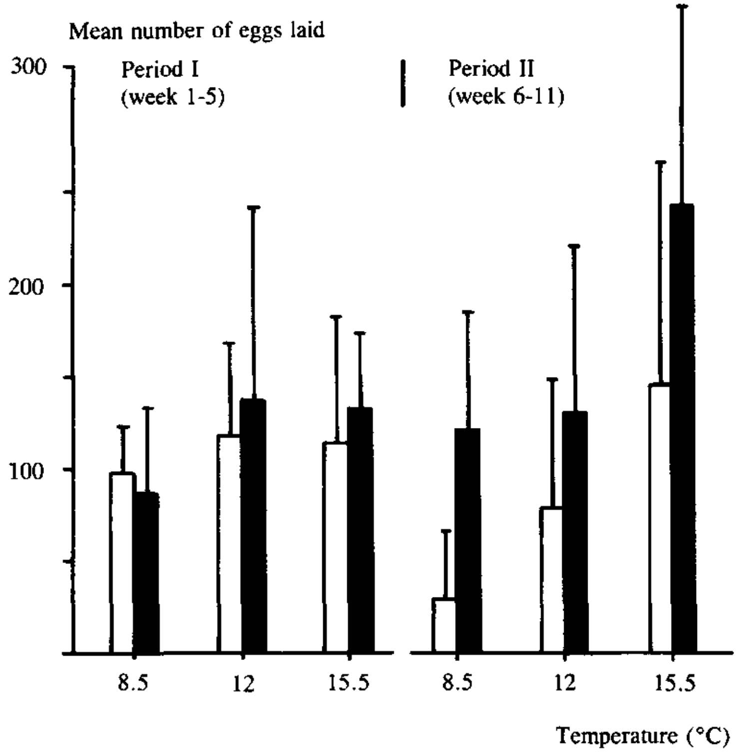

Fig. 31. *Calathus melanocephalus*. Mean egg production of short winged females from Kraloo (white bars) and long winged females from Oost-Flevoland (black bars) at three constant temperatures in 1981 during two successive periods of 5 and 6 weeks of the main oviposition period respectively (standard errors indicated). For numbers of females used, see table 30.

Table 32. Egg production (number of eggs laid) during five weeks (4 September-9 October 1981) of short and long winged *Calathus melanocephalus* at four temperatures. N: number of females

	short winged				long winged	
	Oost-Flevoland		Kraloo		Oost-Flevoland	
Temperature	N	Mean (± s.e.)	N	Mean (± s.e.)	N	Mean (± s.e.)
8.5 °C	9	97.1 (± 8.54)	10	89.2 (± 9.95)	10	106.8 (± 10.79)
12 °C	10	177.4 (± 15.30)	10	154.0 (± 11.05)	10	201.0 (± 10.48)
15.5 °C	10	252.9 (± 27.28)	10	170.3 (± 18.17)	10	255.7 (± 25.55)
outside [a)]	8	177.1 (± 9.77)	10	184.2 (± 20.38)	9	197.7 (± 21.94)

[a)] mean temperature: 13.9 ± 2.1 °C

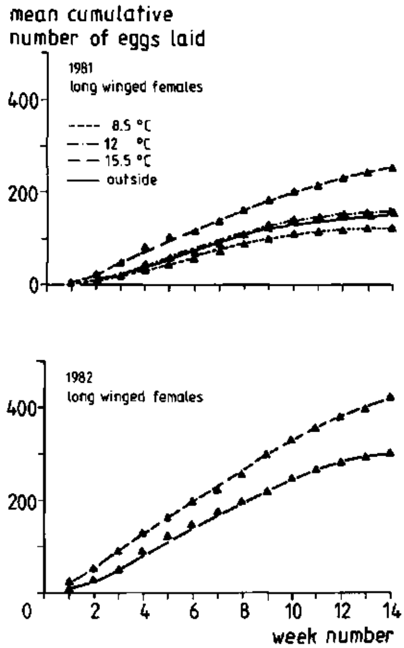

Fig. 32. *Calathus mollis*. Mean egg production of at different temperature conditions cumulated over weeks in the main oviposition period in 1981 (10 August - 25 November) and 1982 (13 August - 18 November). For numbers of females used, see table 30.

dependent also (table 31), and significantly higher in 1982 than in 1981. Egg production under approximately outside conditions (mean temperatures of 11.3 ± 4.6 and 12.3 ± 3.4 °C in 1981 and 1982 respectively) was consistent with the results at constant temperatures (fig. 32).

DISCUSSION

The most striking feature of egg production estimates (the number of eggs laid and the length of the oviposition period) of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* undoubtedly is the enormous amount of variation (see tables 30, 32-34 and fig. 31), which was already observed by Van Dijk (1979, 1982, 1983) in the case of *C. melanocephalus*. Nelemans (1987) and Desender (1989a) also reported a high amount of individual variation in the egg production of the carabids *Nebria brevicollis* (Fabricius) and *Pogonus chalceus* (Marsham) respectively.

In all three species egg production at constant temperatures was significantly lower in 1981/1982 (field collected beetles), than in 1982/1983 (laboratory bred beetles). This difference probably was due to a better condition of the laboratory bred stock. On the other hand, differences in quality and quantity of food or of substrate moisture might influence egg production substantially, making comparisons of egg production between different years difficult. Table 33, for instance, illustrates the effect of different levels of food-supply on the egg production of *Calathus melanocephalus*.

It must be emphasized here, that the conclusions concerning the fecundity of the three species are only valid for young females reproducing for the first time, whereas field populations of these species are composed of beetles of different year-classes (Aukema, 1990). However, for short winged females of *Calathus melanocephalus*, Van Dijk (1979, 1982) concluded that 'there exists no consistent difference between the number of eggs produced by young and by old females'. Concerning the oviposition period, the same author found that under field conditions old beetles usually started egg production earlier than young ones, and sometimes also continued longer (Van Dijk, 1982).

The data on egg production of *Calathus melanocephalus* presented here show that it is very important to measure egg production during the whole oviposition period to get a reliable impression of the differences between wing-morphs in this respect. Studies of, for instance, Zera (1984) and Zera & Rankin (1989) on morph-dependent fecundity differences in the pondskater *Limnoporus canaliculatus* (Heteroptera, Gerridae) and in the cricket *Gryllus rubens* (Orthoptera, Gryllidae) respectively, are considered insufficient because they only considered a small and early part of the oviposition period.

The rather fixed short and early oviposition period in *Calathus melanocephalus* most likely represents an adaptation to cold climatic conditions with a relatively short breeding season. Such an effect is also reflected in differences between the species in their general distribution: *C. melanocephalus* occurs at both higher latitudes and higher altitudes than *C. cinctus* and *C. mollis* (Aukema, 1990). The observation of Baars & Van Dijk (1984), that in *C. melanocephalus* high temperatures during both reproductive and spring period correspond with low survival and low recruitment, points in the same direction.

Van Dijk (1979, 1982, 1983) calculated the egg production of short winged *Calathus melanocephalus* as the number of eggs produced per female per week, whereas in this study the total egg production per female is considered. In four experiments by Van Dijk (pers. comm.) the number of eggs produced per short winged female per week under outside conditions with an excess of food varied between 31.9 ± 20.3 and 36.8 ± 16.9. Similar calculations for the egg production of *C. cinctus*, *C. melanocephalus* and *C. mollis* are presented in table 34. The value found for short winged *C. melanocephalus* in 1981 is well within the range found by Van Dijk. Both in 1981 and 1982 long winged females of this species, however, produced more eggs per female per week than was ever found by Van

Table 33. Egg production (number of eggs laid) during 5 weeks (19 August - 22 - September 1982) of short and long winged *Calathus melanocephalus* at two different levels of food-supply. N: number of females. Low food-supply: 8 mg maggots of blowfly per day; high food-supply: 16 mg maggots of blowfly per day

	Low food-supply				High food-supply			
	short winged		long winged		short winged		long winged	
	Kraloo		Oost-Flevoland		Kraloo		Oost-Flevoland	
Temp.	N	Mean (± s.e.)	N	Mean (± s.e.)	N	Mean (± s.e.)	N	Mean (± s.e.)
8.5 °C	10	52.9 (± 3.32)	5	82.0 (± 9.87)	10	84.6 (± 6.14)	5	151.8 (± 11.09)
15.5 °C	10	103.7 (± 5.66)	4	81.5 (± 3.24)	10	192.4 (± 22.81)	4	257.8 (± 5.03)
outside [a])	10	79.4 (± 6.14)	4	86.3 (± 2.73)	10	160.3 (± 9.77)	4	216.5 (± 15.78)

[a]) mean temperature: 14.8 ± 1.6 °C

however, produced more eggs per female per week than was ever found by Van Dijk.

Calculated in this way, mean egg production in *Calathus melanocephalus* was higher than in *C. cinctus*.

The observed difference in egg production between short winged females of *Calathus melanocephalus* collected in Oost-Flevoland and at Kraloo obviously is due to different genotype frequencies at the two localities. The short winged population at Kraloo contains a very low fraction of long winged and heterozygous genotypes, whereas that in Flevoland will contain a very high percentage of exactly these genotypes. Obviously the phenotypically short winged but genetically long winged genotypes and/or the heterozygous short winged beetles produce more eggs than the short winged homozygous ones.

The higher egg production of long winged *Calathus cinctus* and *C. melanocephalus* partly may be attributed to general differences in body size between the wing-morphs: long winged females are somewhat bigger on the average than short winged ones (Aukema, 1990). Ernsting & Huyer (1984) found a strong positive correlation between body size and fecundity in the carabid *Notiophilus biguttatus* (Fabricius), and Desender (1989) suggested that observed differences in fecundity between 'macropterous' and 'brachypterous' females of the wing polymorphic *Pogonus chalceus* might be due to the significantly larger body size of beetles with larger wings. For females of the F_1-generation of *Calathus cinctus*, reared in the laboratory and used for this study in 1982/1983, however, no relation between body size and egg production was found. Furthermore, Van Dijk (pers. comm.) was not able to find such a relationship for short winged females of *C. melanocephalus*.

Table 34. Mean number of eggs laid per female per week under outside conditions. N: number of females; W: number of weeks with egg production

Species	Wing-morph	Year	N	W	Mean (± s.e.)
cinctus	short winged	1981	27	350	24.8 (± 1.02)
		1982	16	204	33.2 (± 1.43)
	long winged	1981	2	28	29.1 (± 4.53)
		1982	12	159	36.1 (± 1.62)
melanocephalus	short winged	1981	14	142	32.1 (± 1.58)
	long winged	1981	4	40	40.5 (± 4.26)
		1982	4	41	40.1 (± 2.92)
mollis	long winged	1981	12	149	12.2 (± 0.82)
		1982	17	214	23.7 (± 0.87)

Roff (1986) summarised available data on differences in fecundity between short and long winged females of 22 wing-dimorphic species of different insect groups (mainly Hemiptera and Orthoptera) and concluded that the brachypterous morph is both more fecund and reproduces earlier than the macropterous morph (see also Harrison, 1980 and Dingle, 1985 for comparable reviews). Notable exceptions, however, were the feather winged beetles *Ptinella apterae* (Guérin-Méneville) and *P. errabunda* Johnson (Coleoptera, Ptiliidae), in which the winged morph produced significantly more eggs (Taylor, 1978) than the wingless one. Desender (1989a) also found a higher egg production in 'macropterous' females of the wing-polymorphic carabid *Pogonus chalceus*, than in 'brachypterous' ones. So, at least in Coleoptera an opposite trend may occur, implying a higher relative fitness of the long winged morph. General differences in timing of wing-muscle development and/or flight activities between the principal taxonomic groups (viz. Hemimetabola versus Holometabola) might explain the different trends found in these groups.

From the data on fecundity of short and long winged *Calathus cinctus* and *C. melanocephalus* presented here, it is evident that in both species not the brachypterous morph, but the macropterous one has a higher relative Darwinian fitness. In both species wing dimorphism, however, will be maintained by the dominance of the short winged condition. Net emigration of long winged beetles apparently is the most plausible explanation for the observed shift towards brachyptery in ageing populations of these wing-dimorphic species. The higher fecundity of these migrants obviously will favour the (re)settlement of new populations.

CONCLUSIONS

1. *Calathus cinctus*, *C. melanocephalus* and *C. mollis* show specific differences in egg production and in timing and length of the oviposition period, which can be characterized as high, late and long in *C. cinctus*, intermediate, early and short in *C. melanocephalus* and low, early and long in *C. mollis* respectively.
2. Laboratory bred females of the three species produce substantially more eggs than females collected in the field.
3. In both *Calathus cinctus* and *C. melanocephalus* the egg production of long winged females is higher than in short winged females. In both species also the mean length of the oviposition period was longer in long winged females, but the difference was only significant in *C. cinctus*.
4. Consequently the observed shift in the proportion of long winged beetles in ageing populations of these species towards brachyptery cannot be contributed to a higher Darwinian fitness of the short winged morph. On the contrary, in terms of a higher egg production and/or a longer oviposition period the long winged morph has a higher fitness.
5. The higher fecundity of the long winged morph of both *Calathus cinctus* and *C. melanocephalus* is considered to favour their colonizing abilities.

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REFERENCES

Aukema, B., 1987. Differences in egg production and egg-laying period between long and short winged Calathus erythroderus (Coleoptera, Carabidae) in relation to wing-morph frequencies in natural populations.- *Acta Phytopathologica et Entomologica Hungarica* 22: 45-56.

Aukema, B., 1990. Taxonomy, life-history and distribution of three closely related species of the genus Calathus (Coleoptera: Carabidae).- *Tijdschrift voor Entomologie* 133:

121-141.

Aukema, B., 1991. Winglength determination in two wing-dimorphic Calathus species (Coleoptera: Carabidae).- *Hereditas* 113: 189-202.

Baars, M. A. & Th. S. van Dijk, 1984. Population dynamics of two carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal.- *Journal of Animal Ecology* 53: 375-388.

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae).- *Oecologia* 4: 1-28.

Boer, P. J. den, 1977. Dispersal power and survival: carabids in a cultivated countryside.- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J., T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism as stages in an evolutionary process (Coleoptera, Carabidae).- *Entomologia Generalis* 6: 107-134.

Desender, K., 1989a. Heritability of wing development and body size in a carabid beetle, Pogonus chalceus Marsham, and its evolutionary significance.- *Oecologia* 78: 513-520.

Desender, K., 1989b. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Dijk, Th. S. van, 1979. On the relationship between reproduction, age and survival in two carabid beetles: Calathus melanocephalus L. and Pterostichus coerulescens L (Coleoptera, Carabidae).- *Oecologia* 40: 63-80.

Dijk, Th. S. van, 1982. Individual variability and its significance for the survival of animal populations. In: *Environmental adaptation and evolution* (D. Mossakowski & G. Roth, eds): 233-251. Fischer, Stuttgart, New York.

Dijk, Th. S. van, 1983. The influence of food and temperature on the amount of reproduction in carabid beetles. In: Ecology of carabids: the synthesis of field study and laboratory experiment (P. Brandmayr, P.J. den Boer & F. Weber, eds).- *Report 4th Symposium of Carabidologists* 1981 (1983): 105-123.

Dingle, H., 1985. Migration. In: *Comprehensive insect physiology, biochemistry and pharmacology* (G. Kerkut & L.I. Gilbert, eds) 9: 375-416. Pergamon, New York.

Ernsting, G. & F. A. Huyer, 1984. A laboratory study on temperature relations of egg production and development in two related species of carabid beetle.- *Oecologia* 62: 361-367.

Haeck, J., 1971. The immigration and settlement of carabids in the new IJsselmeerpolders. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 8: 33-53.

Harrison, R. G., 1980. Dispersal polymorphisms in insects.- *Annual Review of Ecology and Systematics* 11: 95-118.

Honek, A., 1981. Wing polymorphism in Notiophilus biguttatus in Bohemia (Coleoptera, Carabidae).- *Věstník Československé Společnosti Zoologické* 45: 81-86.

Honek, A. & J. Pulpán, 1983. The flight of Carabidae (Coleoptera) to light trap.- *Věstník Československé Společnosti Zoologické* 47: 13-26.

Huizen, T. H. P. van, 1980. Species of Carabidae (Coleoptera) in which occurrence of dispersal by flight of individuals has been shown.- *Entomologische Berichten, Amsterdam* 40: 166-168.

Lindroth, C. H., 1946. Inheritance of wing dimorphism in Pterostichus anthracinus Ill.- *Hereditas* 32: 37-40.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae. 3. Allgemeiner Teil.- *Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar* 6, Ser. B 4 (3): 1-911.

McCullagh, P. & J. A. Nelder, 1989. *Generalized linear models* (2nd ed.). Chapman and Hall, London, New York.

Mols, P. J. M., Th. S. van Dijk & Y. Jongema, 1981. Two laboratory techniques to separate eggs of carabids from a substrate.- *Pedobiologia* 21: 500-501.

Nelemans, M. N. E., 1987. On the life-history of the carabid beetle Nebria brevicollis (F.). Egg production and larval growth under experimental conditions.- *Netherlands Journal of Zoology* 37: 26-42.

Palmén, E., 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor.- *Annales Societatis Zoologicae Botanicae-Fennicae 'Vanamo'* 10: 1-262.

Roff, D. E., 1986. The evolution of wing dimorphism in insects.- *Evolution* 40: 1009-1020.

Taylor, V. A., 1978. A winged elite in a subcortical beetle as a model for a protermite.- *Nature* 276: 73-75.

Zera, A. J., 1984. Differences in survivorship, development rate and fertility between the long winged and wingless morphs of the waterstrider, Limnoporus canaliculatus.- *Evolution* 38: 1023-1032.

Zera, A. J. & M. A. Rankin, 1989. Wing dimorphism in Gryllus rubens: genetic basis of morph determination and fertility differences between morphs.- *Oecologia* 80: 249-255.

V. DEVELOPMENT TIMES AND GROWTH IN RELATION TO WING-MORPH IN THREE CLOSELY RELATED SPECIES OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE)

ABSTRACT

Development times of short and long winged *Calathus cinctus* and *C. melanocephalus* and of long winged *C. mollis* were established for both males and females in relation to temperature. Growth was established for long winged genotypes of *C. cinctus*, *C. melanocephalus* and *C. mollis*. Development times in all three species were strongly influenced by temperature, but in both *C. cinctus* and *C. melanocephalus* neither for wing-morph nor sex was any general relationship between temperature and development time found.

Development time and growth of long winged genotypes of *Calathus melanocephalus* were strongly influenced by food-supply: in general shorter development times and higher hatching weights were found at a higher food supply. Moreover, long winged beetles of both sexes developed faster and were heavier than short winged ones, whereas females weighed more than males. Higher weight increases of adult beetles, however, were found at a lower food-supply. Short winged phenotypes showed a higher weight increase after hatching than long winged ones, and the weight increase of adults was higher in females than in males.

Key words: Carabidae - Wing dimorphism - development - growth - *Calathus* - *cinctus* - *melanocephalus* - *mollis*

INTRODUCTION

Populations of wing-dimorphic carabid beetles show considerable variation in the proportion of long winged beetles, and it is supposed that this proportion tends to decrease in ageing populations of these species. Both differences in flight ability between the short and long winged morph, and differences in Darwinian fitness between both morphs (a higher fitness of the brachypterous morph) have been used to explain this supposed trend towards brachyptery in ageing populations of the species concerned (see Aukema, 1991 for a review).

Wing dimorphism in the carabids *Calathus (Neocalathus) cinctus* Motschulsky (= *C. (N.) erythroderus* Gemminger & Harold) and *C. (N.) melanocephalus* (Linnaeus) was found to be determined genetically according to a single-locus model with brachyptery dominant to macroptery (Aukema, 1990b). In *C. melanocephalus*, however, environmental factors (temperature and food-supply) modify the expression of the long winged genotype, whereas in *C. cinctus* the long winged genotype is always expressed (Aukema, 1990b). The fecundity (egg production and oviposition period) of the long winged morph was found to be higher than those of the short winged morph (Aukema, 1990b). Consequently, differences in fecundity between the morphs cannot contribute to the supposed shift towards brachyptery in ageing populations of these species. Net emigration of long winged beetles is considered the most plausible explanation of this shift (Aukema, 1991). However, differences in growth and development time between the morphs also might influence the proportion of long winged beetles in populations of wing-dimorphic species (Roff, 1986).

Development times of short and long winged beetles of *Calathus cinctus* and *C. melanocephalus* were compared to detect possible differences in fitness between the two wing-morphs in this respect. Furthermore, in *C. melanocephalus* the effect of both development time and growth of immature stages on the expression of the long winged genotype was studied. Since the development of immature stages in carabids was found to be highly temperature dependent (see for instance Boye Jensen, 1990; Van Dijk, 1994; Ernsting & Huyer, 1984; Heessen et al., 1982 and Nelemans, 1987, 1988), both development time and growth were established in relation to temperature. Comparable data for the long winged morph of a third species, the closely related *Calathus (Neocalathus) mollis*, are included.

Van Dijk & Den Boer (1992) published data on the survival of eggs and the mortality during development of short winged *Calathus melanocephalus* in relation to substrate moisture and temperature, and Van Dijk (1994) studied development times and growth of developmental stages of short winged beetles of the same species at different temperature and food conditions.

MATERIAL AND METHODS

Species

Details on habitat, life-history and distribution of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* are given by Aukema (1990a), and data on wing dimorphism in these species can be found in Aukema (1990b). All three species are autumn breeders with a thermic hibernation parapause of the larvae (Thiele, 1977).

Data on timing of the oviposition period are given by Aukema (1991). *Calathus melanocephalus* starts egg production in the first week of August and stops after 12-14 weeks in October. *Calathus cinctus* starts 3-4 weeks later, but is able to proceed much longer than *C. melanocephalus*. *Calathus mollis* is intermediate in this respect with an early start (as in *C. melanocephalus*) and a long oviposition period (as in *C. cinctus*).

Data on development times of 1st and 2nd instar larvae of *Calathus melanocephalus* and *C. mollis* are given by Kůrka (1972) but are not reliable because of possible confusion with *C. cinctus* (Aukema, 1990a).

Experiments

Development times of immature stages (eggs, larvae and pupae) of short and long winged *Calathus cinctus* and *C. melanocephalus* and of long winged *C. mollis* were estimated in relation to temperature (experiment 1). The effect of temperature and food-supply on development times, growth rate, and weight of long winged genotypes of *C. melanocephalus* in relation to wing-morph was studied in experiment 2.

In 1981/1982 experiment 1 started with 10 single pairs of short and long winged *Calathus cinctus* and *C. melanocephalus* and long winged *C. mollis* kept in petri dishes (diameter 8.8 cm) with moist ground peat litter in incubators at 8.5 and 12 °C and natural daylength (adjusted weekly), as well as under approximately outside conditions in an outdoor insectary with overwintering in a wooden box sunk in the ground (see Aukema, 1990b, 1991). After a period of acclimatization the beetles were placed daily in new petri dishes with an excess of small blowfly larvae as food. Eggs were separated daily from the peat in the old petri dishes according to the sieve wash method of Mols et al. (1981) and incubated individually in small caps in petri dishes on moist filter paper. They were daily checked for hatching. Larvae were reared individually in moist peat litter. They were fed twice a week with small blowfly larvae and the larval development was checked weekly. Older third instar larvae were placed in small glass tubes and checked daily for pupation and emergence of adults.

In 1983/1984 the effect of food-supply on development of immature stages and larval growth of long winged genotypes of *Calathus melanocephalus* in relation to wing-morph was established in experiment 2 by rearing newly hatched larvae of the same eight pairs of long winged beetles under six temperature conditions and with two food-supply levels. The eggs were incubated at 19 °C. The larvae were fed three times a week with small blowfly larvae and about half of them were weighed twice a week (once before and once one day after feeding). Each time larvae of the high food-supply group got about their own weight in small blowfly larvae, whereas larvae of the low food-supply group only got two milligrams during their whole development (see also Aukema, 1990b). Pupae were

Table 35. Development time (days) of immature stages of short and long winged *Calathus cinctus* (cin) and *C. melanocephalus* (mel) and of long winged *C. mollis* (mol) at three temperatures in 1981/1982. WP: wing-morph parents; WO: wing-morph offspring; N: number of beetles. Oviposition periods: 24 September - 6 October (cin), 29 August - 6 September (mel) and 25 August - 4 September (mol).

						Mean development time in days (± SE)		
Temp.	Spec.	WP	WF	Sex	N	Egg	Larva I	Larva II
8.5 °C	cin	SW/LW	SW	♂	85	42.1 (± 0.30)	35.5 (± 0.92)	33.7 (± 0.53)
			SW	♀	86	42.4 (± 0.32)	37.6 (± 0.89)	35.9 (± 0.73)
			LW	♂	67	43.3 (± 0.55)	37.2 (± 0.82)	32.7 (± 0.65)
			LW	♀	62	42.5 (± 0.41)	35.9 (± 0.74)	32.5 (± 0.70)
	mel	SW	SW	♂	73	45.8 (± 0.23)	52.9 (± 1.16)	37.4 (± 0.80)
			SW	♀	51	45.2 (± 0.26)	49.4 (± 1.29)	39.5 (± 0.91)
		LW	SW	♂	54	45.4 (± 0.25)	50.2 (± 0.96)	38.6 (± 0.78)
			SW	♀	56	45.3 (± 0.24)	52.0 (± 1.36)	40.9 (± 1.11)
			LW	♂	4	46.2 (± 1.11)	58.0 (± 4.08)	41.0 (± 3.34)
			LW	♀	14	44.8 (± 0.35)	49.2 (± 1.69)	39.7 (± 2.19)
	mol	LW	LW	♂	71	46.9 (± 0.17)	44.3 (± 1.09)	31.7 (± 0.70)
			LW	♀	49	47.1 (± 0.25)	47.1 (± 1.24)	32.2 (± 0.80)
12 °C	cin	SW/LW	SW	♂	40	31.2 (± 0.66)	34.0 (± 1.55)	24.0 (± 0.65)
			SW	♀	43	29.4 (± 0.51)	35.2 (± 1.59)	27.3 (± 0.78)
			LW	♂	45	31.8 (± 0.74)	33.6 (± 1.42)	27.1 (± 0.82)
			LW	♀	55	30.0 (± 0.51)	38.7 (± 1.26)	27.0 (± 0.73)
	mel	SW	SW	♂	67	29.4 (± 0.40)	46.0 (± 1.49)	27.4 (± 0.83)
			SW	♀	58	28.6 (± 0.36)	43.3 (± 1.52)	27.9 (± 0.79)
			LW	♀	7	27.4 (± 0.75)	52.9 (± 4.77)	25.1 (± 1.81)
		LW	SW	♂	34	28.8 (± 0.42)	52.4 (± 2.41)	25.2 (± 0.82)
			SW	♀	19	29.9 (± 0.66)	49.7 (± 3.66)	28.9 (± 1.34)
			LW	♂	38	29.6 (± 0.28)	46.4 (± 2.56)	27.4 (± 1.03)
			LW	♀	30	28.7 (± 0.42)	47.6 (± 2.44)	26.5 (± 1.02)
	mol	LW	LW	♂	59	30.9 (± 0.24)	34.4 (± 1.57)	28.5 (± 1.14)
			LW	♀	68	30.7 (± 0.17)	33.8 (± 1.61)	28.2 (± 1.04)
outside	cin	SW/LW	SW	♂	39	47.8 (± 0.79)	87.9 (± 2.07)	65.2 (± 1.16)
			SW	♀	48	48.4 (± 0.68)	89.8 (± 1.74)	66.9 (± 1.39)
			LW	♂	29	53.0 (± 1.18)	87.8 (± 2.00)	58.1 (± 1.79)
			LW	♀	24	52.4 (± 1.09)	85.2 (± 2.98)	65.1 (± 2.65)
	mel	SW	SW	♂	70	19.6 (± 0.15)	44.2 (± 2.35)	77.2 (± 2.62)
			SW	♀	54	19.5 (± 0.08)	47.4 (± 2.83)	82.4 (± 3.01)
			LW	♂	1			
			LW	♀	4			
		LW	SW	♂	53	19.3 (± 0.14)	48.5 (± 2.11)	90.2 (± 3.44)
			SW	♀	47	19.5 (± 0.25)	46.4 (± 2.38)	88.8 (± 3.63)
			LW	♂	12	19.7 (± 0.28)	43.8 (± 4.77)	78.1 (± 6.77)
			LW	♀	16	19.4 (± 0.26)	45.6 (± 4.85)	86.6 (± 4.12)
	mol	LW	LW	♂	61	21.1 (± 0.27)	32.1 (± 1.84)	67.1 (± 1.52)
			LW	♀	86	21.2 (± 0.21)	33.5 (± 1.61)	66.4 (± 1.28)

Table 35, continued.

						Mean development time in days (± SE)		
Temp.	Spec.	WP	WF	Sex	N	Larva III	Pupae	Total
8.5 °C	cin	SW/ LW	SW	♂	85	105.7 (± 2.42)	47.0 (± 0.43)	264.1 (± 2.44)
			SW	♀	86	103.4 (± 2.21)	46.0 (± 0.47)	264.5 (± 2.16)
			LW	♂	67	125.3 (± 2.65)	61.2 (± 0.49)	299.3 (± 2.61)
			LW	♀	62	126.0 (± 2.61)	61.2 (± 0.49)	298.0 (± 2.59)
	mel	SW	SW	♂	73	120.5 (± 2.48)	45.4 (± 0.27)	301.9 (± 2.17)
			SW	♀	51	126.5 (± 3.05)	44.3 (± 0.37)	304.8 (± 2.80)
		LW	SW	♂	54	137.2 (± 2.85)	48.5 (± 0.30)	320.0 (± 3.13)
			SW	♀	56	136.0 (± 2.96)	47.8 (± 0.31)	322.1 (± 3.02)
			LW	♂	4	127.0 (± 7.01)	50.0 (± 0.58)	322.2 (± 2.93)
			LW	♀	14	132.3 (± 6.21)	47.2 (± 0.90)	313.2 (± 7.41)
	mol	LW	LW	♂	71	87.6 (± 1.60)	40.5 (± 0.66)	251.0 (± 1.43)
			LW	♀	49	86.5 (± 2.16)	39.9 (± 0.71)	250.4 (± 1.97)
12 °C	cin	SW/ LW	SW	♂	40	83.7 (± 2.08)	30.3 (± 0.25)	203.1 (± 2.42)
			SW	♀	43	86.6 (± 1.85)	29.8 (± 0.31)	208.3 (± 2.52)
			LW	♂	45	79.4 (± 1.68)	30.0 (± 0.72)	203.0 (± 2.31)
			LW	♀	55	84.0 (± 2.03)	29.5 (± 0.56)	208.9 (± 2.22)
	mel	SW	SW	♂	67	92.2 (± 1.81)	26.8 (± 0.19)	221.8 (± 1.65)
			SW	♀	58	98.7 (± 2.12)	26.4 (± 0.19)	225.0 (± 1.93)
			LW	♀	7	86.4 (± 5.20)	26.9 (± 0.34)	218.7 (± 2.15)
		LW	SW	♂	34	89.7 (± 2.34)	21.8 (± 0.36)	218.3 (± 2.76)
			SW	♀	19	96.4 (± 3.37)	21.6 (± 0.53)	226.5 (± 3.28)
			LW	♂	38	85.7 (± 1.70)	20.7 (± 0.43)	209.8 (± 2.40)
			LW	♀	30	86.2 (± 2.16)	20.7 (± 0.39)	209.8 (± 2.12)
	mol	LW	LW	♂	59	84.2 (± 1.28)	25.1 (± 0.38)	203.1 (± 0.53)
			LW	♀	68	86.8 (± 1.29)	24.0 (± 0.36)	203.4 (± 0.54)
outside	cin	SW/ LW	SW	♂	39	47.0 (± 1.39)	14.1 (± 0.37)	262.0 (± 0.54)
			SW	♀	48	43.7 (± 1.05)	15.9 (± 0.37)	264.7 (± 0.94)
			LW	♂	29	45.0 (± 1.51)	14.2 (± 0.52)	258.1 (± 0.88)
			LW	♀	24	42.4 (± 1.96)	15.3 (± 0.61)	260.4 (± 1.39)
	mel	SW	SW	♂	70	128.4 (± 4.45)	14.3 (± 0.32)	283.7 (± 0.97)
			SW	♀	54	120.0 (± 5.24)	13.9 (± 0.32)	283.3 (± 0.94)
			LW	♂	1			(275.0)
			LW	♀	4			(279.5)
		LW	SW	♂	53	111.7 (± 5.05)	14.9 (± 0.33)	284.5 (± 1.08)
			SW	♀	47	115.9 (± 4.90)	14.3 (± 0.41)	284.8 (± 1.18)
			LW	♂	12	128.3 (± 9.58)	12.3 (± 0.43)	282.1 (± 1.42)
			LW	♀	16	115.5 (± 6.43)	12.7 (± 0.27)	279.8 (± 1.11)
	mol	LW	LW	♂	61	137.6 (± 3.16)	17.8 (± 0.27)	275.9 (± 0.51)
			LW	♀	86	137.9 (± 2.50)	17.8 (± 0.17)	276.8 (± 0.45)

not weighed, because they are too vulnerable, but freshly hatched beetles were weighed within a day after hatching. The rearing conditions were either constant temperatures (8.5, 12, 15.5 and 19 °C) with natural photoperiod (adjusted once a week), or one alternating temperature (12 hours light at 15.5 °C and 12 hours dark at 8.5 °C), or approximately outside conditions in an outdoor insectary (comparable to the earlier experiments). After hatching the beetles were kept under the same conditions for at least six weeks with food ad libitum three times a week and they were weighed twice a week, just before feeding and the day after feeding.

In a similar experiment additional groups of larvae of long winged pairs of *Calathus cinctus*, *C. melanocephalus* (the same parents as the other groups) and *C. mollis* were reared with an excessive food-supply ($>$ 10 mg twice a week) at 15.5 °C only.

Data on total development time and growth rate were analysed by means of regression analysis based on a generalized linear model (GLM) with a Poisson distribution (McCullagh & Nelder, 1989) with GENSTAT.

RESULTS

Development

a) General

Timing of the development of immature stages (eggs, larvae I, II, III and pupae) of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* both in the outdoor insectary and at constant temperatures of 8.5 and 12 °C are depicted in figs 31-32, together with the weekly mean temperatures from the meteorological station of the KNMI at Eelde and with the temperatures in the wooden box used for overwintering of the larvae. Data on development times are given in table 35.

In accordance with data on their life-histories (see Aukema, 1990a), the eggs of *Calathus cinctus* were incubated about four weeks later (24 September - 6 October) than those of *C. melanocephalus* and *C. mollis* (29 August - 6 September and 25 August - 4 September respectively).

Under outside conditions *Calathus cinctus* overwintered mainly in the first instar, whereas both *C. melanocephalus* and *C. mollis* did so mainly in the second instar (fig. 32). Despite this initial delay in development, the total development time of *C. cinctus* was about three to two weeks shorter than that of *C. melanocephalus* and *C. mollis* respectively (table 35). From May onwards, however, the development of all three species proceeded very quickly (fig. 32: high median values of the third instar and very short pupal stages).

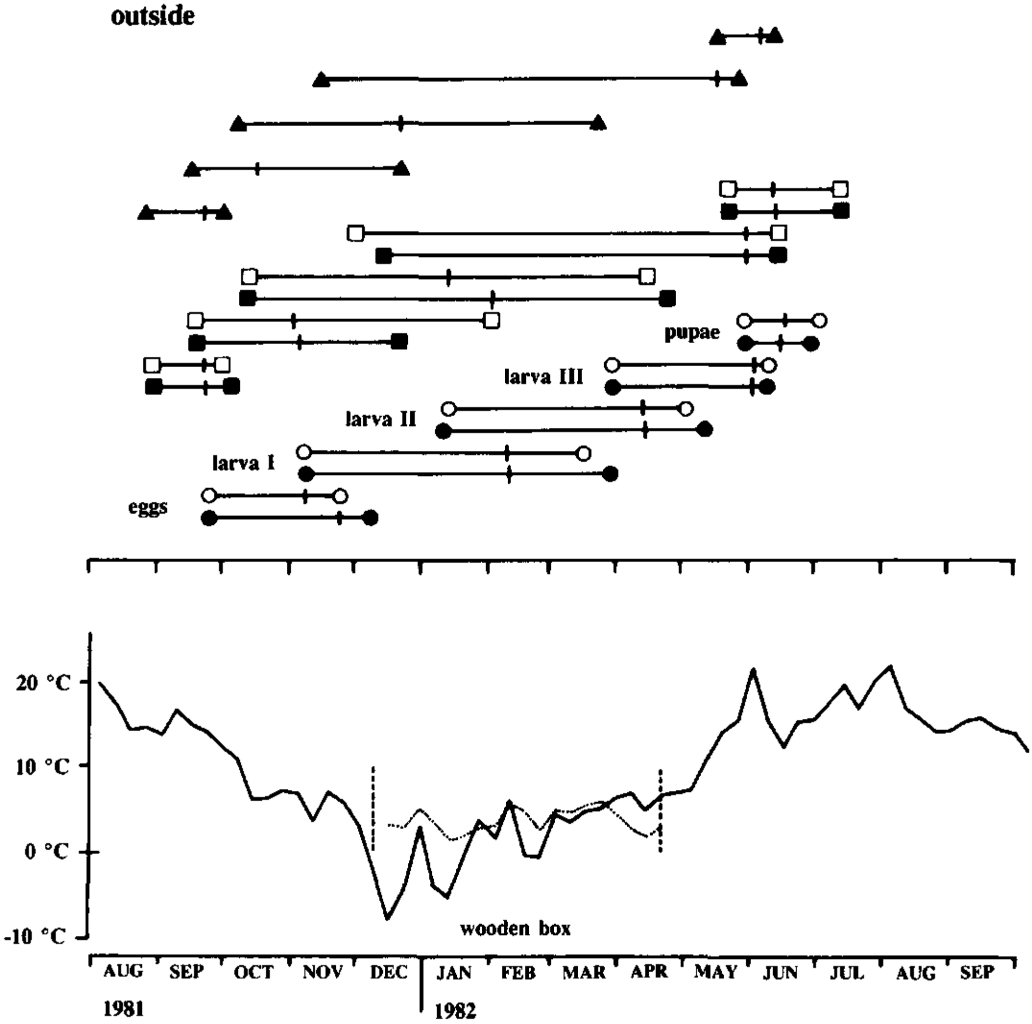

Fig. 32. Development times of eggs, larvae and pupae of *Calathus cinctus* (circles), *C. melanocephalus* (squares), and *C. mollis* (triangles) under outside conditions (experiment 1). Open symbols: short winged beetles; closed symbols: long winged beetles; median values indicated by a cross-bar. Lower part: mean weekly temperatures estimated in Eelde (dotted line: temperatures in the underground wooden box during overwintering).

Development at 8.5 °C was slower and at 12 °C faster than under outside conditions (fig. 33). Under these constant conditions the timing of the development of the stages was more regular than in the outdoor insectary. At both temperatures *Calathus mollis* showed the shortest development time and *C. melanocephalus* the longest one (table 35).

Eggs.- The eggs needed about 4 weeks to develop at 12 °C and 6-7 weeks at 8.5 °C. Note the long development time of the (late incubated) eggs of *Calathus*

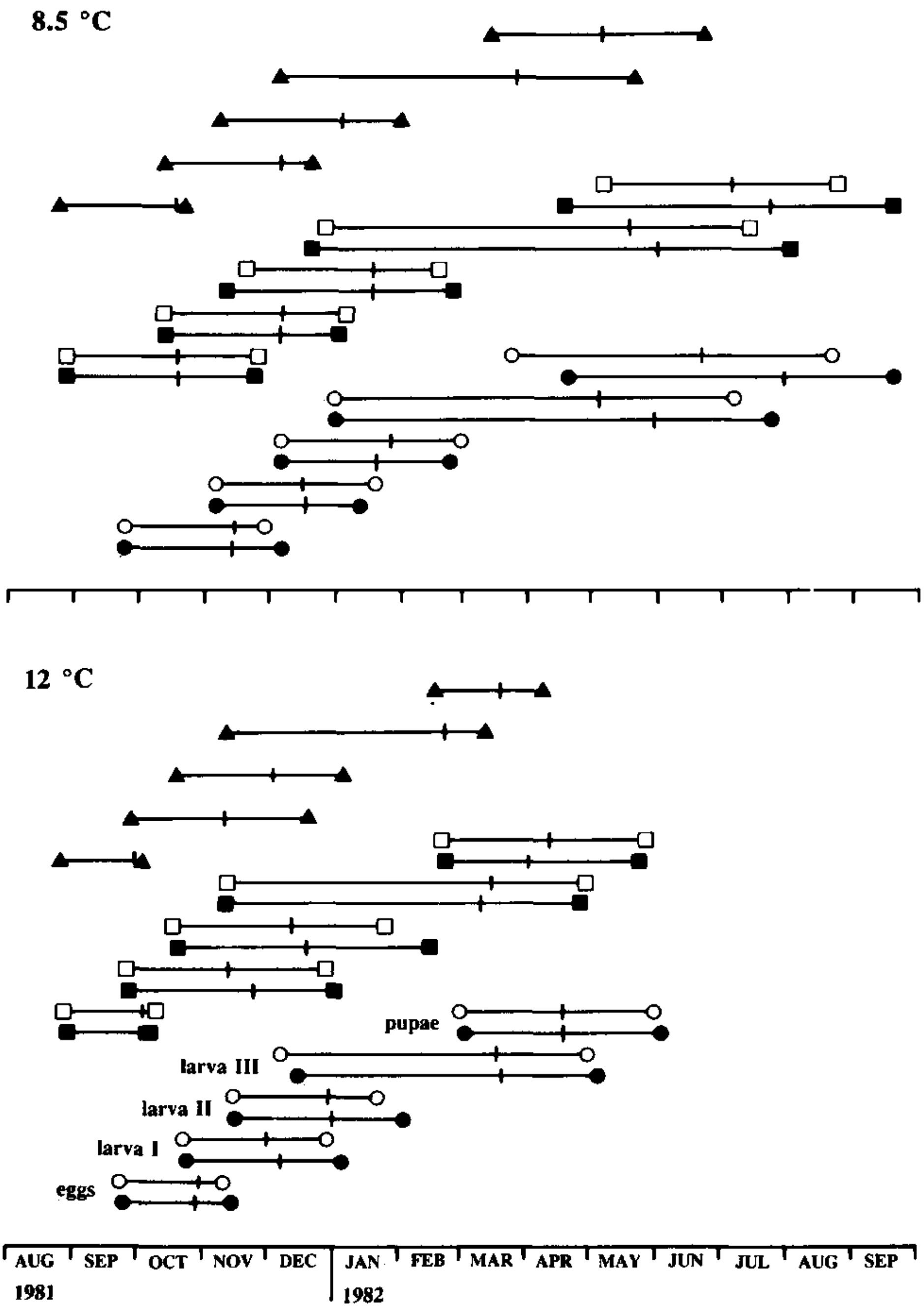

Fig. 33. Development times of eggs, larvae and pupae of Calathus cinctus (circles), C. melanocephalus (squares), and C. mollis (triangles) at 8.5 and 12 °C (experiment 1). Symbols: see fig. 32.

cinctus under outside conditions (table 35).

First instar.- First instar larvae of *Calathus cinctus* needed about 5 weeks on the average for their development both at 8.5 and at 12 °C. Under the colder outside conditions (fig. 32) this period was extended to 12-13 weeks (table 35). Mean development times of first instar larvae of *C. melanocephalus* and *C. mollis* were similar both under outside conditions and at 12 °C (6-7 and 4-5 weeks respectively) and only slightly longer at 8.5 °C (7-8 and 6-7 weeks respectively).

Second instar.- Mean development times of the second instar larvae of the three species at 8.5 and 12 °C were about similar (4 and 4.5-6 weeks respectively), but under outside conditions they appeared to be much longer: about 9.5 weeks in *Calathus cinctus* and *C. mollis* and 11-13 weeks in *C. melanocephalus* (table 35).

Third instar.- Mean development times of the third instar larvae of the three species at 12 °C were about similar (12-13 weeks). The development time of third instar larvae of *Calathus mollis* at 8.5 °C was similar to that at 12 °C, but those of *C. cinctus* and *C. melanocephalus* were much longer at 8.5 °C than at 12 °C (table 35: about 15-18 and 18-20 weeks respectively). Note the large difference in mean development time of about 3 weeks between short and long winged *C. cinctus*. Under outside conditions the third instar larvae of *C. cinctus* developed remarkable fast (6-7 weeks) and those of *C. mollis* very slowly (about 19.5 weeks). Third instar larvae of *Calathus melanocephalus* needed 16-18 weeks on average for their development.

Pupae.- Mean duration of the pupal stage at 12 °C was about 3-4 weeks (table 35: lowest values in *C. melanocephalus* and highest values in *C. cinctus*). The development of the pupae at 8.5 °C lasted about two times as long and again long winged *C. cinctus* needed substantially more time (about two weeks) for their development than short winged ones. Under outside conditions the pupal stage only lasted about 2 weeks in all three species (table 35).

Total development.- Mean total development (DT) lasted 29-33 weeks at 12 °C ($\mathrm{DT}_{mollis} \leq \mathrm{DT}_{cinctus} < \mathrm{DT}_{melanocephalus}$), 36-46 weeks at 8.5 °C ($\mathrm{DT}_{mollis} < \mathrm{DT}_{cinctus} < \mathrm{DT}_{melanocephalus}$) and 37-41 weeks under outside conditions ($\mathrm{DT}_{cinctus} < \mathrm{DT}_{mollis} < \mathrm{DT}_{melanocephalus}$). Differences in total development time between wing-morphs will be discussed in more detail for each species separately.

Mortality.- Data on mortality are given in table 36. In general mortality of eggs and first instar larvae was relatively low, and in most cases the mortality of second

Table 36. Mortality among developmental stages of offspring of short and long winged *Calathus cinctus* (cin) and *C. melanocephalus* (mel) and of long winged *C. mollis* (mol) at three temperatures in 1981/1982. SW: short winged; LW: long winged; NE: number of eggs used; EM: egg mortality (%); NL: number of larvae; LI, LII, LIII: first, second and third larval stage respectively. Oviposition period: see table 35.

						Mortality (%)				
Temperature	Species	Morph	NE	EM	NL	LI	LII	LIII	Pupae	Total
8.5 °C	cin	SW	257	9.3	196	8.2	2.0	2.0	0.5	12.7
		LW	210	3.8	170	8.8	6.5	5.3	3.5	24.1
	mel	SW	234	5.1	158	6.3	3.8	7.6	2.5	20.2
		LW	263	6.8	162	6.2	4.9	6.2	3.7	21.0
	mol	LW	264	11.7	154	6.5	5.8	4.5	5.2	22.1
12 ° C	cin	SW	270	5.6	133	13.5	3.0	3.0	8.3	27.8
		LW	299	4.0	118	11.0	1.7	6.8	6.8	26.3
	mel	SW	257	6.2	156	9.0	0.0	1.9	4.5	15.4
		LW	264	4.5	131	9.9	0.8	0.0	4.6	15.3
	mol	LW	256	10.9	150	9.3	2.0	2.0	2.0	15.3
outside	cin	SW	270	8.5	169	7.7	20.2	1.2	2.4	31.4
		LW	168	6.5	98	3.1	30.6	10.2	2.0	45.9
	mel	SW	257	14.8	186	5.9	5.9	16.7	2.1	30.6
		LW	259	10.0	195	9.7	4.1	20.5	0.0	34.4
	mol	LW	257	10.9	206	6.3	3.4	17.0	1.9	28.6

and third larval stages and of pupae was even lower. A relatively high mortality in the second larval stage was observed among offspring of both short and long winged *Calathus cinctus* under outside conditions, whereas offspring of both *C. melanocephalus* and *C. mollis* showed a significantly increased mortality in the third larval stage under outside conditions. The highest total mortality of all three species was found under outside conditions. The survival of both *Calathus melanocephalus* and *C. mollis* was relatively high at 12 °C, whereas especially the short winged morph of *C. cinctus* performed better at 8.5 °C. The effect of food supply-level on the mortality of long and short winged *C. melanocephalus* during experiment 2 is illustrated in table 37. In general the mortality at the low food-supply level was significantly higher than at the high food-supply level. High mortality rates were observed in the third larval stage for all temperatures higher than 8.5 °C at the low food-supply level, and for 19 °C at the high food-supply

Table 37. Mortality among developmental stages of *Calathus melanocephalus* reared from the same parental long winged single-pair crosses under six temperature conditions and with two food-supply levels (1983/1984). NL: number of larvae; LI: larva I, LII: larva II; LIII: larva III.

			Mortality (%)				
Food-supply	Temperatures	NL	LI	LII	LIII	pupae	total
Low	8.5 °C	70	7.1	0.0	1.4	20.0	28.6
	12 °C	70	8.6	1.4	24.2	12.9	47.1
	15.5 °C	64	3.1	0.0	26.6	1.6	31.2
	19 °C	67	3.0	4.5	26.9	11.9	46.3
	15.5/8.5 °C	67	6.0	3.0	17.9	7.5	34.3
	Outside	66	12.1	4.5	7.6	3.0	27.3
High	8.5 °C	68	2.9	1.5	1.5	0.0	5.9
	12 °C	72	12.5	2.8	2.8	0.0	18.0
	15.5 °C	63	7.9	0.0	3.2	3.2	14.3
	19 °C	68	7.3	10.3	22.1	13.2	52.9
	15.5/8.5 °C	63	3.2	1.6	3.2	0.0	7.9
	Outside	67	6.0	1.5	7.5	0.0	14.9

level. The mortality of the pupae was remarkably low at 8.5 °C and a low food-supply.

b) *Calathus cinctus*

Data on development times of eggs, larval instars and pupae as well as total development time (DT) of *Calathus cinctus* in relation to temperature for 1981/1982 are summarised in table 35. Analysis of the data on total development time (table 38) showed a highly significant difference between wing-morphs, i.e. longer total development times of long winged beetles than of short winged ones, and a highly significant effect of temperature on development time ($DT_{12} < DT_{outside} = DT_{8.5}$ for both short and long winged beetles). Although males at outside conditions and 12 °C tended to develop somewhat faster than females, in general no significant difference was found between sexes.

The difference in total development time between wing-morphs, however, was strongly influenced by the highly significant interaction between temperature and wing-morph, which was mainly due to the extreme long development time of long winged beetles at 8.5 °C: almost 300 days against about 265 days for short winged beetles (table 35). At 12 °C no difference in development time was found between short and long winged beetles, whereas under outside conditions both short winged males and females needed about four days longer for their development on the

Table 38. Testing results of regression analysis of data on total development time of short and long winged *Calathus cinctus* (cin) and *C. melanocephalus* (mel) and long winged *C. mollis* (mol) under three temperature conditions in 1981/1982, and *C. melanocephalus* under six temperature conditions and with a high food-supply in 1983/1984. SW: short winged; LW: long winged; n.s. = not significant; ***: P<0.001; *: P<0.05.

	Species				
	cin	mel	mel	mel	mol
Wing-morph parents	SW, LW	LW	SW, LW	LW	LW
Wing-morph offspring	SW, LW	SW, LW	SW	SW, LW	LW
Year	1981/82	1981/82	1981/82	1983/84	1981/82
Source of variation					
temperature	***	***	***	***	***
wing-morph offspring	***	***	—	n.s.	—
wing-morph parents	—	—	***	—	—
sex	n.s.	n.s.	*	n.s.	n.s.
temperature x wing-morph	***	n.s.	***	n.s.	—
temperature x sex	n.s.	n.s.	n.s.	n.s.	n.s.
wing-morph x sex	n.s.	n.s.	n.s.	*	—
temperature x wing-morph x sex	n.s.	n.s.	n.s.	n.s.	—

average than long winged ones (table 35). So, apparently in *Calathus cinctus* no simple relation exists between wing-morph, temperature and total development time.

c) *Calathus melanocephalus*

As could be expected from the inheritance of wing dimorphism in *Calathus melanocephalus* (Aukema, 1990b) both short and long winged parents produced short as well as long winged offspring (table 35). Since the number of long winged offspring of short winged parents was very low (8.5 °C: 2 ♀; 12.5 °C: 7 ♀; outside: 1 ♂, 4 ♀), differences in development time between wing-morphs were studied from data of offspring of long winged females only.

In this species a highly significant difference in development time between wing-morphs was again found (table 38), but in this case the difference was caused by shorter development times of long winged beetles than those of short winged ones (table 35). The effect of temperature was highly significant ($DT_{12} < DT_{outside} < DT_{8.5}$), and no differences in development time between the sexes were found.

When comparing short winged offspring of both short and long winged parents, offspring of long winged parents appeared to develop significantly more slowly than those of short winged parents, and males tended to develop faster than females (table 38). However, the longer development time of short winged male offspring of short winged parents under outside conditions (table 35) obscured this trend.

Development times at low and high food-supply levels (experiment 2) are given in table 39. Both temperature and food-supply level were found to have a highly significant effect on the development time of offspring of long winged *Calathus melanocephalus*. In general development times were shorter at higher temperatures ($DT_{19} < DT_{15.5} < DT_{12} < DT_{8.5}$) and at a high food-supply level. At the high food-supply level the development under the changing day-night temperature condition and under outside conditions fit very well in this range ($DT_{19} < DT_{15.5} < DT_{8.5/15.5} < DT_{12} < DT_{8.5} < DT_{outside}$). The results at the low food-supply level, however, are less clear, mainly caused by the extremely long development times of females at 8.5 °C and under the changing day-night temperature condition (mean values of 327.3 and 244.1 days respectively). Because of the high amount of interaction between the factors temperature, food-supply and sex at the low food-supply level, analysis was limited to the data obtained at the high food-supply level (table 38). No significant effects of wing-morph or sex were found. The significant interaction between wing-morph and sex was due to the relatively short development times of long winged males (the lowest mean values at 12, 8.5/15.5 and 15.5 °C, see table 39).

d) *Calathus mollis*

In *Calathus mollis* also a highly significant effect of temperature on development time ($DT_{12} < DT_{8.5} < DT_{outside}$, see table 35) and no difference in development time between the sexes were found (table 38).

Growth

Data on larval growth of short and long winged offspring of long winged *Calathus melanocephalus,* reared at two food-supply levels and six temperature conditions,

Table 39. Development times (days) of immature stages of offspring of long winged *Calathus melanocephalus* reared at two food-supply levels and six temperatures in 1983/1984. SW: short winged; LW: long winged; N: number of beetles.

					Mean development time in days (± SE)		
Food-supply	Sex	Wing-morph	Temp.	N	Larva I	Larva II	Larva III
low 1)	♂	SW	outside	20	37.1 (± 1.34)	58.3 (± 2.09)	143.2 (± 2.48)
			8.5 °C	25	27.8 (± 0.39)	30.0 (± 0.47)	163.6 (± 9.58)
			12 °C	20	22.9 (± 0.55)	25.4 (± 0.34)	162.9 (± 12.68)
			8.5/15.5 °C	25	19.5 (± 0.37)	24.6 (± 0.83)	142.2 (± 7.20)
			15.5 °C	20	15.7 (± 0.47)	22.0 (± 0.43)	94.0 (± 2.95)
			19 °C	27	14.9 (± 0.63)	22.3 (± 0.80)	82.9 (± 2.23)
	♀	SW	outside	28	36.8 (± 0.73)	62.6 (± 2.11)	141.6 (± 2.03)
			8.5 °C	25	29.0 (± 0.41)	31.0 (± 0.68)	228.8 (± 11.00)
			12 °C	16	22.9 (± 0.36)	25.1 (± 0.74)	168.7 (± 15.22)
			8.5/15.5 °C	19	19.2 (± 0.63)	25.8 (± 0.96)	173.6 (± 13.78)
			15.5 °C	23	16.7 (± 0.47)	22.5 (± 0.45)	96.5 (± 1.99)
			19 °C	9	15.4 (± 0.90)	21.9 (± 1.18)	76.6 (± 4.39)
high 2)	♂	SW	outside	24	40.8 (± 2.40)	57.5 (± 1.76)	132.3 (± 4.40)
			8.5 °C	30	28.8 (± 0.33)	27.7 (± 0.35)	140.8 (± 2.68)
			12 °C	29	21.9 (± 0.34)	23.7 (± 0.38)	121.8 (± 2.87)
			8.5/15.5 °C	17	19.5 (± 0.62)	22.2 (± 0.62)	110.5 (± 5.50)
			15.5 °C	10	14.6 (± 0.64)	20.6 (± 0.65)	80.2 (± 3.32)
			19 °C	10	13.9 (± 1.12)	18.4 (± 1.17)	54.8 (± 1.98)
		LW	outside	6	33.7 (± 2.03)	55.2 (± 1.64)	144.3 (± 2.63)
			8.5 °C	1	25.0	29.0	109.0
			12 °C	7	21.9 (± 0.40)	23.4 (± 0.57)	115.4 (± 4.41)
			8.5/15.5 °C	6	18.8 (± 0.54)	22.3 (± 0.92)	97.2 (± 5.95)
			15.5 °C	17	15.5 (± 0.45)	20.1 (± 0.71)	68.5 (± 1.94)
			19 °C	6	12.5 (± 1.65)	19.3 (± 0.84)	55.8 (± 5.60)
	♀	SW	outside	14	38.3 (± 0.84)	57.2 (± 2.13)	133.4 (± 2.98)
			8.5 °C	30	28.7 (± 0.29)	28.9 (± 0.67)	141.7 (± 3.37)
			12 °C	13	22.1 (± 0.33)	24.2 (± 0.51)	127.4 (± 5.18)
			8.5/15.5 °C	20	18.8 (± 0.49)	22.9 (± 0.38)	107.6 (± 4.59)
			15.5 °C	8	16.6 (± 0.68)	19.8 (± 0.86)	77.5 (± 3.50)
			19 °C	9	12.1 (± 0.54)	20.3 (± 0.90)	56.8 (± 4.62)
		LW	outside	13	35.6 (± 1.71)	55.8 (± 1.10)	135.6 (± 2.91)
			8.5 °C	3	28.3	30.0	146.0
			12 °C	11	23.5 (± 0.41)	25.5 (± 0.77)	117.7 (± 4.13)
			8.5/15.5 °C	15	19.0 (± 0.61)	22.2 (± 0.42)	118.5 (± 5.74)
			15.5 °C	19	15.6 (± 0.41)	19.7 (± 0.55)	75.1 (± 2.15)
			19 °C	7	13.1 (± 0.88)	17.6 (± 0.81)	58.1 (± 3.17)

1) 2 mg of small blowfly larvae twice a week

2) larval weight in small blowfly larvae twice a week

Table 39, continued.

Food-supply	Sex	Wing-morph	Temp.	N	Mean development time in days (± SE)	
					Pupa	Larva I - Adult
low 1)	♂	SW	outside	20	20.7 (± 0.23)	259.2 (± 1.55)
			8.5 °C	25	39.1 (± 0.53)	259.2 (± 9.91)
			12 °C	20	28.1 (± 0.36)	239.2 (± 12.71)
			8.5/15.5 °C	25	25.0 (± 0.21)	211.4 (± 7.19)
			15.5 °C	20	17.2 (± 0.15)	148.8 (± 2.66)
			19 °C	27	12.2 (± 0.15)	132.2 (± 2.50)
	♀	SW	outside	28	20.9 (± 0.35)	262.0 (± 1.53)
			8.5 °C	25	38.6 (± 0.59)	327.3 (± 10.98)
			12 °C	16	28.3 (± 0.33)	244.9 (± 15.41)
			8.5/15.5 °C	19	25.5 (± 0.29)	244.1 (± 14.09)
			15.5 °C	23	16.6 (± 0.16)	152.3 (± 2.08)
			19 °C	9	12.3 (± 0.17)	126.2 (± 4.87)
high 2)	♂	SW	outside	24	21.7 (± 0.28)	252.3 (± 1.54)
			8.5 °C	30	38.5 (± 0.26)	235.8 (± 2.89)
			12 °C	29	28.5 (± 0.20)	195.9 (± 2.74)
			8.5/15.5 °C	17	24.8 (± 0.20)	176.9 (± 5.50)
			15.5 °C	10	17.7 (± 0.15)	133.1 (± 3.66)
			19 °C	10	12.9 (± 0.23)	100.0 (± 2.24)
		LW	outside	6	21.2 (± 0.40)	254.3 (± 1.69)
			8.5 °C	1	38.0	201.0
			12 °C	7	29.1 (± 0.26)	189.9 (± 4.65)
			8.5/15.5 °C	6	25.0 (± 0.26)	163.3 (± 6.01)
			15.5 °C	17	17.3 (± 0.11)	121.4 (± 2.05)
			19 °C	6	12.8 (± 0.17)	100.5 (± 5.37)
	♀	SW	outside	14	20.8 (± 0.15)	249.6 (± 1.86)
			8.5 °C	30	38.0 (± 0.26)	237.3 (± 3.21)
			12 °C	13	27.4 (± 0.21)	201.1 (± 4.95)
			8.5/15.5 °C	20	23.9 (± 0.18)	173.1 (± 4.95)
			15.5 °C	8	16.4 (± 0.18)	130.3 (± 4.03)
			19 °C	9	12.2 (± 0.22)	101.4 (± 5.13)
		LW	outside	13	21.3 (± 0.33)	248.3 (± 1.39)
			8.5 °C	3	37.3	241.7
			12 °C	11	28.8 (± 0.26)	195.6 (± 4.11)
			8.5/15.5 °C	15	24.7 (± 0.67)	184.4 (± 6.44)
			15.5 °C	19	16.7 (± 0.12)	127.1 (± 2.33)
			19 °C	7	12.6 (± 0.20)	101.4 (± 3.08)

1) 2 mg of small blowfly larvae twice a week

2) larval weight in small blowfly larvae twice a week

Table 40. *Calathus melanocephalus*: starting weights of larvae (WSTART), maximum weights of larva I, II and III (WLI, WLII and WLIII respectively) and mean weights of freshly hatched beetles (WHATCH) in mg at two food-supply levels and six temperatures in 1983/1984. FS: food-supply; WM: wing-morph; N: number weighed.

				WSTART		WLI		WLII	
FS	Sex	WM	Temp.	N	Mean (± SE)	N	Mean (± SE)	N	Mean (± SE)
low	♂	SW	outside	16	0.23 (± 0.0002)	12	1.08 (± 0.007)	10	3.62 (± 0.037)
			8.5 °C	25	0.23 (± 0.0001)	13	1.06 (± 0.004)	12	3.46 (± 0.043)
			12 °C	19	0.24 (± 0.0002)	7	1.15 (± 0.009)	8	3.49 (± 0.046)
			8.5/15.5 °C	13	0.21 (± 0.0002)	10	1.00 (± 0.006)	10	3.44 (± 0.050)
			15.5 °C	15	0.22 (± 0.0001)	11	1.04 (± 0.005)	11	3.41 (± 0.078)
			19 °C	26	0.22 (± 0.0001)	11	0.97 (± 0.007)	11	3.33 (± 0.059)
	♀	SW	outside	26	0.23 (± 0.0001)	13	1.07 (± 0.005)	17	3.96 (± 0.058)
			8.5 °C	23	0.22 (± 0.0002)	17	1.11 (± 0.005)	16	3.62 (± 0.066)
			12 °C	16	0.23 (± 0.0002)	10	1.18 (± 0.012)	10	3.29 (± 0.093)
			8.5/15.5 °C	12	0.22 (± 0.0001)	10	1.00 (± 0.002)	10	3.66 (± 0.049)
			15.5 °C	17	0.23 (± 0.0001)	10	1.02 (± 0.015)	11	3.40 (± 0.187)
			19 °C	9	0.24 (± 0.0001)	5	1.04 (± 0.007)	4	3.23 (± 0.045)
high	♂	SW	outside	21	0.22 (± 0.0002)	12	1.10 (± 0.005)	12	4.28 (± 0.107)
			8.5 °C	29	0.21 (± 0.0001)	15	1.07 (± 0.003)	13	4.04 (± 0.107)
			12 °C	29	0.23 (± 0.0002)	17	1.16 (± 0.005)	17	4.22 (± 0.074)
			8.5/15.5 °C	8	0.22 (± 0.0001)	9	1.12 (± 0.006)	9	3.94 (± 0.110)
			15.5 °C	7	0.23 (± 0.0001)	5	1.08 (± 0.005)	4	3.68 (± 0.115)
			19 °C	10	0.24 (± 0.0001)	3	1.18	4	4.03 (± 0.113)
		LW	outside	6	0.23 (± 0.0001)	4	1.12 (± 0.004)	4	4.41 (± 0.303)
			8.5 °C			1	1.11	1	4.08
			12 °C	6	0.25 (± 0.0002)	2	1.24	4	4.64 (± 0.069)
			8.5/15.5 °C	4	0.23 (± 0.0004)	3	0.97	3	3.91
			15.5 °C	11	0.23 (± 0.0002)	6	1.13 (± 0.018)	6	3.73 (± 0.278)
			19 °C	6	0.23 (± 0.0002)	2	1.09	6	3.85 (± 0.077)
	♀	SW	outside	12	0.23 (± 0.0001)	8	1.17 (± 0.006)	7	4.45 (± 0.061)
			8.5 °C	30	0.22 (± 0.0001)	15	1.12 (± 0.001)	14	4.44 (± 0.062)
			12 °C	13	0.24 (± 0.0001)	5	1.25 (± 0.005)	6	4.75 (± 0.059)
			8.5/15.5 °C	13	0.21 (± 0.0003)	10	1.08 (± 0.008)	9	3.74 (± 0.150)
			15.5 °C	7	0.21 (± 0.0001)	4	1.11 (± 0.008)	5	4.36 (± 0.103)
			19 °C	9	0.22 (± 0.0004)	4	1.06 (± 0.002)	5	4.11 (± 0.314)
		LW	outside	11	0.24 (± 0.0007)	5	1.15 (± 0.001)	5	4.70 (± 0.076)
			8.5 °C	3	0.25	3	1.27	3	4.77
			12 °C	11	0.24 (± 0.0001)	7	1.34 (± 0.004)	5	4.83 (± 0.054)
			8.5/15.5 °C	12	0.22 (± 0.0002)	8	1.10 (± 0.000)	9	4.04 (± 0.061)
			15.5 °C	15	0.23 (± 0.0002)	11	1.16 (± 0.005)	12	4.14 (± 0.090)
			19 °C	7	0.23 (± 0.0002)	2	1.13	2	4.46

Table 40, continued.

				WLIII		WHATCH	
FS	Sex	WM	Temp.	N	Mean (± SE)	N	Mean (± SE)
low	♂	SW	outside	20	9.06 (± 0.111)	20	11.51 (± 0.441)
			8.5 °C	25	9.04 (± 0.051)	25	11.06 (± 0.205)
			12 °C	19	9.23 (± 0.057)	19	10.61 (± 0.693)
			8.5/15.5 °C	24	8.91 (± 0.013)	24	10.17 (± 0.610)
			15.5 °C	19	9.01 (± 0.144)	18	11.08 (± 0.175)
			19 °C	25	8.28 (± 0.122)	26	9.82 (± 0.302)
	♀	SW	outside	27	9.21 (± 0.027)	27	12.15 (± 0.231)
			8.5 °C	23	8.99 (± 0.059)	23	10.35 (± 0.338)
			12 °C	17	9.61 (± 0.175)	17	11.37 (± 0.780)
			8.5/15.5 °C	18	9.11 (± 0.048)	18	10.50 (± 0.248)
			15.5 °C	23	9.21 (± 0.080)	24	11.80 (± 0.194)
			19 °C	9	9.51 (± 0.360)	9	11.18 (± 0.420)
high	♂	SW	outside	24	10.87 (± 0.536)	24	14.16 (± 0.718)
			8.5 °C	29	12.75 (± 0.134)	29	14.84 (± 0.310)
			12 °C	29	12.90 (± 0.117)	29	15.19 (± 0.177)
			8.5/15.5 °C	16	12.41 (± 0.142)	16	14.02 (± 0.399)
			15.5 °C	9	12.70 (± 0.194)	9	14.28 (± 0.366)
			19 °C	10	10.97 (± 0.225)	10	13.13 (± 0.555)
		LW	outside	6	11.63 (± 0.407)	6	14.90 (± 0.448)
			8.5 °C	1	12.56	1	16.26
			12 °C	7	13.49 (± 0.393)	7	16.49 (± 0.406)
			8.5/15.5 °C	6	12.70 (± 0.098)	6	15.43 (± 0.638)
			15.5 °C	16	13.31 (± 0.267)	16	16.36 (± 0.385)
			19 °C	6	11.31 (± 0.492)	6	14.50 (± 0.513)
	♀	SW	outside	14	11.94 (± 0.167)	14	15.97 (± 0.486)
			8.5 °C	30	13.18 (± 0.100)	30	15.94 (± 0.426)
			12 °C	13	13.77 (± 0.218)	13	16.33 (± 0.371)
			8.5/15.5 °C	20	12.91 (± 0.083)	20	15.14 (± 0.240)
			15.5 °C	8	14.58 (± 0.340)	8	17.88 (± 0.516)
			19 °C	9	11.59 (± 0.293)	9	14.13 (± 0.909)
		LW	outside	12	12.44 (± 0.076)	12	17.06 (± 0.094)
			8.5 °C	3	13.32	3	17.34
			12 °C	11	13.51 (± 0.177)	11	17.50 (± 0.300)
			8.5/15.5 °C	15	13.36 (± 0.133)	15	16.41 (± 0.258)
			15.5 °C	19	13.85 (± 0.395)	19	17.67 (± 0.749)
			19 °C	7	12.43 (± 0.493)	7	16.48 (± 0.953)

Table 41. *Calathus melanocephalus*: adult weights six weeks after hatching and kept at two food-supply levels and six temperatures in 1983/1984. FS: food-supply; WM: wing-morph; N: number of beetles weighed; WHATCH: hatching weight; WMIN: minimum weight; WMAX: maximum weight; RMAX: maximum weight increase (WMAX/WHATCH).

				Temperature					
				Outside		8.5 °C		12 °C	
FS	Sex	WM	Weight	N	Mean (± SE)	N	Mean (± SE)	N	Mean (± SE)
low	♂	SW	WHATCH	13	12.09 (± 0.437)	16	11.40 (± 0.399)	14	11.49 (± 0.524)
			WMIN	13	13.03 (± 0.741)	16	12.07 (± 0.596)	14	12.89 (± 0.560)
			WMAX	13	16.82 (± 0.669)	16	14.86 (± 0.506)	14	15.85 (± 0.838)
			RMAX	13	1.39 (± 0.040)	16	1.30 (± 0.022)	14	1.38 (± 0.033)
	♀	SW	WHATCH	23	12.16 (± 0.475)	5	11.39 (± 1.243)	10	12.53 (± 0.344)
			WMIN	24	13.65 (± 0.705)	5	11.29 (± 2.897)	10	14.13 (± 0.637)
			WMAX	24	19.23 (± 0.805)	5	15.71 (± 1.732)	10	19.23 (± 0.767)
			RMAX	23	1.59 (± 0.054)	5	1.38 (± 0.108)	10	1.54 (± 0.076)
high	♂	SW	WHATCH	19	14.44 (± 0.885)	28	14.83 (± 0.488)	30	15.21 (± 0.360)
			WMIN	19	15.95 (± 1.000)	29	14.91 (± 0.819)	30	16.29 (± 0.536)
			WMAX	19	19.25 (± 1.019)	29	18.63 (± 0.575)	30	19.87 (± 0.422)
			RMAX	19	1.34 (± 0.029)	28	1.26 (± 0.017)	30	1.31 (± 0.024)
		LW	WHATCH	5	15.13 (± 1.227)	1	16.26	7	16.49 (± 0.959)
			WMIN	5	16.39 (± 1.599)	1	16.10	7	17.15 (± 0.645)
			WMAX	5	20.01 (± 1.877)	1	18.66	7	21.58 (± 1.427)
			RMAX	5	1.32 (± 0.074)	1	1.15	7	1.31 (± 0.069)
	♀	SW	WHATCH	13	16.08 (± 0.806)	31	15.92 (± 0.554)	12	16.39 (± 0.755)
			WMIN	13	18.69 (± 0.827)	31	17.70 (± 0.788)	12	17.95 (± 0.986)
			WMAX	13	24.29 (± 1.417)	31	22.56 (± 0.840)	12	23.62 (± 1.224)
			RMAX	13	1.51 (± 0.064)	31	1.42 (± 0.028)	12	1.44 (± 0.041)
		LW	WHATCH	11	17.07 (± 0.403)	3	17.34	11	17.50 (± 0.670)
			WMIN	11	19.45 (± 0.755)	3	18.63	11	18.79 (± 1.571)
			WMAX	11	25.34 (± 1.001)	3	23.98	11	25.18 (± 0.739)
			RMAX	11	1.49 (± 0.058)	3	1.38	11	1.44 (± 0.035)

are given in table 40. These clearly illustrate the effect of both food-supply, sex and wing-morph on the weights of fully grown larvae and freshly hatched adult beetles.

In general freshly hatched beetles reared at a high food-supply level were significantly heavier than those reared at a low food-supply level: the mean hatching weights (WHATCH) of beetles of the first group varied between 13.13 and 17.88 mg, whereas those of the low food-supply group were between 9.82 and 12.15 mg. At both food-supply levels females weighed more than males, but this

Table 41, continued.

				Temperature					
				8.5/15.5 °C		15.5 °C		19 °C	
FS	Sex	WM	Weight	N	Mean (± SE)	N	Mean (± SE)	N	Mean (± SE)
low	♂	SW	WHATCH	17	10.80 (± 0.485)	10	11.15 (± 0.523)	9	10.66 (± 0.601)
			WMIN	17	11.94 (± 0.697)	10	12.64 (± 0.439)	9	11.43 (± 0.458)
			WMAX	17	15.38 (± 0.785)	10	15.72 (± 0.691)	9	15.13 (± 0.936)
			RMAX	17	1.42 (± 0.044)	10	1.42 (± 0.091)	9	1.39 (± 0.069)
	♀	SW	WHATCH	11	10.80 (± 0.400)	11	12.00 (± 0.525)	1	11.11
			WMIN	11	13.19 (± 0.538)	11	13.67 (± 0.614)	1	11.99
			WMAX	11	17.17 (± 0.906)	11	18.85 (± 1.112)	1	20.45
			RMAX	11	1.58 (± 0.077)	11	1.57 (± 0.081)	1	1.84
high	♂	SW	WHATCH	15	14.08 (± 0.682)	9	14.36 (± 0.759)	8	13.22 (± 1.096)
			WMIN	16	15.22 (± 0.660)	9	15.57 (± 0.805)	8	13.00 (± 1.121)
			WMAX	16	19.10 (± 0.652)	9	19.03 (± 1.329)	8	17.50 (± 1.931)
			RMAX	15	1.36 (± 0.050)	9	1.33 (± 0.083)	8	1.32 (± 0.085)
		LW	WHATCH	5	15.78 (± 1.240)	17	16.17 (± 0.660)	4	15.03 (± 1.125)
			WMIN	5	16.38 (± 1.140)	17	16.57 (± 0.686)	4	14.82 (± 2.196)
			WMAX	5	20.45 (± 1.497)	17	20.70 (± 0.950)	4	19.23 (± 1.783)
			RMAX	5	1.30 (± 0.093)	17	1.28 (± 0.042)	4	1.28 (± 0.101)
	♀	SW	WHATCH	20	15.14 (± 0.485)	8	17.88 (± 1.010)	7	14.72 (± 1.069)
			WMIN	20	17.31 (± 0.656)	8	19.37 (± 0.679)	7	15.32 (± 0.602)
			WMAX	20	22.31 (± 0.818)	8	24.10 (± 1.281)	7	21.11 (± 0.946)
			RMAX	20	1.47 (± 0.038)	8	1.35 (± 0.050)	7	1.44 (± 0.086)
		LW	WHATCH	14	16.56 (± 0.484)	15	17.91 (± 1.003)	7	16.48 (± 1.469)
			WMIN	14	18.08 (± 0.564)	15	18.91 (± 1.084)	7	16.59 (± 1.470)
			WMAX	14	23.42 (± 0.711)	15	24.99 (± 1.298)	7	23.29 (± 1.605)
			RMAX	14	1.42 (± 0.048)	15	1.40 (± 0.081)	7	1.42 (± 0.060)

Identical trends were found when comparing the minimum and maximum weights (WMIN and WMAX respectively) of beetles during six weeks after hatching and kept with excess food (table 41). The mean maximum weight increase (RMAX = WMAX/WHATCH) varied between 1.25 and 1.60 and values for males were generally smaller (1.26-1.42) than those for females (1.35-1.59) reared at the same food-supply level and under similar temperature conditions ($RMAX_{males} < RMAX_{females}$).

For both males and females the maximum weight increases were smaller at

Table 42. *Calathus*: adult weights of long winged beetles six weeks after hatching at a high food-supply level and a temperature of 15.5 °C in 1983/1984. Acronyms: see table 41.

		cinctus		*melanocephalus*		*mollis*	
Sex	weight	N	Mean (± SE)	N	Mean (± SE)	N	Mean (± SE)
males	WHATCH	18	14.75 (± 0.760)	13	15.43 (± 0.684)	26	16.04 (± 0.492)
	WMIN	18	13.96 (± 0.802)	13	16.42 (± 0.928)	26	15.72 (± 0.533)
	WMAX	18	19.60 (± 0.748)	13	20.44 (± 0.719)	26	20.41 (± 0.743)
	RMAX	18	1.33 (± 0.038)	13	1.33 (± 0.042)	26	1.28 (± 0.027)
females	WHATCH	29	16.88 (± 0.671)	14	17.38 (± 0.564)	24	19.45 (± 0.433)
	WMIN	29	16.36 (± 0.874)	14	17.73 (± 0.881)	24	19.60 (± 0.483)
	WMAX	29	23.80 (± 0.997)	14	23.65 (± 0.902)	24	26.38 (± 0.766)
	RMAX	29	1.41 (± 0.027)	14	1.36 (± 0.043)	24	1.36 (± 0.025)

high food-supply levels (1.26-1.36 for males and 1.35-1.51 for females) than at low food supply levels (1.30-1.42 and 1.38-1.59) under similar temperature conditions ($\mathrm{RMAX}_{\text{high food-supply}} < \mathrm{RMAX}_{\text{low food-supply}}$).

At the high food-supply level for both males and females the maximum weight increases generally were smaller for long winged beetles (1.28-1.31 and 1.38-1.49 for males and females respectively) than for short winged ones (1.26-1.36 and 1.35-1.51 respectively) reared under similar conditions ($\mathrm{RMAX}_{\text{long winged}} < \mathrm{RMAX}_{\text{short winged}}$).

Data for long winged offspring of *Calathus cinctus* and *C. mollis* showed similar trends when comparing the effects of temperature, food-supply and weight (table 42). As far as the tested populations are concerned, clear differences in hatching weight exist between the species for both males and females: $\mathrm{WHATCH}_{cinctus} < \mathrm{WHATCH}_{melanocephalus} < \mathrm{WHATCH}_{mollis}$. This trend is reflected in their body dimensions (Aukema, 1990a).

DISCUSSION

Development times, growth and mortality of eggs, larvae and pupae depend on many biotic and abiotic factors. In this study it is shown that environmental factors such as temperature and food-supply (i.e. the quantity of food) are very important in this respect, but there may be more, as for instance quality of food and moisture of the rearing substrate during larval development.

The data presented by Van Dijk & Den Boer (1992), who published data on the survival of eggs and the mortality during development of short winged *Calathus melanocephalus*, show that both temperature and substrate moisture are

Table 43. *Calathus melanocephalus*: mean development times (larva-adult) of short winged beetles at two food-supply levels and three temperatures in two different studies. Sources: A, Van Dijk (1994); B, this study.

		Low food-supply		High food-supply	
Sex	Temperature	A	B	A	B
males	8.5 °C	301.9	259.2	294.9	235.8
	15.5 °C	185.1	148.8	135.0	133.1
	outside	274.2	259.2	274.6	252.3
females	8.5 °C	285.3	327.3	291.9	237.3
	15.5 °C	190.7	152.3	149.7	130.3
	outside	277.3	262.0	270.9	249.6

important limiting factors for the survival of larvae of this species. Medium moisture conditions of the substrate (65 % water content) combined with relatively low temperatures (8.5-15.5 °C) resulted in a high survival. In this study no special attention was paid to the substrate moisture, but the relatively low total mortality at both 8.5 and 12 °C (20.2 and 15.4 %, respectively) indicates that the rearing conditions were more favourable than those used in the experiments included in Van Dijk and Den Boer (1992), who experienced mortalities of about 28 and 34 % under the most favourable conditions at similar temperatures.

This means that it will be quite ambiguous to compare this work with the results of apparently similar studies. Indeed, the data presented by Van Dijk (1994), who reared offspring of short winged *Calathus melanocephalus* under three temperature conditions (constant temperatures of 8.5 and 15.5 °C and outside conditions) and two food-supply levels (2-3 and >8 mg/2 days), differ substantially from the data presented here, although the general trend is the same (table 43). Van Dijk (1994) only found a significant difference in total development time (larva-adult) between low and high amounts of food at 15.5 °C. Obviously, at lower temperatures the effect of food shortage is less severe than at higher temperatures. The same trend is found in the data presented here (table 43) and this is reflected in the observed mortality rates, which are lowest at 8.5 °C and under outside conditions (table 37).

The high mortality found under outside conditions can be explained by the results of Van Dijk & Den Boer (1992), who found increasing mortalities at both temperatures lower than 8.5 °C and higher than 15.5 °C. The first condition occurs frequently in autumn and the second one is common in September when first instar larvae hatch, and in April/May when third instar larvae pupate. In both cases the mortality will be high, in particular under wet soil conditions.

In general the mortality among first instar larvae will be relatively high, caused by the transfer of the larvae at the start of the experiment and by handling this vulnerable stage during weighing. The availability of food immediately after hatching is also an important condition to keep the young larvae alive. The relatively high mortality among third instar larvae reared under less favourable conditions such as high temperatures or a low food-supply can be explained by the fact that their development last longer and that they had already also experienced less favourable conditions in early stages as well.

The hatching weights of short winged *Calathus melanocephalus* at the low food-supply level (table 40) are in accordance with the data presented by Van Dijk (1994: table 2): 10.35-12.15 mg against 10.31-12.26 mg and the two data sets show only very small differences between males and females and between temperatures. At the high food-supply level, however, in this study the hatching weights of short winged phenotypes were considerably higher than those estimated by Van Dijk: 14.16-17.88 mg against 11.49-15.82 mg. These differences might be due to differences in quantity and/or quality of the food, but the possibility that in this respect long winged genotypes with short wings differ from short winged genotypes in this respect cannot be excluded. A comparison between the data on weight increase after hatching (table 41: WMIN, WMAX) with data of Van Dijk (1994: table 6) is not possible, because different methods were used. Moreover, the weight range given by Van Dijk for beetles from the field (18-24 mg) is not supported by his own data on 'Field' beetles, which show a lot of variation and indicate a much wider range (mean values of 14,75-16,18 mg for males and 19,23-19,97 for females, respectively).

Food shortage during larval development may only be compensated partly during adult life. This can be explained by the fact that body weight is related to body dimensions, which physically limit the gain of weight, for instance for building up fat bodies or ovarian development.

The higher weight of both long winged males and females in *Calathus melanocephalus* is not only due to the presence of well-developed wings, but also goes with larger body dimensions of long winged beetles (Aukema, 1990a). The higher fecundity of long winged females thus may at least partly be attributed to their higher body weights.

After breeding seasons with relatively high temperatures and a relatively high food-supply in populations of *Calathus melanocephalus*, there will be a relatively high dispersal potential, as expressed in the presence of a large proportion of long winged individuals. Whether or not this will actually lead to a high level of dispersal (many flying beetles) further depends on favourable conditions for building up flight muscles and on weather conditions that enable actual flight.

CONCLUSIONS

1. Development times of *Calathus cinctus*, *C. melanocephalus*, and *C. mollis* are strongly influenced by temperature: shorter development times were found at higher temperatures and longer ones at lower temperatures.
2. In all three species no general differences in development time between males and females were found.
3. In both *Calathus cinctus* and *C. melanocephalus* no simple relation between wing morph, temperature and total development time was found.
4. For long winged genotypes of *Calathus melanocephalus* it is concluded that:
   a. long winged beetles of both sexes develop faster and are heavier than short winged ones
   b. food-supply strongly influences development time, mortality, and growth rate: shorter development times, a lower mortality, and higher hatching weights at a higher food-supply.
   c. females weigh more than males.
   d. the maximum weight increase of adult beetles is larger at a lower food-supply level and larger in females than in males.
   e. the maximum weight increase of short winged phenotypes is larger than that of long winged phenotypes.
5. For both males and females long winged adults of *Calathus cinctus* are lighter and those of *C. mollis* are heavier than those of *C. melanocephalus*.

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REFERENCES

Aukema, B., 1990a. Taxonomy. life history and distribution of three closely related species of the genus Calathus (Coleoptera: Carabidae).- *Tijdschrift voor Entomologie* 133: 121-141.

Aukema, B., 1990b. Winglength determination in two wing-dimorphic Calathus species.- *Hereditas* 113: 189-141

Aukema, B., 1991. Fecundity in relation to wing-morph of three species of the melanocephalus group of the genus Calathus (Coleoptera: Carabidae).- *Oecologia* 87:

118-126.

Boye Jensen, L., 1990. Effect of temperature on the development of the immature stages of Bembidion lampros (Coleoptera: Carabidae).- *Entomophaga* 35: 277-281.

Dijk, Th. S. van, 1994. On the relationship between food, reproduction and survival of two carabid beetles: Calathus melanocephalus and Pterostichus versicolor.- *Ecological Entomology* 19: 263-270.

Dijk, Th. S. van & P. J. den Boer, 1992. The life histories and population dynamics of two carabid beetles. I. Fecundity and the mortality of immature stages.- *Oecologia* 90: 340-352.

Ernsting G. & F. A. Huyer, 1984. A laboratory study on temperature relations of egg production and development in two related species of carabid beetle.- *Oecologia* 62: 361-367.

Heessen, H. J. L., M. A. Wildschut & A. M. H. Brunsting, 1982. Duration of developmental stages and timing of the end of the reproductive season of Pterostichus oblongopunctatus (Fabricius) (Col., Carabidae) and Philonthus decorus (Gravenhorst) (Col., Staphylinidae).- *Netherlands Journal of Zoology* 32: 49-62.

Kůrka, A., 1972. Bionomy of the Czechoslovakian species of the genus Calathus Bon., with notes on their rearing (Coleoptera: Carabidae).- *Věstník Československé Společnosti Zoologické* 36: 101-114.

McCullagh P. & J. A. Nelder, 1989. *Generalized linear models (2nd ed.)*: i-xix, 1-511. Chapman and Hall, London, New York.

Mols, P. J. M., Th. S. van Dijk & Y. Jongema, 1981. Two laboratory techniques to separate eggs of carabids from a substrate.- *Pedobiologia* 21: 500-501.

Nelemans, M. N. E., 1987. On the life-history of the carabid beetle Nebria brevicollis (F.).- *Netherlands Journal of Zoology* 37: 26-42.

Nelemans, M. N. E., 1988. Surface activity and growth of larvae of Nebria brevicollis (F.) (Coleoptera, Carabidae).- *Netherlands Journal of Zoology* 38: 74-95.

Roff, D. A., 1986. The evolution of wing dimorphism in insects.- *Evolution* 40: 1009-1020.

Thiele, H.-U., 1977. *Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour*: i-xvii, 1-369. Springer, Berlin.

VI. FLIGHT AND FLIGHT MUSCLE DEVELOPMENT IN THREE CLOSELY RELATED SPECIES OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE)

ABSTRACT

Long winged males and females of the wing-dimorphic *Calathus cinctus* and *C. melanocephalus*, as well as beetles of the monomorph macropterous *C. mollis* were able to built up functional flight muscles and were capable of flight under laboratory conditions. Flight activity in the field, however, was only observed in *C. cinctus*. In the latter species both building up flight muscles and flight occurred before breeding, but mating and even ovarian development may occur in the flight period.

These findings are discussed in relation to the dispersal strategies of the species.

Key words: Carabidae, *Calathus*, *cinctus*, *melanocephalus*, *mollis*, Flight muscle development, Flight, Dispersal.

INTRODUCTION

The carabid beetles *Calathus (Neocalathus) cinctus* Motschulsky (= *C. (N.) erythroderus* Gemminger & Harold) and *C. (N.) melanocephalus* (Linnaeus) are both wing-dimorphic and *C. (N.) mollis* (Marsham) is always macropterous. Information on their taxonomy, life history and distribution is given in Aukema (1990a), fecundity in relation to wing-morph is treated in Aukema (1991), and data on wing dimensions are given in Den Boer & al., (1980: only *C. cinctus*), Desender (1989) and Aukema (1990a, 1990b). Brachypterous beetles of the three species always have strongly reduced hind wings and are not able to fly, whereas macropterous beetles have well-developed hind wings. Capability of flight, however, among others depends on their relative wing size, which may be well estimated by the quotient of wing surface (length of wing x width of wing) and elytrum surface (length of elytrum x width of elytrum) (Den Boer, 1977). Whether or not long winged beetles of wing-dimorphic and macropterous species with sufficiently large wings will actually fly is finally determined by the possession of fully developed wing muscles and suitable weather conditions (Van Huizen, 1979).

Den Boer (1977) listed carabid beetles according to their dispersal power. Species showing frequent flight activities were classified as having a high dispersal power (B-species); they showed large relative wing sizes (> 1.7). Species with smaller relative wing sizes (< 1.5) were included as A-species, a group with a low dispersal power. The remaining species were classified as species with uncertain dispersal power (C-species).

A lot of variation in the presence of flight muscles exists among wing-dimorphic and macropterous species of Carabidae, which is complicated by the phenomenon of a seasonal flight muscle-dimorphism, i.e. only part of the long winged beetles will develop functional flight muscles temporarily (Van Huizen, 1979; Desender, 1989). Nelemans (1987) showed that flight muscle development in the autumn breeding carabid beetle *Nebria brevicollis* (Fabricius) is induced by favourable environmental conditions, as for instance a high amount of available food during larval development and short day conditions, whereas Van Schaick Zillesen & Brunsting (1984) suggested the opposite in the spring breeder *Pterostichus oblongopunctatus* (Fabricius), i.e. the development of flight muscles in response to unfavourable environmental conditions, as for instance food shortage during larval development and a photoperiod deviating from natural conditions.

Suitable weather conditions for flight of carabid beetles were defined by Van Huizen (1979) in terms of temperature (daily maximum temperatures above 16 °C), rainfall ($\leq$ 0.1 mm per day) and wind velocity ($\leq$ 7 m/s).

Flight activity under field conditions can be detected either directly by making flight observations in the field, or indirectly by sampling flying individuals in light traps or window traps, or by sampling drowned dispersers washed ashore. Field observations of flying specimens of these species, however, were never recorded quantitatively. The identity of the few published catches of *Calathus melanocephalus* in light traps (Honek & Pulpán 1983, Kádár & Szél, 1989) is questionable, because of confusion of the three species concerned in the past (see Aukema, 1990a). The same applies to material of *C. melanocephalus* washed ashore on the southwestern coast of Finland (Palmén, 1944).

As no reliable data existed on actual flight, *Calathus melanocephalus* was classified as a species with a relatively low dispersal power (Den Boer, 1977: A-species) or as a species with an uncertain dispersal power (Aukema, 1990a: C-species). Development of functional flight muscles in *Calathus melanocephalus* was observed by Desender (1989), and a mean relative wing surface of 3.08 and 2.82 in males and females respectively (calculated according Den Boer, 1977 from the data presented in Aukema, 1990a) is considered sufficient for flight.

Calathus cinctus was caught in window traps in the surroundings of Wijster, Drenthe (Van Huizen, 1979, 1980a; Den Boer et al., 1980) and was consequently classified as a species with a high dispersal power (Van Dijk, 1986: B-species). The mean relative wing surface (calculated as for *C. melanocephalus*) was 2.71 in males and 2.62 in females.

Although being invariably macropterous, flight activity of *Calathus mollis* was never mentioned, and consequently this species was also classified as a species with an uncertain dispersal power (Aukema, 1990a: C-species). Desender (1989) listed *C. mollis* as a species without flight muscle development and uncertain flight capacity. The mean relative wing surfaces of 2.67 and 2.63 for males and females respectively (calculated as for *C. melanocephalus*), however, are considered sufficient for flight.

MATERIAL AND METHODS

Window traps

Flight activity of carabids was monitored by means of window traps as described by Den Boer (1971), Haeck (1971) and Meijer (1971), and modified by Van Huizen (1980b).

Wing-dimorphic populations of *Calathus cinctus* with a high proportion of long winged beetles at Nuil (Ruinen, province of Drenthe) and Schoongelegen (Dwingeloo, province of Drenthe) (see Aukema, 1990a) were sampled with window traps between 1973 and 1980 as part of the routine sampling program of the Biological Station, Wijster (see Van Huizen, 1979).

A wing-dimorphic population of *Calathus melanocephalus* in the recently reclaimed polder Oost-Flevoland (Ecological Nature Reserve, see Aukema, 1990b for data on wing-morph frequencies) was sampled during four successive years (1981-1984) with window traps.

Trapped beetles were dissected to establish flight muscle development, age and development of reproductive organs.

Flight muscle development

Flight muscle development was studied by dissecting beetles from field samples of *Calathus cinctus* and *C. melanocephalus* collected in pitfalls at Schoongelegen in the years 1973-1978 (see Aukema, 1990a), samples of *C. cinctus* and *C. melanocephalus* collected in pitfalls at the West Frisian Island of Texel in 1986-1987, a sample of *C. mollis* collected by hand at Haamstede (Schouwen, province of Zeeland) in 1989 (see Aukema, 1990b), and samples of *C. melanocephalus* collected in pitfalls at Oost-Flevoland, the Ecological Nature Reserve, in 1982-1984. Further, a small number of laboratory bred beetles were dissected, especially of *C. cinctus* and *C. mollis*. Direct and indirect flight muscles were examined and classified according to Tietze (1963). Beetles with well-developed direct and indirect flight muscles in the classes IV and V (almost full-grown and full-grown muscles respectively) were assumed to be able to fly (see also Nelemans, 1987).

Table 44. Ecological Nature Reserve, Oost-Flevoland. Number of carabids caught in window traps. Nomenclature according to Turin (1990). 1981: 2 traps, operated 3 June-30 October; 1981: 4 traps, 22 April-28 October; 1983: 4 traps, 22 April-10 November; 1984: 4 traps, 14 April-25 October. DG: dynamic group; D: wing-dimorphic; M: macropterous.

		Year				
Species	DG	1981	1982	1983	1984	Total
Acupalpus exiguus (Dejean)	M				1	1
Agonum marginatum (Linnaeus)	M			1		1
Agonum moestum (Duftschmid)	D			1		1
Agonum muelleri (Herbst)	M			1		1
Agonum thoreyi Dejean	D			1		1
Amara aenea (De Geer)	M		5	24	62	91
Amara anthobia (A. Villa & G.B. Villa)	M				1	1
Amara apricaria (Paykull)	M	1				1
Amara aulica (Panzer)	M		7	140	13	160
Amara bifrons (Gyllenhal)	M	1			1	2
Amara communis (Panzer)	M		5		21	26
Amara convexiuscula (Marsham)	M	1	1			2
Amara familiaris (Duftschmid)	M		33	16	104	153
Amara lucida (Duftschmid)	M		3		7	10
Amara lunicollis (Schiødte)	M		5	5	10	20
Amara majuscula Chaudoir	M			3		3
Amara plebeja (Gyllenhal)	M		1			1
Amara similata (Gyllenhal)	M		1	1	11	13
Amara spreta Dejean	M		1			1
Anisodactylus binotatus (Fabricius)	M			1	1	2
Bembidion guttula (Fabricius)	D				7	7
Bembidion properans (Stephens)	D			3	6	9
Bembidion tetracolum Say	D			1		1
Bradycellus harpalinus (Serville)	D	2		3	4	9
Bradycellus verbasci (Duftschmid)	M	21	7	9	6	43
Clivina fossor (Linnaeus)	D		2	2	2	6
Dromius angustus Brullé	M				1	1
Harpalus affinis Schrank	M			1	3	4
Harpalus rufipes De Geer	M			1	1	2
Harpalus rufitarsus Duftschmid	M		1	1	1	3
Loricera pilicornis (Fabricius)	M		1			1
Pterostichus nigrita (Paykull)	M				1	1
Pterostichus vernalis (Panzer)	M			1	1	2
Pterostichus versicolor (Sturm)	M			1	1	2
Trechus obtusus Erichson	D		1		1	2
Trechus quadristriatus (Schrank)	M	4	1	1		6
Trichocellus placidus (Gyllenhal)	M				3	3
Number of specimens		30	75	218	270	593
Number of species		6	16	22	25	37

Flight experiments

Flight capability of laboratory bred males and females of the three species was tested by means of tethered flight experiments in the laboratory, as described by Nelemans (1987): beetles were hung up with a small thread, stuck to the pronotum with a small clump of bee wax. The beetles were tested for at least 30 minutes under an electric light bulb (60 watt) in a slight air current produced by a hair-dryer. A small part of the non-flyers, especially of *Calathus cinctus* and *C. mollis* were dissected to establish their flight muscle development.

Males and females of *Calathus melanocephalus* reared at three temperatures (constant temperatures of 15.5 and 19 °C, and outside conditions) and a high food-supply level (see Chapter 5 for rearing conditions) were tested. Furthermore beetles of *Calathus cinctus, C. melanocephalus* and *C. mollis* reared at a constant temperature of 15.5 °C and natural daylength (adjusted once a week) and food ad libitum (see Chapter 5 for rearing conditions) were tested at more or less regular time intervals.

Development times from egg to adult of all tested beetles were established (see Chapter 5), and they were weighed twice a week during larval development and after hatching (see Chapter 5). Development times and weights of flyers and non-flyers were compared to establish possible differences in development time, hatching weight (WHATCH), and weight increase of adult beetles (WMIN, WMAX, RMAX) between the two groups.

RESULTS

Window traps

Catches of females of *Calathus cinctus* between 1969 and 1977 in window traps, operated as part of the regular sampling program of the Biological Station, Wijster, were already published by Van Huizen (1979) and Den Boer & al. (1980). In this period 4 males and 8 females were captured between 21 May and 14 August. Two of the females were inseminated and one was carrying ripe eggs in the ovaries. No flight activity was recorded during the oviposition period (late August until November, see Aukema, 1990a, 1991). One of the females had already reproduced at least during one previous breeding season (Van Huizen, 1979). The relative wing size of beetles captured in window traps showed a similar distribution to those collected in pitfall traps (Den Boer & al., 1980).

At the Ecological Nature Reserve, Oost-Flevoland, a total of 593 carabids belonging to 37 species were captured in the window traps in the years 1981-1984 (table 44), but no specimens of *Calathus melanocephalus* were trapped, as was

Table 45. *Calathus cinctus* and *C. melanocephalus*. Flight muscles of beetles sampled with pitfalls at Schoongelegen (Dwingeloo, province of Drenthe) in 1973-1978, and at the Ecological Nature Reserve, Oost-Flevoland in 1982-1984. SW: short winged; LW: long winged; +: well-developed flight muscles; 0: flight muscles reduced or absent; -: no observations.

			Month															
			<<		Jun		Jul		Aug		Sep		Oct		>>		Total	
Species	Sex	Morph	+	0	+	0	+	0	+	0	+	0	+	0	+	0	+	0
Schoongelegen																		
cinctus	males	SW	-	-	-	2	-	6	-	10	-	8	-	1	-	1	-	28
		LW	-	-	4	9	5	9	-	22	-	31	-	12	-	4	9	87
	females	SW	-	-	-	6	-	3	-	10	-	5	-	3	-	3	-	30
		LW	-	2	14	13	3	9	3	21	-	12	-	6	-	6	20	69
melanocephalus	males	SW	-	1	-	2	-	16	-	54	-	81	-	21	-	4	-	179
		LW	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	females	SW	-	6	-	12	-	21	-	35	-	37	-	23	-	3	-	137
		LW	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2
Oost-Flevoland																		
melanocephalus	males	SW	-	-	-	2	-	9	-	76	-	42	-	2	-	11	-	142
		LW	-	-	-	-	-	1	-	29	-	9	-	1	-	3	-	43
	females	SW	-	-	-	1	-	10	-	110	-	34	-	11	-	14	-	180
		LW	-	-	-	-	1	-	-	70	-	17	-	8	-	8	1	104

expected. It is not known whether this is due to the absence of flight activities in this species, or to specific flight habits which reduce the chance of flying beetles being caught in window traps.

Flight muscle development

Field samples of *Calathus cinctus* and *Calathus melanocephalus* from a mixed population at Schoongelegen consisted of both short and long winged *C. cinctus* (77 and 75 % long winged in males and females respectively), and of mainly short winged *C. melanocephalus* (no long winged males and 2 long winged females only).

Flight muscle development of beetles from these populations sampled in pitfalls between 1973 and 1979 is given in table 45. In both short winged males and females of *Calathus cinctus* and *C. melanocephalus* no flight muscle development was observed. In long winged *Calathus cinctus* well developed flight muscles were only found before breeding in late June, July and early August. The first specimens with well developed flight muscles were trapped on 21 June, and the last ones on 13 August. About half of the males trapped in both June and July possessed well developed flight muscles, whereas in August none of the 22 males caught did so. About 50% of the females caught in June possessed well developed flight muscles, but this figure decreases to 33% in July and 12.5% in August. Two of the females with well developed flight muscles, collected on 19 July and 13 August respectively, carried developed eggs, six of them were inseminated, and one of them had reproduced already at least once.

Field samples of *Calathus melanocephalus* collected in 1982-1984 from a population at the Ecological Nature Reserve, Oost-Flevoland consisted of both short and long winged beetles (21 and 30% long winged in males and females respectively, see Aukema, 1990b). A large number of these beetles were dissected and their flight muscle development is given in table 45. In short winged beetles no flight muscle development was found, whereas none of the 43 long winged males and only one of the 103 long winged females possessed well-developed flight muscles. The female concerned was a young specimen trapped on 7 July, showing no ovarian development at all.

No specimens with well-developed flight muscles were found in samples of *Calathus cinctus* (11♂, 11 ♀ long winged; 20 ♂, 20 ♀ short winged) and of *C. melanocephalus* (20 ♂, 20 ♀ short winged; 7 ♂, 20 ♀ long winged) collected at Texel between 6 May and 19 December. A sample of long winged *C. mollis*, collected by hand in the dunes near Haamstede on 10 June (20 ♂, 20 ♀) contained only one male with full-grown flight muscles.

A small part of laboratory bred beetles of *Calathus cinctus* and *C. mollis* used for tethered flight experiments were dissected as a check on these experiments.

Table 46. *Calathus cinctus* (cin), *C. melanocephalus* (mel) and *C. mollis* (mol). Tethered flight experiments with beetles reared at a high food-supply level or food ad libitum, and kept at 15.5 °C and food ad libitum after hatching. +: positive flight tests; 0: negative flight tests; -: no observations; N: number of beetles (number of flying beetles), used in the experiments.

				Flight tests/period (weeks after hatching)														
				1-3		4-6		7-9		10-12		13-15		16-18		Total		
Species	Group	Start	Sex	+	-	+	-	+	-	+	-	+	-	+	-	+	-	N
High food-supply																		
mel	15.5 °C	14 March	males	1	-	6	25	8	31	1	31	-	26	-	5	16	118	17 (5)
			females	-	3	13	27	9	31	3	36	2	21	1	6	28	124	18 (9)
	19 °C	28 February	males	-	-	-	8	-	9	-	9	-	9	-	3	-	38	4 (-)
			females	-	-	1	12	-	13	1	12	-	9	-	8	2	54	6 (1)
	outside	24 July	males	-	-	-	6	-	6	-	2	-	-	-	-	-	14	3 (-)
			females	-	-	-	18	-	23	1	8	-	-	-	-	1	49	11 (1)
Food ad libitum																		
cin	15.5 °C	15 February	males	-	1	-	12	-	24	-	30	-	20	-	20	-	107	19 (-)
			females	-	1	-	16	2	57	-	34	-	34	-	28	2	170	32 (2)
mel	15.5 °C	14 March	males	-	1	3	9	3	17	-	17	-	19	-	8	6	71	12 (3)
			females	-	-	2	17	1	21	-	20	-	25	-	7	3	90	14 (1)
mol	15.5 °C	15 February	males	-	-	5	37	2	31	1	13	1	13	-	17	9	111	26 (6)
			females	-	-	1	27	2	37	7	10	3	11	2	21	15	106	22 (6)

After 3-4 negative flight tests (7-12 weeks after hatching) 3 males and 6 females of *C. cinctus* were dissected and indeed none of the specimens possessed developed flight muscles. After 1-5 negative flight tests (5-12 weeks after hatching) 12 males and 10 females of *C. mollis* were also dissected. Two of the dissected males possessed fully developed flight muscles (after one and two negative tests respectively), whereas the other 10 males and the 10 females tested did not show any flight muscle development at all.

Flight experiments

Tethered flight was found in all three species and in all groups tested (table 46). In general females tended to fly more frequently than males. Great differences in flight behaviour were observed. Some beetles flew spontaneously at the start of the test and some of these flew continuously until the end of the test (more than 30 minutes), whereas others only flew for a very short period (a few seconds), and after many trials.

In *Calathus cinctus* none of the males and only 2 of the females tested showed tethered flight. In both females flight was restricted to week 7 after hatching.

In *Calathus melanocephalus* most flyers were found in the group reared at 15.5 °C and a high food supply: 29% of the males and 50% of the females showed tethered flight. The number of flying beetles in the group reared at a similar temperature and food ad libitum was about similar in males (25%), but much lower in females (7%). None of the males and only one of the tested females (6 and 11 respectively) among the beetles reared at 19 °C and under outside conditions and a high food-supply showed tethered flight. In the group reared at a high food-supply flight occurred in week 3-10 after hatching in males and in week 5-16 after hatching in females. Especially among females great individual differences in flight were found. In 8 of the 9 flying females flight was restricted to the period between 5 and 8 weeks after hatching, and 3 of those females only flew once between day 23 and 30 after hatching. The 9th female, however, was able to fly no less than 10 times in the period between 5 and 16 weeks after hatching (day 33, 38, 48, 58, 66, 75, 81, 89, 95 and 108). All flying beetles reared at food ad libitum (3 males, 1 female) flew between 5 and 9 weeks after hatching.

In *Calathus mollis* 6 males (23%) and 6 females (27%) showed tethered flight. Five males flew in the period of 5-8 weeks after hatching and number six flew 9-13 weeks after hatching. Females flew 10-16 weeks after hatching with the exception of one early and one late flight at 46 and 125 days after hatching respectively.

Mean development time from egg to adult, and mean hatching weight (WHATCH)

Table 47. *Calathus melanocephalus* and *C. mollis*. Development time (days) of non-flyers and flyers, kept at 15.5 °C and natural daylength with food ad libitum.

		C. melanocephalus		*C. mollis*	
Sex	Group	N	Mean (± SE)	N	Mean (± SE)
males	non-flyers	12	121.7 (± 6.29)	19	108.2 (± 3.22)
	flyers	5	118.4 (± 6.43)	6	107.2 (± 7.16)
females	non-flyers	9	129.3 (± 8.89)	15	108.0 (± 2.80)
	flyers	9	126.5 (± 6.17)	6	112.2 (± 7.10)

and mean weight increase of adult beetles (WMIN, WMAX and RMAX) of non-flying and flying males and females of both *Calathus melanocephalus* and *C. mollis* reared at food ad libitum are given in table 47 and 48 respectively. For both species in both sexes no significant differences between non-flyers and flyers were found either in development time, hatching weight, or in weight increase of adult beetles (Mann-Whitney *U*-test, two-sided, $p<0.05$).

DISCUSSION

Apparently, in the three species studied development (and subsequent autolysis) of flight muscles only takes place before breeding. Since during this period walking activities usually are low the chance to catch beetles with well-developed flight muscles in pitfall traps is correspondingly low, resulting in an underestimation of the number of beetles actually developing functional flight muscles.

It is not surprising that during the routine sampling program of the Biological Station, Wijster, no flight activity of *Calathus melanocephalus* was ever recorded by means of catches in window traps, because the frequency of macropters in the populations sampled was extremely low: 0.23% (Den Boer, 1977: 30,887 specimens examined). Desender (1989) lists a somewhat higher figure of 1.6% (5,455 specimens examined) for Belgian populations, mainly caused by the fact that in his study more unstable habitats, such as meadows and agricultural fields, were included. As during a short period only a limited number of the macropters actually will develop functional flight muscles, which can only be used during suitable weather conditions, the chance of trapping a flying beetle will be extremely low indeed!

On the other hand, the presence of high numbers of macropters in newly

Table 48. *Calathus melanocephalus* and *C. mollis*. Weights (mg) of non-flyers and flyers six weeks after hatching and kept at 15.5 °C and natural daylength with food ad libitum. WHATCH: hatching weight; WMIN: minimum weight; WMAX: maximum weight; RMAX: maximum weight increase (WMAX/WHATCH)

			C. melanocephalus		*C. mollis*	
Sex	Group	Weight	N	Mean (± SE)	N	Mean (± SE)
males	non-flyers	WHATCH	12	16.47 (± 0.875)	20	16.08 (± 0.591)
		WMIN	12	17.04 (± 0.756)	20	15.88 (± 0.672)
		WMAX	12	21.09 (± 1.131)	20	20.51 (± 0.820)
		RMAX	12	1.28 (± 0.047)	20	1.28 (± 0.028)
	flyers	WHATCH	5	15.43 (± 0.810)	6	15.91 (± 1.222)
		WMIN	5	15.40 (± 1.153)	6	15.79 (± 0.973)
		WMAX	5	19.77 (± 2.289)	6	20.28 (± 2.179)
		RMAX	5	1.28 (± 0.136)	6	1.27 (± 0.088)
females	non-flyers	WHATCH	9	17.68 (± 1.170)	16	19.52 (± 0.557)
		WMIN	9	18.64 (± 1.627)	16	19.79 (± 0.632)
		WMAX	9	24.77 (± 1.362)	16	24.58 (± 0.957)
		RMAX	9	1.41 (± 0.138)	16	1.32 (± 0.031)
	flyers	WHATCH	9	18.01 (± 1.479)	6	19.55 (± 0.916)
		WMIN	9	18.82 (± 1.421)	6	19.46 (± 0.829)
		WMAX	9	24.57 (± 2.154)	6	27.46 (± 1.645)
		RMAX	9	1.36 (± 0.059)	6	1.40 (± 0.043)

established populations, implies that flight occurs, and that it is important for (re)colonization of unoccupied habitats. For instance, at a locality in the recently reclaimed polder Oost-Flevoland, which ran dry in spring 1957, 34% of the 152 specimens of *Calathus melanocephalus* trapped between March 1964 and March 1965 were long winged! (Den Boer, 1970). Even higher figures were found in 1968 for small populations at the grounds of the planned Ecological Nature Reserve (5 macropters among 7 specimens), and at an isolated spot at the end of the dyke of the planned Markerwaard, made in 1963 (4 macropters among 9 specimens) (Haeck, 1971). The population at the Ecological Nature Reserve was sampled regularly between 1975 and 1984 (Aukema, 1990a) and through the years showed a fluctuating but relatively high frequency of macropters, varying between 18.5 and 34.2 % in males and between 27.3 and 45.0% in females.

But even under these conditions the chance to trap flying beetles of *Calathus melanocephalus* obviously is rather low. No specimens were caught in window traps operating in the new polders in 1968 and 1969 (Haeck, 1971), and even in the study presented here, where the traps were placed directly within a population with high numbers of macropters, the result was the same. Similar observations were made by Nelemans (1987) for *Nebria brevicollis*.

However, these results are in accordance with the general picture we got about the two species concerned (see Aukema, 1990b). In *Calathus cinctus* the dispersal potential (i.e. the expression of the long winged genotype) is always realized, allowing short-term 'between sites movements', resulting in a high turnover of populations (see the examples of Nuil, Schoongelegen and Texel in Aukema, 1990a). A high level of flight activity is supposed to be essential in this way of life. In *Calathus melanocephalus* the dispersal potential is under environmental control and usually only a small fraction is realized, favouring long-term 'within sites movements', resulting in a low turnover of populations. Therefore, in *Calathus melanocephalus* the level of flight activity is expected to be much lower than in *Calathus cinctus*.

The fact that females of *Calathus cinctus* are able to fly inseminated and/or with developing or even ripe eggs in the ovaries favours their colonizing abilities.

The factors governing flight muscle development still remain obscure, though the results from groups of *Calathus melanocephalus* reared at less favourable temperatures (8.5 and 19 °C) indicate that these circumstances not only suppress the expression of the long winged genotype (Aukema, 1990b), but also the development of functional flight muscles in adult beetles. These results further show that in beetles reared at 15.5 °C neither development time nor weight (either hatching weight or weight increase of adult beetles) discriminate between flyers and non-flyers. Flight muscle development might well be under hormonal control in a way similar to that of the expression of the long winged genotype (Aukema, 1990b), but at this stage of the investigations a genetic determination of the observed flight muscle dimorphism also cannot be excluded.

CONCLUSIONS

Both males and females of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* are able to built up functional flight muscles.

In *Calathus cinctus* flight muscle development and flight were recorded under both field and laboratory conditions, whereas in *Calathus melanocephalus* and *C. mollis* both flight muscle development and flight were only recorded under laboratory conditions. In *C. cinctus* flight muscle development and flight occur before breeding, but mating and ovarian development may already take place during the flight period.

Flyers and non-flyers of both *Calathus melanocephalus* and *C. mollis* did not show differences in development time, hatching weight or weight increase after hatching. In *C. melanocephalus* favourable conditions during larval development may stimulate not only the expression of the long winged genotype, but also the ability of adult beetles to develop flight muscles. The factors influencing flight muscle development in these species are still unknown.

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REFERENCES

Aukema, B., 1990a. Taxonomy, life history and distribution of three closely related species of the genus Calathus (Coleoptera: Carabidae).- *Tijdschrift voor Entomologie* 133: 121-141.

Aukema, B., 1990b. Wing-length determination in two wing-dimorphic Calathus species (Coleoptera: Carabidae).- *Hereditas* 113: 189-202.

Aukema, B., 1991. Fecundity in relation to wing-morph of three closely related species of the melanocephalus group of the genus Calathus (Coleoptera: Carabidae).- *Oecologia* 87: 118-126.

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae).- *Oecologia* 4: 1-28.

Boer, P. J. den, 1971. On the dispersal power of carabid beetles and its possible significance. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 8: 119-137.

Boer, P. J. den, 1977. Dispersal power and survival. Carabids in a cultivated countryside.- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae).- *Entomologia Generalis* 6: 107-134.

Desender, K., 1989. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Dijk, Th. S. van, 1986. Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments.- *Netherlands Journal of Zoology* 36: 413-437.

Haeck, J., 1971. The immigration and settlement of carabids in the new IJsselmeer-Polders. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).-

Miscellaneous Papers Landbouwhogeschool Wageningen 8: 33-52.

Honek, A. & J. Pulpán, 1983. The flight of Carabidae (Coleoptera) to light trap.- *Věstník Československé Společnosti Zoologické* 47: 13-26.

Huizen, T. H. P. van, 1979. Individual and environmental factors determining flight in carabid beetles. In: On the evolution of behaviour in carabid beetles (P. J. den Boer, H.-U. Thiele & F. Weber eds).- *Miscellaneous Papers of the Agricultural University Wageningen* 18: 199-211.

Huizen, T. H. P. van, 1980a. Species of Carabidae in which the occurrence of dispersal by flight of individuals has been shown.- *Entomologische Berichten, Amsterdam* 40: 167-168.

Huizen, T. H. P. van, 1980b. Why not use window traps for collecting Coleoptera and other flying insects?- *Entomologische Berichten, Amsterdam* 40: 131-132.

Kádár, F. & G. Szél, 1989. Carabid beetles (Coleoptera, Carabidae) collected by light traps in apple orchards and maize stands in Hungary.- *Folia Entomologica Hungarica* 50: 27-36.

Meijer, J., 1971. Immigration of arthropods into the new Lauwerszee Polder. In: Dispersal and dispersal power of carabid beetles (P.J. den Boer, ed.).- *Miscellaneous Papers Landbouwhogeschool Wageningen* 8: 53-64.

Nelemans, M. N. E., 1983. Flight-muscle development of the carabid beetle Nebria brevicollis (F.). In: Ecology of carabids: the synthesis of field study and laboratory experiment (P. Brandmayr, P. J. den Boer & F. Weber eds).- *Report 4th Meeting of European Carabidologists:* 45-53.

Nelemans, M. N. E., 1987. Possibilities for flight in the carabid beetle Nebria brevicollis (F.). The importance of food during larval growth.- *Oecologia* 72: 502-509.

Palmén, E., 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor.- *Annales Zoologici Societatis Zoologico-Botanicae Fennicae 'Vanamo'* 10: 1-262.

Schaick Zillesen, P. G. van & A. M. H. Brunsting, 1984. The influence of food quantity and photoperiod during the pre-adult stages on flight muscle development in adult Philonthus decorus (Coleoptera: Staphylinidae) and Pterostichus oblongopunctatus (Coleoptera: Carabidae).- *Entomologia Generalis* 9: 143-147.

Tietze, F., 1963. Untersuchungen über die Beziehungen zwischen Flügelreduktion und Ausbildung des Metathorax bei Carabiden unter besonderer Berücksichtigung der Flugmuskulatur (Coleoptera, Carabidae).- *Beiträge zur Entomologie* 13: 88-167.

Turin, H., 1990. Naamlijst voor de Nederlandse loopkevers (Coleoptera: Carabidae).- *Entomologische Berichten, Amsterdam* 50: 61-72.

VII. GENERAL DISCUSSION

In this thesis different aspects of wing dimorphism in three closely related ground beetle species of the *Calathus melanocephalus*-group, *Calathus cinctus*, *C. melanocephalus* and *C. mollis*, were studied in relation to dispersal by flight. Detailed discussions on material, methods and results were given in the foregoing chapters: taxonomy, nomenclature, life history and distribution in Chapter II, wing morph determination in Chapter III, differences between wing morphs in Chapters IV (fecundity) and V (development time and growth), and flight and flight muscle development in Chapter VI.

Here the discussion will be focused on more general aspects of wing dimorphism: its evolution, genetic basis, environmental control, trade-offs between life history traits and wing development, and maintenance of wing dimorphism.

THE EVOLUTION OF WING DIMORPHISM

Wing reduction is supposed to evolve in favourable, isolated habitats with reduced heterogeneity, both spatial and temporal (Southwood, 1977; Den Boer et al., 1980). In these kinds of 'stable' habitats species can dispense with energetically costly dispersal activity and allocate more energy into reproduction, receiving a fitness advantage (Roff, 1990, 1994). Under these circumstances we may expect that selection will quickly favour the elimination of flight, if not essential (Roff & Fairbairn, 1991). Mountain habitats, for instance, have been considered 'more stable' and also isolated and therefore more suitable for the evolution of brachyptery (Darlington, 1943). Roff (1990) indeed found a significant correlation between the incidence of brachyptery and habitat stability when studying mainly literature data. The method, however, was criticized by Liebherr (1992), who argued that the fact "that all these brachypterous species inhabit a certain type of habitat is due not so much to present day ecological conditions as to the singular event by which their common ancestor became monomorph brachypterous while inhabiting a particular habitat type. Subsequent speciation without further evolution of the flight apparatus or change in habitat preference will lead to correlation of habitat and brachyptery". So, correlation tests assuming each species to represent an independent datum here are quite inappropriate. Extensive comparisons of sister groups alternately characterized by macroptery and brachyptery are the method for testing this process (Liebherr, 1991, 1992; Wagner & Liebherr, 1992).

Isolation may also play an important role in the evolution of flightlessness, because dispersers from isolated habitats will face a higher mortality risk than residents. Especially in Coleoptera the high proportion of flightless species on islands was noticed (Wollaston, 1854; Darwin, 1859; Darlington, 1943) and lead to the first theories on the causes of loss of flight. However, Roff (1990), from a comparison between the frequency of flightlessness on oceanic islands versus mainland, considering differences in altitude and latitude, concluded that, with respect to Carabidae, there is no evidence of a correlation between the incidence of flightlessness and island status. Similar findings were reported for other insect groups (Roff, 1990).

However, isolation may affect the evolution of flightlessness not only on islands, but also in several other habitats as for instance caves, inland sand dunes, and high montane and coastal strand communities (Wagner & Liebherr, 1992).

In carabid beetles Den Boer et al. (1980) showed a clear relationship between the capabilities to disperse and the degree of stability of the habitats occupied by these species: high dispersal capabilities in instable habitats and low capabilities in stable ones. Obviously, in Carabidae the dispersal power is predominantly determined by natural selection: flight activity will result in the loss of 'dispersal genes' from the population and this loss will not be compensated fully by arriving immigrants. Especially in isolated populations these selection forces are supposed to be significant. Evolution towards wing polymorphism is supposed to occur if both stable and unstable habitats are inhabited. Wing dimorphism may result from a process of disruptive selection if under these circumstances the effect of the unstable sites decreases. Moreover, the same disruptive selection may concentrate the genes for wing size in such a way that being short winged becomes a single dominant character. Populations thus will gradually evolve from macropterous to brachypterous if the habitats occupied become more and more stable and wing polymorphism and dimorphism are considered as stages in this evolutionary process. Preliminary data on *Calathus cinctus* presented in this study, were included by Den Boer et al. (1980: as *Calathus mollis erythroderus*).

THE GENETIC BASIS OF WING DIMORPHISM

Two types of genetic determination of wing dimorphism are found among insects: single locus systems, typically with the short winged condition dominant, and polygenic systems (Roff, 1986; Roff & Fairbairn, 1991; Fairbairn, 1994). Single locus systems were listed for 10 cases among the following orders: Coleoptera (5), Diptera (1), Hemiptera (2), and Hymenoptera (2). Polygenic systems are known from 19 cases: Coleoptera (3), Hemiptera (4), Homoptera (5), Orthoptera (5), and Dermaptera (2).

Preliminary data for *Calathus cinctus* and *C. melanocephalus* from this study (Aukema, 1986) were included by Roff (1986), but those for *C. melanocephalus* at the time were interpreted as being 'polygenic'.

Both types of inheritance can be subsumed in a physiological threshold model with wing form under hormonal control (Roff, 1986; Roff & Fairbairn, 1991). The titre of juvenile hormone is supposed to trigger wing development: short winged morphs will be produced if a critical threshold during a particular stage of development is exceeded (fig. 35).

In *Calathus cinctus* and *C. melanocephalus* wing dimorphism is inherited according to a single locus, two-allele system with the short winged condition dominant. In *Calathus cinctus* the long winged genotype (bb in fig. 35) is always expressed, whereas the short winged genotypes (Bb and BB) are always short winged.

The expression of the long winged genotype in *Calathus melanocephalus* is under environmental control, but again both short winged genotypes are always short winged. Therefore, both cases thus at least make up special cases of the threshold model (fig. 36). Observed differences between males and females of *Calathus melanocephalus* in the expression of the long winged genotype accordingly can be explained by differences in thresholds between the sexes: females are more frequently long winged than males due to a higher threshold in females than in males. Similar differences were observed by Carter (1976) in *Agonum retractum* Leconte and Bengtson & Erikstad (1984) in *Amara quenseli* (Schönherr). Thus far no reasonable explanation was found for the asymmetric wing development in *C. melanocephalus* and a few other wing dimorphic species (see also Desender, 1989a), but it is supposed to be linked to the environmental control of wing

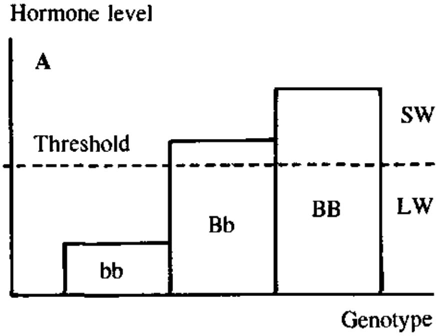

Fig. 35. Threshold model for the determination of wing-morph by a single locus, two-allele system with short winged dominant. SW: short winged; LW: long winged (source: Roff, 1986).

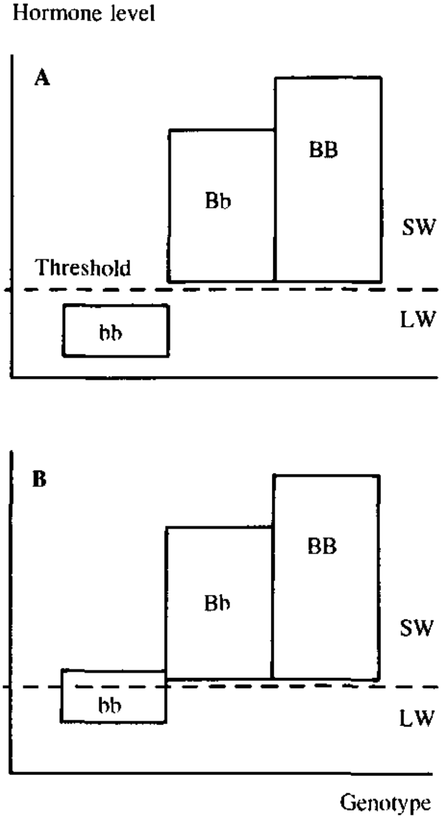

Fig. 36. See fig. 35. A, *Calathus cinctus*; B, *C. melanocephalus*. SW: short winged; LW: long winged.

development.

Whether juvenile hormone is (always) involved in the expression of the different genotypes is still rather speculative, because up to the present only one possible case has been published (Zera & Tiebel, 1989) and other morphogenetic hormones may be involved (Zera, personal communication). Moreover, the prediction of Roff & Fairbairn (1991) that the short winged morph should take longer to develop than the long winged one because of different levels of juvenile hormone, does not hold for *Calathus cinctus* and *C. melanocephalus*: no relations between sex, wing-morph and temperature could be established in these two species.

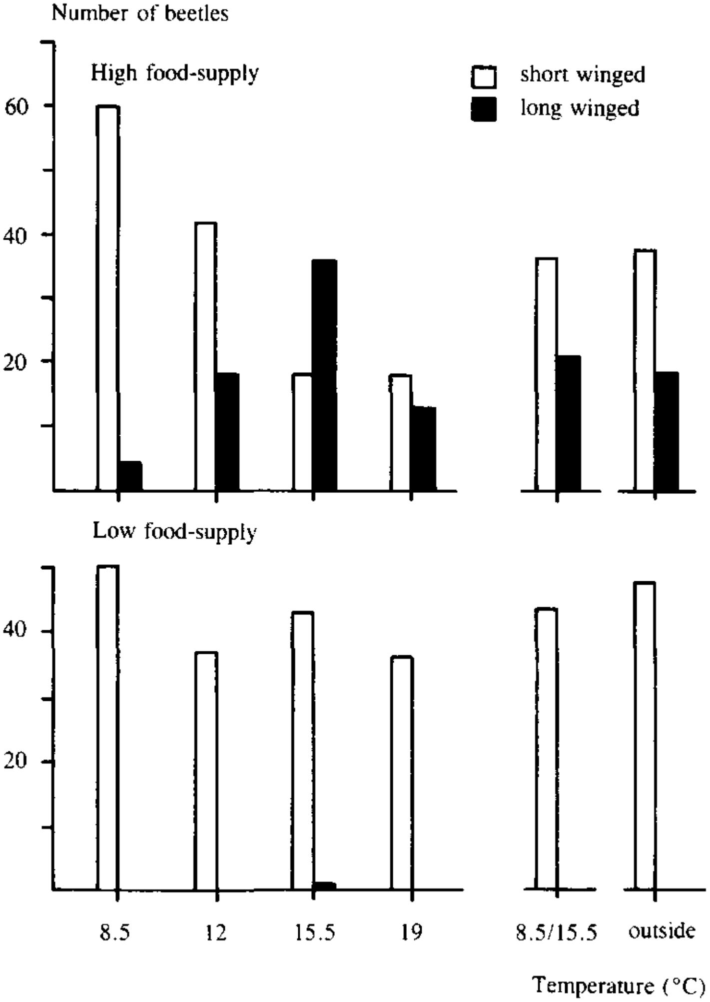

Fig. 37. Phenotypes of offspring of long winged parents of *Calathus melanocephalus* in relation to temperature and food-supply level (see Chapter III, table 28).

ENVIRONMENTAL FACTORS AND WING DIMORPHISM

Both abiotic and biotic factors were frequently found to influence wing and flight muscle development in insects (see Harrison, 1980 for a review). Dispersal activities, the development of dispersal morphs included, are thought to be associated with adverse conditions, i.e. with detoriating environments.

In this study in *Calathus melanocephalus* the opposite was found, the dispersal morph being produced more frequently under relatively favourable conditions, such as high temperatures and abundant food (fig. 37). In the closely related *C. cinctus* no effect of the same environmental factors was found on wing development at all.

Concerning Carabidae there is still little and contradicting information on this point. Nelemans (1987) studied the effect of food supply, temperature and daylength during larval growth on the development of flight muscles in the autumn breeder *Nebria brevicollis* (Fabricius). In this species functional flight muscles were only developed under favourable conditions during larval development. Van Schaick Zillesen & Brunsting presented a seemingly opposite case in the spring breeder *Pterostichus oblongopunctatus* (Fabricius): shortage of food and deviating photoperiods during larval development was supposed to result in increasing numbers of beetles with functional flight muscles. However, their data do not allow unambiguous conclusions.

Differences between spring and autumn breeders in this respect may result from a more general difference in response to environmental factors between quickly developing summer larvae (*Pterostichus oblongopunctatus*) and slowly developing and overwintering winter larvae (*Calathus melanocephalus* and *Nebria brevicollis*).

TRADE-OFFS AND WING DIMORPHISM

Trade-offs between flight capability and other fitness components are frequently supposed to explain the existence of forms with reduced flight capability (Roff & Fairbairn, 1991; Roff, 1994). Development time, adult longevity, age at first reproduction, and total fecundity are commonly supposed to benefit from a reduction of flight capability (Liebherr, 1992; Roff, 1986, 1990; Roff & Fairbairn, 1991). However, no consistent pattern was found with respect to differences in development time and adult longevity between long and short winged individuals of the same species, but highly significant differences were found in several species for age at first reproduction and total fecundity (Roff, 1986; Roff & Fairbairn, 1991). Roff (1986) listed 26 intraspecific comparisons of wing-polymorphic species, 21 of which, mostly in Homoptera, were characterized by more fecund brachypters and 3 had more fecund macropters. No carabids are listed and among the four species of Coleoptera listed the long winged morph was more fecund in two species and less fecund in two other species.

In both *Calathus cinctus* and *C. melanocephalus* no differences in start of the oviposition period were detected and concerning total fecundity the opposite was found: a higher fecundity of long winged females. Similar results were obtained by Desender (1989b) for the wing-polymorphic carabid *Pogonus chalceus* Marsham.

Moreover, at least in *Calathus cinctus* flight and reproduction were not fully separated in time as suggested by the oogenesis-flight syndrome of Johnson (1969) (see also Van Huizen, 1979).

MAINTENANCE OF WING-DIMORPHISM

Since populations of wing-dimorphic carabids tend to develop towards brachyptery, wing-dimorphism will only be maintained if new populations, producing predominantly or exclusively 'dispersal genes', can be founded regularly (Den Boer et al., 1980; Den Boer, 1990). Roff (1994) presented simulation models to illustrate the hypothesis that wing dimorphism is maintained by a trade-off between the costs of being long winged and capable of flight, and the long-term benefits of migration in a heterogeneous environment. In his simulation habitat persistence, the cost of being macropterous, the proportion of migrants and the probability of locating other suitable patches were all important in determining the frequency of macroptery, but habitat persistence and the costs of being macropterous were the most important factors. However, since the model assumes reduced fecundity of the long winged morph, which is not the case in the two carabid species studied thus far, it cannot be applied.

In *Calathus cinctus*, a species living in temporary, unstable habitats like, for instance (abandoned) agricultural fields and waste sites, a high turnover and a short survival time of populations in combination with a high frequency of (re)establishing new populations with high proportions of long winged beetles is expected. The higher fecundity of long winged females will favour the (re)establishment of new populations, and thus contribute to the maintenance of wing dimorphism in this species.

However, in *Calathus melanocephalus*, a species living in more stable habitats, such as heaths and grasslands, we expect a low turnover and a long survival time of populations in combination with a low frequency of (re)establishing populations. Since a large part of the long winged genotypes will not be expressed, dispersal activities will be low and the resident population will always include many 'hidden macropters', which will contribute to the maintenance of wing dimorphism in the population. Also in this species the higher fecundity of long winged females will favour the (re)establishment of new populations, but the contribution to the maintenance of wing dimorphism through reverse gene-flow is supposed to be much lower in this species than in *C. cinctus*. Estimates of turnover and survival time of populations of *C.*

melanocephalus in Den Boer (1990) support this view.

Moreover, since flight is optional for long winged beetles of both species, depending on flight muscle development, fuel budget, and suitable weather conditions, also many long winged beetles often will stay in the resident population, contributing to the maintenance of wing dimorphism not only by their genetic contribution, but also by their higher fecundity.

It has been suggested that in *Calathus melanocephalus* mating preference among wing morphs might exist (Meijer in Haeck, 1971) and thus prevent the introduction of brachyptery through the air. However, as shown in this study, brachyptery in this species will be present in the first generation after founding and there will be no clear relationship between the proportion of long winged beetles and the age of the populations concerned. In *Calathus cinctus* no mating preference between wing morphs could be established in the laboratory (Aukema, unpublished data).

REFERENCES

Aukema, B., 1986. Wing length determination in relation to dispersal by flight in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae).- In: *Carabid beetles. Their adaptations and dynamics* (P. J. den Boer, M. L. Luff, D. Mossakowski & F. Weber, eds): 91-99. Fischer, New York.

Boer, P. J. den, 1990. Density limits and survival of local populations in 64 carabid species with different powers of dispersal.- *Journal of Evolutionary Biology* 3: 19-48.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae).- *Entomologia Generalis* 6: 107-134.

Bengtson, S.-A. & K. E. Erikstad, 1984. Wing polymorphism in Amara quenseli (Schönherr) (Coleoptera: Carabidae) in Iceland.- *Entomologica Scandinavica* 15: 179-183.

Carter, A., 1976. Wing polymorphism in the insect species Agonum retractum Leconte (Coleoptera, Carabidae).- *Canadian Journal of Zoology* 54: 1375-1382.

Darlington, P. J., 1943. Carabidae of mountains and islands.- *Ecological Monographs* 13: 37-61.

Desender, K., 1989a. Dispersievermogen en ecologie van loopkevers (Coleoptera: Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Desender, K., 1989b. Heritability of wing development and body size in a carabid beetle, Pogonus chalceus Marsham, and its evolutionary significance.- *Oecologia* 78: 513-520.

Fairbairn, D. J., 1994. Wing dimorphism and the migratory syndrome: correlated traits for dispersal tendency in wing dimorphic insects.- *Proceedings of the Memorial and International Symposium on Dispersal Polymorphism of Insects, its Adaptation an Evolution, Okayama, Japan*: 143-152.

Haeck, J., 1971. The immigration and settlement of carabids in the new IJsselmeer-polders.

In: Dispersal and dispersal power of carabid beetles (P.J. den Boer ed.).- *Miscellaneous Papers Lanbouwhogeschool Wageningen* 8: 33-52.

Harrison, R. G., 1980. Dispersal polymorphism in insects.- *Annual Review of Ecology and Systematics* 103: 547-570.

Huizen, T. H. P. van, 1979. Individual and environmental factors determining flight in carabid beetles. In: On the evolution of behaviour in carabid beetles (P.J. den Boer, H.U. Thiele & F. Weber, eds).- *Miscellaneous Papers of the Agricultural University Wageningen* 18: 199-211.

Johnson, C. G., 1969. *Migration and dispersal of insects by flight*: 1-763. Methuen, London.

Liebherr, J. K., 1991. Phylogeny and revision of the Anchomenus clade: the genera Tetraleucus, Anchomenus, Sericoda, and Elliptoleus (Coleoptera: Carabidae: Platynini).- *Bulletin of the American Museum of Natural History* 202: 1-163.

Liebherr, J. K., 1992. Phylogeny and revision of the Platynus degallieri species group (Coleoptera: Carabidae: Platynini).- *Bulletin of the American Museum of Natural History* 214: 1-115.

Nelemans, M. N. E., 1987. Possibilities for flight in the carabid beetle Nebria brevicollis (F.). The importance of food during adult life.- *Oecologia* 72: 502-509.

Roff, D. A., 1986. The evolution of wing dimorphism in insects.- *Evolution* 40: 1009-1020.

Roff, D. A., 1990. The evolution of flightlessness in insects.- *Ecological Monographs* 60: 389-421.

Roff, D. A., 1994. Habitat persistence and the evolution of wing dimorphism in insects.- *The American Naturalist* 144: 772-798.

Roff, D. A. & D. J. Fairbairn, 1991. Wing dimorphism and the evolution of migratory polymorphisms among the insecta.- *American Zoologist* 31: 243-251.

Schaick Zillesen, P. G. van & A. M. H. Brunsting, 1984. The influence of food quantity and photoperiod during the pre-adult stages on flight muscle development in adult Philonthus decorus (Coleoptera: Staphylinidae) and Pterostichus oblongopunctatus (Coleoptera: Carabidae).- *Entomologia Generalis* 9: 143-147.

Southwood, T. R. E., 1977. Habitat, the templet for ecological strategies.- *Journal of Animal Ecology* 46: 337-365.

Wagner, D. L. & J. K. Liebherr, 1992. Flightlessness in insects.- *Tree* 7: 216-220.

Zera, A. J. & K. C. Tiebel, 1989. Differences in juvenile hormone esterase activity between presumptive longwinged and shortwinged Gryllus rubens: implications for the hormonal control of winglength polymorphism.- *Journal of Insect Physiology* 35: 7-18.

VIII. SUMMARY

Factors governing wing dimorphism in ground beetles (Coleoptera: Carabidae) of the *Calathus melanocephalus* complex have been studied in relation to dispersal by flight. In Western Europe this complex consists of three well-defined species, as was shown by cross-breeding experiments and morphological studies: *Calathus cinctus* Motschulsky (= *C. erythroderus* Gemminger & Harold), *Calathus melanocephalus* (Linnaeus) and *Calathus mollis* (Marsham). The synonymy of *Calathus erythroderus* with *C. cinctus* was established. To stabilize the nomenclature of the species involved lectotypes were designated for *Carabus melanocephalus* Linnaeus and *Carabus mollis* Marsham. Action undertaken to conserve the specific name of *Carabus mollis* Marsham was approved by the International Commission on Zoological Nomenclature. Data on morphology, life history and distribution of the three species involved were listed and an identification key is included.

Calathus cinctus and *C. melanocephalus* are wing-dimorphic with either strongly reduced wings (short winged or brachypterous) or fully developed wings (long winged or macropterous), whereas *C. mollis* is always macropterous. Long winged beetles are considered potential flyers, representing the dispersal morph of these species. Populations of *C. cinctus* and *C. melanocephalus* showed different proportions of long winged beetles.

Wing dimorphism in *Calathus cinctus* and *C. melanocephalus* was found to be genetically determined and to be inherited in a simple Mendelian fashion with brachyptery dominant to macroptery. In *C. cinctus* the long winged genotype is always expressed, whereas in *C. melanocephalus* the expression of the long winged genotype is under environmental control. It was shown that at least temperature and food-supply affected the expression of the long winged genotype in *C. melanocephalus*: more favourable temperatures (i.e. relatively high temperatures) and a higher food-supply resulted in a higher number of long winged beetles compared with less favourable temperatures (i.e. both low and extremely high temperatures) and a lower food-supply.

Wing-morph frequencies in populations of wing-dimorphic species may also be affected by differences in fitness between short and long winged beetles. Fecundity (egg production and oviposition period), development time, and growth were studied in this respect.

In both *Calathus cinctus* and *C. melanocephalus* long winged females showed a significantly higher egg production than short winged females, and they also tended to produce eggs during a longer period. Considerable differences in fecundity were observed between the species: the highest egg production was found in *Calathus cinctus*, a species with a late start and a long oviposition period, and the lowest egg

production was found in *C. mollis*, a species with an early start and a comparably long oviposition period. *Calathus melanocephalus* showed an egg production intermediate between those of *C. cinctus* and *C. mollis*, with an early start and a relatively short oviposition period.

In all three species development times were generally shorter at higher temperatures and longer at lower temperatures, but in both *Calathus cinctus* and *C. melanocephalus* a general relationship between temperature and development time was found neither for wing-morph nor for sex. Development time and growth of long winged genotypes of *Calathus melanocephalus* were strongly influenced by food-supply: with a higher food-supply shorter development times and higher hatching weights were found. Long winged beetles of both sexes developed faster and were heavier than short winged ones reared under similar conditions, and females weighed more than males.

Under laboratory conditions both long winged males and females of the three species studied built up functional flight muscles and were capable of flight. Flight activity in the field, however, was only observed in *Calathus cinctus*. Building up flight muscles, flight, and subsequent resorption of flight muscles only occurred in the pre-oviposition period, but mating and even ovarian development may occur during the flight period too.

The dispersal abilities of the three species studied are supposed to be different because there are large differences in flight potential between the species. In *Calathus cinctus* and *C. melanocephalus* only part of the individuals is long winged and has flight potential, whereas in *Calathus mollis* all individuals have this ability. Moreover, in *Calathus cinctus* the long winged genotype, and so the potential for flight, is always expressed, whereas in *C. melanocephalus* the expression of the long winged genotype depends on environmental conditions, such as temperature and food-supply, and therefore the flight potential for flight is partly expressed only.

Differences in flight potential were clearly associated with differences in life histories and habitat selection. *Calathus cinctus* occupies temporary habitats, showing a high potential for flight and a high turnover of populations, whereas *C. melanocephalus* occurs in less temporary habitats, showing a much lower potential for flight and a relatively low turnover of populations. *Calathus mollis* inhabits coastal dunes and blowing sands, showing a maximum potential for flight, obviously to keep pace with changes in this extreme environment.

The higher fecundity of long winged females, closely linked with larger body size and higher weight, is considered to benefit the colonization abilities of the species.

The wing-morph determination found in *Calathus cinctus* and *C. melanocephalus* fitted the current model, but a trade-off between flightlessness and fecundity was not found. Both flight capability and high fecundity are considered to represent closely linked characters of species adapted to unstable, temporary habitats.

Wing dimorphism is supposed to be maintained by a 'balance' between the loss of long winged genotypes by flight activities and the frequency of successful (re)colonizations. In *Calathus cinctus* both the loss of long winged genotypes and the colonization success is supposed to be high (a short term, opportunistic 'strategy'), whereas in *C. melanocephalus* both the loss of long winged genotypes and the colonization success is supposed to be low. However, in the latter species the maintenance of wing dimorphism is favoured by the environmental control of the expression of long winged genotypes (a long term, more ensuring 'strategy').

IX. SAMENVATTING

Factoren die de vleugeldimorfie bij loopkevers (Coleoptera: Carabidae) van de *Calathus melanocephalus*-groep bepalen, werden bestudeerd in relatie tot dispersie als gevolg van vliegactiviteit. Met behulp van kruisings-proeven en morfologisch onderzoek werd aangetoond dat het bestudeerde soortencomplex in West-Europa uit drie afzonderlijke soorten bestaat. De betreffende soorten zijn *Calathus cinctus* Motschulsky (= *Calathus erythroderus* Gemminger & Harold), *Calathus melanocephalus* (Linnaeus) en *Calathus mollis* (Marsham). De synoniemie van *Calathus erythroderus* met *Calathus cinctus* werd vastgesteld. Teneinde de nomenclatuur te stabiliseren werden lectotypes aangewezen voor *Carabus melanocephalus* en *Carabus mollis* Marsham. Tevens werd met succes een verzoek ingediend bij de Internationale Commissie voor de Zoölogische Nomenclatuur om de naam *Carabus mollis* Marsham te behouden. Gegevens over de morfologie, de leefwijze en de verspreiding van de betrokken soorten werden samengevat, terwijl tevens een determinatiesleutel werd verstrekt.

Calathus cinctus en *C. melanocephalus* zijn beide vleugeldimorf met hetzij sterk gereduceerde vleugels (kortvleugelig of brachypteer), of volledig ontwikkelde vleugels (langvleugelig of macropteer), terwijl *C. mollis* uitsluitend langvleugelig is. Langvleugelige kevers worden beschouwd als mogelijke vliegers en zij vormen daarmee de dispersievorm van deze soorten. Populaties van *C. cinctus* en *C. melanocephalus* vertoonden grote verschillen in het aandeel langvleugelige kevers.

De vleugeldimorfie in *Calathus cinctus* en *C. melanocephalus* bleek genetisch bepaald te zijn en overerving vond plaats via een eenvoudige Mendelsplitsing met kortvleugelig dominant. In *Calathus cinctus* vind expressie van het langvleugelig genotype altijd plaats, terwijl bij *Calathus melanocephalus* de expressie van het langvleugelig genotype afhankelijk is van omgevingsfactoren. Zowel temperatuur als voedsel aanbod bleken daarbij van invloed: relatief gunstige omstandigheden (relatief hoge temperatuur en een groot voedselaanbod) resulteerden in een groter aantal langvleugelige kevers dan relatief ongunstige omstandigheden (lage en hoge temperaturen en een beperkt voedselaanbod).

De verhouding tussen de aantallen kort- en langvleugelige kevers in populaties van vleugeldimorfe soorten kan mogelijk ook beïnvloed kunnen worden door verschillen in fitness tussen de beide vleugelvormen. Vruchtbaarheid (eiproduktie en duur van de eilegperiode), ontwikkelingsduur en groei werden in dit opzicht bestudeerd.

Zowel bij *Calathus cinctus* als bij *C. melanocephalus* bleken Langvleugelige vrouwtjes meer eieren te produceren gedurende een langere periode dan kortvleugelige vrouwtjes. Tussen de soorten bleken grote verschillen te bestaan: de hoogste eiproduktie werd waargenomen bij *C. cinctus*, een soort waarbij de eiproduktie laat in het seizoen op gang komt, maar lang doorgaat. *Calathus mollis* vertoonde de laagste eiproduktie in combinatie met een vroege start en een vergelijkbaar lange legperiode, terwijl de eiproduktie bij *C. melanocephalus* intermediair was met een vroege start en een relatief korte legperiode.

Bij alle drie de soorten was de ontwikkelingsduur van ei tot kever in het algemeen korter bij hogere temperaturen en langer bij lagere temperaturen. Er bleek echter geen duidelijk relatie te bestaan tussen temperatuur en ontwikkelingsduur enerzijds en vleugelontwikkeling of geslacht anderzijds. De ontwikkelingsduur en de groei van langvleugelige genotypen van *Calathus melanocephalus* werd sterk beïnvloed door het voedselaanbod: een groter voedselaanbod resulteerde in een kortere ontwikkelingsduur en een hoger geboortegewicht. Langvleugelige kevers van beide geslachten ontwikkelden zich sneller en wogen meer dan kortvleugelige kevers, die onder dezelfde omstandigheden gekweekt werden, en vrouwtjes meer wogen dan mannetjes.

Langvleugelige mannetjes en vrouwtjes van alle drie de soorten bleken in staat om onder laboratoriumomstandigheden functionele vliegspieren op te bouwen en om daadwerkelijk te vliegen. In het veld werd vliegactiviteit echter alleen waargenomen bij *Calathus cinctus*. De opbouw van vliegspieren, vliegactiviteit en de daarop volgende resorptie van de vliegspieren vinden plaats tijdens een korte periode voor de eilegperiode. Paring en ovariumontwikkeling kunnen echter al wel plaatsvinden tijdens de vliegperiode.

Op basis van de grote verschillen in mogelijke vliegactiviteit tussen de soorten, worden aanzienlijke verschillen in verbreidingsvermogen tussen de drie bestudeerde soorten verondersteld. Bij *Calathus cinctus* en *C. melanocephalus* zijn slechts een beperkt aantal kevers langvleugelig en tot vliegen in staat, terwijl dit bij *C. mollis* voor alle dieren geldt. Bij *Calathus cinctus* is bovendien de expressie van het langvleugelig genotype en daarmee van het aantal potentiële vliegers volledig, terwijl bij *C. melanocephalus* slechts een deel van de langvleugelige genotypen tot expressie komt.

Deze verschillen in verbreidingsvermogen komen duidelijk naar voren in verschillen in leefwijze en habitatselectie. *Calathus cinctus* komt voor in tijdelijke habitats en vertoont relatief veel vliegactiviteit en een hoge frequentie van het (her)vestigen en verdwijnen van populaties, terwijl *C. melanocephalus* in meer permanente habitats voorkomt en minder vlieg-activiteit en een lagere frequentie van het (her)vestigen en verdwijnen van populaties vertoont. *Calathus mollis* komt uitsluitend voor in onze kustduinen en in zandverstuivingen. Het grote verbreidingsvermogen van deze soort vormt een duidelijke aanpassing aan dit ten dele zeer veranderlijke en extreme habitat.

De wijze waarop de vleugelontwikkeling bij *Calathus cinctus* en *C. melanocephalus* tot stand komt overeen met het gangbare model, maar er bleek geen sprake te zijn van een "trade-off" tussen vleugelreductie en eiproduktie.

Zowel het vliegvermogen als een hoge eiproduktie worden beschouwd als nauw gerelateerde eigenschappen van soorten, die zijn aangepast aan een instabiele, tijdelijke leefomgeving.

Vleugeldimorfie blijft gehandhaafd dankzij een evenwicht tussen enerzijds het verlies van langvleugelige genotypen als gevolg van vliegactiviteiten en anderzijds de frequentie van succesvolle (her)kolonisaties. Bij *Calathus cinctus* worden een groot verlies van langvleugelige genotypen en een hoge frequentie van (her)kolonisaties verondersteld (een opportunistische "korte-termijn-strategie"), terwijl bij *C. melanocephalus* een gering verlies aan langvleugelige genotypen en een lage frequentie van (her)kolonisaties worden verondersteld. Bij *Calathus melanocephalus* werkt echter de invloed van de omgeving via de gedeeltelijke expressie van het langvleugelig genotype ten gunste van handhaving van de vleugeldimorfie (een meer behoudende "lange-termijn strategie").

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Curriculum vitae

De auteur werd op 22 november 1949 te Zaandam geboren. Na het doorlopen van de H.B.S. werd in 1969 de studie biologie aan de Vrije Universiteit aangevangen. Na het behalen van het doctoraal diploma (B1 met wiskunde) in 1978 werd tot eind 1984 het onderhavige onderzoek verricht aan het Biologisch Station te Wijster. In de periode 1986-1988 werd in het kader van een tijdelijke aanstelling bij de vakgroep Toxicologie van de Landbouwuniversiteit geparticipeerd in onderzoek naar neveneffecten van bestrijdingsmiddelen op ongewervelden, met name spinnen, in terrestrische ecosystemen. In 1990 volgde aanstelling in de huidige functie van hoofd van de Sectie Entomologie van de Plantenziektenkundige Dienst te Wageningen.

Naast de professionele betrokkenheid bij de entomologie richtte de auteur zich al op jeugdige leeftijd op de studie van de (Nederlandse) wantsen. Hij is editor van de nieuw uit te geven Catalogue of Palaearctic Heteroptera, lid van de redactie van Entomologische Berichten en bestuurslid van de afdeling Nederland van de European Invertebrate Survey.

APPENDICES

APPENDIX A

THE NOMENCLATURE OF THE *MELANOCEPHALUS* GROUP OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE) *

ABSTRACT

Type material of *Calathus melanocephalus*, *C. mollis* and *C. cinctus* is examined in order to stabilize nomenclature in the *melanocephalus* group of the subgenus *Neocalathus*. Lectotypes are designated for *Carabus melanocephalus* Linnaeus and *Carabus mollis* Marsham. *Calathus cinctus* Motschulsky appears to be a senior synonym of *Calathus erythroderus* Gemminger & Harold nov. syn.

INTRODUCTION

The taxonomic status and the identification of the West Palaearctic representatives of the so-called *melanocephalus* group of the subgenus *Neocalathus* Ball & Negre of the genus *Calathus* Bonelli have given many problems (see Aukema (1990) for a review).

Lucht (1987) lists two species, both represented by two subspecies: *melanocephalus*, represented by *melanocephalus melanocephalus* (Linnaeus) and *melanocephalus alpinus* Dejean, and *mollis*, represented by *mollis mollis* (Marsham) and *mollis erythroderus* Gemminger & Harold.

Cross-breeding experiments and morphological studies, however, showed that in fact there are three good species: *melanocephalus*, *mollis* and *erythroderus* (Aukema, 1990).

To stabilize the nomenclature in this group of closely related species the types of the species involved were examined.

Calathus melanocephalus

Carabus melanocephalus was described by Linnaeus in 1758 from 'Europe'. In the collection of Linnaeus, now in the keeping of the Linnean Society of London at

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[Communication No. 432 of the Biological Station, Wijster, The Netherlands]

Burlington House, *melanocephalus* is represented by a single female, labelled "15 melanocephalus" and "22". Both labels are narrow horizontal stripes. The first one is an original label in the hand of Linnaeus (for a review of Linnean labels see Day & Fitton, 1978 and Robinson & Schmidt Nielsen, 1983), the number referring to the serial number of *melanocephalus* in the 10th edition of his Systema Naturae (Linnaeus, 1758). The second label, referring to the serial number of *melanocephalus* in the 12th edition of the Systema Naturae (Linnaeus, 1767), was put on the specimen after photographs of the collection have been taken in the 1950s.

The specimen is designated as lectotype by labelling it "Lectotype *Carabus melanocephalus* Linnaeus/Design. B. Aukema".

Calathus mollis

Carabus mollis was described by Marsham in 1802 from Ealing, West London. His collection, or at least the bulk of it, was purchased in 1820 by J. F. Stephens and bought in 1853 by the British Museum (Natural History), London (Hammond, 1972).

Stephens' collection contains a small box with fourteen unlabelled specimens (seven males and seven females, all long winged) of *mollis*. A male was designated as lectotype by labelling it "Lectotype *Carabus mollis* Marsham/Design. B. Aukema". The vesica and right paramere were dissected and glued to the card holding the specimen.

Silfverberg (1977), however, showed that *mollis* Marsham is a junior primary homonym of *Carabus mollis* Ström, 1768 (now in the synonymy of *Cymindus vaporariorum* (Linnaeus)) and replaced it by its senior synonym *ochropterus* (Duftschmid, 1812). Unfortunately the collection of Duftschmid is not traceable (Gusenleitner, 1984), and the identity of *ochropterus* could not be checked. Since it is very unlikely that *ochropterus*, described from the Schneeberg near Vienna, Austria, represents the same taxon (*mollis* is limited to coastal dunes and inland blown sands and does not occur in Austria at all, see Aukema, 1990), and since *mollis* is a well-established name for this species, the International Commission on Zoological Nomenclature will be requested to preserve the name *mollis* Marsham for this species (Aukema & Luff, 1990).

Calathus cinctus (= *Calathus erythroderus* **syn. nov.**)

Gautier des Cottes (1868) described *Calathus ruficollis* from Sicily. Gemminger & Harold (1868), however, in preparing their catalog, found this name preoccupied by the Nearctic *C. ruficollis* Dejean, 1828 and replaced it by *erythroderus* (Gautier des Cottes (1869): *erytthroderus* [sic!]). Despite special efforts the *Calathus* types of Gautier des Cottes could not be traced.

Vereshchagina (1985) in her revision of the genus *Calathus* in the USSR synonymised *C. cinctus* Motschulsky, 1850, described from the Caucasus, with *C. mollis*. Since *mollis* is not known from the Caucasus, nor from eastern Europe (Aukema, 1990), records of *mollis* from this region generally will concern *erythroderus*. A check of the lectotype of *cinctus*, kept at the Museum of Moscow University, confirmed this opinion. The male (vesica and right paramere dissected and glued on a separate card) bears four labels: "Derbent", "Calathus cinctus m./ Erivan", "Lectotypus Calathus cinctus Motsch./design. T. Vereschagina" and "Calathus mollis Marsh./ T. Vereschagina det.". Since *cinctus* Motschulsky is a senior synonym of *erythroderus* Gemminger & Harold, the valid name for this taxon accordingly is *cinctus*.

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REFERENCES

Aukema, B., 1990. Taxonomy, life-history and distribution of three closely related species of the genus Calathus (Coleoptera: Carabidae).- *Tijdschrift voor Entomologie* 133: 121-141.

Aukema, B. & M. L. Luff, 1990. Calathus mollis Marsham, 1802 (Insecta, Coleoptera): proposed conservation of the specific name.- *Bulletin of Zoological Nomenclature* 49: 28-29.

Day, M. C. & M. G. Fitton, 1978. Re-curation of the Linnean Hymenoptera (Insecta), with a reassessment of the taxonomic importance of the collection.- *Biological Journal* *of the Linnean Society* 10: 181-198.

Duftschmid, C., 1812. *Fauna Austriae* 2: 1-311.- Linz.

Gemminger, M. & B. De Harold, 1868. *Catalogus Coleopterorum. I. Cicindelidae - Carabidae*: 1-460.- Monachii.

Gautier des Cottes, C., 1868. VIIIme Recueil.- *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 2: 321-327.

Gautier des Cottes, C., 1869. IXe Recueil.- *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 3: 130-151.

Gusenleitner, F., 1984. Das Rätsel um den Verbleib der Caspar Erasmus Duftschmid-Kollektion.- *Koleopterologische Rundschau* 57: 93-95.

Hammond, P. M., 1972. On the type material of Staphylinidae (Col.) described by T. Marsham and J. F. Stephens.- *Entmologist's Gazette* 23: 129-135.

Linnaeus, C., 1758. *Systema Naturae*, 10th ed., i: 1-823.- Holmiae.

Linnaeus, C., 1767. *Systema Naturae*, 12th ed., i(2): 533-1327 & 36 pages.- Holmiae.

Lucht, W. H., 1987. Katalog.- *Die Käfer Mitteleuropas*: 1-342.

Marsham, T., 1802. *Entomologia Brittannica, sistens Insecta Britanniae indigena secundum methodum Linnaeanam disposita 1. Coleoptera*: i-xxxi, 1-547. J. White, London.

Motschulsky, V. von, 1850. *Die Käfer Russlands bearbeitet von Victor von Motschulsky*: i-iv: i-xii, 1-91. W. Gautier, Moscou.

Robinson, G. S. & E. Schmidt Nielsen, 1983. The Microlepidoptera described by Linnaeus and Clerck.- *Systematic Entomology* 8: 191-242.

Silfverberg, H., 1977. Nomenclatoric notes on Coleoptera Adephaga.- *Notulae Entomologicae* 57: 41-44.

Ström, H., 1768. Beskrivelse over Norske Insecter. Andet Stykke.- *Kongelige Norske Videnskabers Selskabs Skrifter* 4: 313-371.

Vereshchagina, T. N., 1985. The genus Calathus Bon. (Coleoptera, Carabidae) in the USSR.- *Entomological Review* 63: 75-94.

APPENDIX B

CARABUS *MOLLIS* MARSHAM, 1802 (CURRENTLY *CALATHUS MOLLIS*; COLEOPTERA: COLEOPTERA): PROPOSED CONSERVATION OF THE SPECIFIC NAME *

Aukema, B. & M. L. Luff

ABSTRACT

The purpose of this application is to conserve the specific name of the ground beetle *Carabus mollis* Marsham, 1802 by suppression of its unused senior homonym *Carabus mollis* Ström, 1768.

1. Ström (1768, p. 330) described *mollis* in the genus *Carabus* Linnaeus, 1758. This name is a junior subjective synonym of *Carabus vaporariorum* Linnaeus, 1758 (p. 415). Since its publication the specific name *mollis* Ström, 1768 has been cited only by Schoyen (1880, p. 179) and Silfverberg (1977, p. 42) as a synonym and as a homonym respectively.

2. In 1802 (p. 456) Marsham described *mollis* in *Carabus*, now placed in *Calathus* Bonelli, 1810, from Ealing, U.K. The species name *Calathus mollis* is well-established. At least 30 different authors have applied this binomen during the last 20 years (e.g. Freude, Harde & Lohse, 1976, p. 206; Kloet & Hincks, 1977, p.4 and Trautner & Geigenmüller, 1987, p. 288). A list of a further 40 references has been given to the Commission Secretariat. A male lectotype for *Carabus mollis*, here designated, is kept in the Natural History Museum, London. It is labelled 'Lectotypus Carabus mollis Marsham/Des. B. Aukema 1990'.

3. Duftschmid (1812, p. 124) described and named *Carabus ochropterus*. Since then *ochropterus* has been treated either as a synonym of *Calathus melanocephalus* (Linnaeus, 1758, p. 356) (see, for example, Schatzmayr, 1937, p. 44 and Jeannel, 1942, p. 845), or as a synonym of *Calathus mollis* (see, for example, Putzeys, 1873). The type of *Carabus ochropterus* is lost (Gusenleiter, 1984)

4. Silfverberg (1977, p. 42) pointed out that, as a junior primary homonym, *Carabus mollis* Marsham, 1802 cannot be used. He suggested to use the name

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Calathus ochropterus (Duftschmid, 1812) for the species. *C. ochropterus* was described from the Schneeberg near Vienna. Since *mollis* Marsham (a species of coastal dunes and blown sands) is not known from Austria (Aukema, 1990), and is unlikely to occur there, it seems highly improbable that *ochropterus* represented the same species as *mollis* Marsham.

5. The International Commission on Zoological Nomenclature is accordingly asked:

(1) to use its plenary powers to suppress the specific name *mollis* Ström, 1768 as published in the binomen *Carabus mollis*, and all uses of the name *Carabus mollis* prior to that by Marsham, 1802, for the purpose of both the Principle of Priority and for the Principle of Homonymy;

(2) to place on the Official list of Specific Names in Zoology the name *mollis* Marsham, 1802, as published in the binomen *Carabus mollis* and as defined by the lectotype designated in para. 2 above;

(3) to place on the Official Index of Rejected and Invalid Specific Names in Zoology the name *mollis* Ström, 1768, as published in the binomen *Carabus mollis* and as suppressed in (1) above.

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REFERENCES

Aukema, B., 1990. Taxonomy, life-history and distribution of three closely related species of the genus Calathus (Coleoptera: Carabidae).- *Tijdschrift voor Entomologie* 133: 121-141

Bonelli, F. A., 1910. Observations entomologiques. I.- *Memorie della Accademia delle Scienze di Torino* 18: 21-78.

Duftschmid, C., 1812. *Fauna Austriae* 2: 1-311. Linz.

Freude, H., K. W. Harde & G. A. Lohse, 1976. Adephaga 1.- *Die Käfer Mitteleuropas* 2: 1-302.

Gusenleitner, F., 1984. Das Rätsel um den Verbleib der Caspar Erasmus Duftschmid-Kollektion.- *Koleopterologische Rundschau* 57: 93-95.

Jeannel, R., 1942. Coléoptères Carabiques.- *Faune de France* 40: 572-1173.

Linnaeus, C., 1758. *Systema Naturae*, 10th ed., I: 1-823. Holmiae.

Kloet, G. S. & W. D. Hincks, 1977. A checklist of British insects. Coleoptera and Strepsiptera.- *Handbooks for the identification of British insects*, 2nd Ed., 11 (3): i-xiv, 1-105.

Marsham, T., 1802. *Entomologia Brittannica, sistens Insecta Britanniae indigena secundum methodum Linnaeanam disposita 1. Coleoptera*: i-xxxi, 1-547. White, London.

Putzeys, J., 1873. Monographie des Calathides.- *Annales de la Société Entomologique de Belgique* 16: 19-96.

Schatzmayr, A., 1937. I Calathus d'Europa.- *Pubblicazioni del Museo Entomologico "Pietro Rossi" Duino* 2: 1-50.

Schoyen, W. M., 1880. Coleopterologiske Notitser.- *Entomologisk Tidskrift* 1: 177-185.

Silfverberg, H., 1977. Nomenclatoric notes on Coleoptera Adephaga.- *Notulae Entomologicae* 57: 41-44.

Ström, H., 1768. Beskrivelse over Norske Insecter. Andet Stykke.- *Kongelige Norske Videnskabers Selskabs Skrifter* 4: 313-371.

Trautner, J. & K. Geigenmüller, 1987. *Tiger beetles - groundbeetles*. Illustrated key to the Cicindelidae and Carabidae of Europe: 1-488. Margraf, Aichtal, Germany.

REFERENCES CITING *CALATHUS MOLLIS* (MARSHAM)

Anderson, R., 1987. Some uncommon Carabidae (Coleoptera) from South Dublin, Wicklow.- *Irish Naturalist Journal* 22: 259-260.

Aukema, B., 1986. Winglength determination in relation to dispersal by flight in two wing dimorphic species of Calathus Bonelli (Coleoptera, Carabidae). In: *Carabid Beetles. Their adaptations and dynamics* (P. J. den Boer, M. L. Luff, D. Mossakowski and F. Weber eds): 91- 99. Fischer, New York.

Aukema, B., 1987. Differences in egg production and egg-laying period between long- and short winged Calathus erythroderus (Coleoptera, Carabidae) in relation to wing morph frequencies in natural populations.- *Acta Phytopathologica et Entomologica Hungarica* 22: 45-56.

Baehr, M., 1982. Die Fauna der Ägäis-Insel Santorin, Teil 3 Carabidae (Coleoptera).- *Stuttgarter Beiträge zur Naturkunde* A 355: 1-6.

Boer, P. J. den, 1977. Dispersal power and survival. Carabids in a cultivated countryside.- *Miscellaneous Papers Landbouwhogeschool Wageningen* 14: 1-190.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae).- *Entomologia Generalis* 6: 107-134.

Boer, P. J. den, 1981. Evolutie van het vliegvermogen bij Carabiden en de gevolgen voor het overleven van soorten.- *Vakblad voor Biologen* 6: 122-129.

Bonadona, P., 1971. Catalogue des Coléoptères Carabiques de France. Supplement.- *Nouvelle Revue d'Entomologie* 1: 1-171.

Desender, K., 1985. Carabid beetles new for the Belgian fauna.- *Bulletin et Annales de la Société (Royale) Entomologique de Belgique* 121: 69-74.

Desender, K., 1985. Naamlijst van de loopkevers en zandloopkevers van België.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 19: 1-36.

Desender, K., 1986. Distribution and ecology of carabid beetles in Belgium (Coleoptera, Carabidae). 4. Species 153-217.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 30: 1-23.

Desender, K., 1989. Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering.- *Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen* 54: 1-136.

Dijk, Th. S. van, 1979a. Calathus mollis erythroderus Gemminger & Harold in Drenthe (Coleoptera, Carabidae).- *Entomologische Berichten, Amsterdam* 38: 151-153.

Freude, H., 1976. Adephaga I.- *Die Käfer Mitteleuropas* 2: 1-302.

Hieke, F. & D. W. Wrase, 1988. Faunistik der Laufkäfer Bulgariens (Coleoptera: Carabidae).- *Deutsche Entomologische Zeitschrift, Neue Folge* 35: 1-171.

Huizen, T. H. P. van, 1980. Species of Carabidae in which the occurrence of dispersal by flight of individuals has been shown.- *Entomologische Berichten, Amsterdam* 40: 167-168.

Jablokoff-Khnzorian, S. M., 1975. Notes entomologiques 2.- *Entomologiste* 31: 24-29.

Jeanne, C. & J. P. Zaballos, 1986. Catalogue des Coléoptères Carabiques de la Peninsule Ibérique.- *Bulletin de la Société Linnéenne de Bordeaux* 14, Supplément: 1-186.

Koch, K., 1989. Ökologie. I.- *Die Käfer Mitteleuropas*: 1-440.

Kûrka, A., 1971. Larvae of the Czechoslovak species of the genus Calathus Bonelli (Coleoptera, Carabidae).- *Acta Entomologica Bohemoslovaca* 68: 233-262.

Kûrka, A., 1972. Bionomy of the Czechoslovak species of the genus Calathus Bon., with notes on their rearing (Coleoptera: Carabidae).- *Vestník Československé Společnosti Zoologické* 36: 101-114.

Lienemann, K., 1981. Calathus erythroderus Gemminger et Harold 1868 (Coleoptera, Carabidae) neu im Rheinland.- *Decheniana* 134: 176.

Lindroth, C. H., 1974. Coleoptera, Carabidae.- *Handbooks for the identification of British Insects* 4(2): 1-148.

Lindroth, C. H., 1979. The theory of glacial refugia. In: *Carabid beetles, their evolution, natural history and classification* (Ball, G. E., T. L. Erwin & D. R. Whitehead eds): 385-394.- Junk, Den Haag.

Lucht, W. H., 1987. Katalog.- *Die Käfer Mitteleuropas*: 1-342.

Luff, M. L., 1981. Diagnostic characters of the eggs of some Carabidae (Coleoptera).- *Entomologica Scandinaviae*, Supplement 15: 317-327.

Luff, M. L., 1982. *Preliminary atlas of British Carabidae*: 1-123. Biological Records Centre, Huntingdon.

Luff, M. L., M. D. Eyre & S. P. Rushton, 1989. Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in north-east England.- *Journal of Biogeography* 16: 121-130.

Mandl, K. & R. Schönmann, 1978. Coleoptera Carabidae 2.- *Catalogus Faunae Austriae* 15b: 1-58.

Moncel, J., 1972. A propos de Calathus mollis (Col. Carabidae) et de sa variété erythroderus.- *Entomologiste* 28: 26-30.

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

Pope, R. D., 1977. Coleoptera. In: G. S. Kloet & W. D. Hinks, A check list of British insects. Coleoptera and Strepsiptera.- *Handbooks for the identification of British insects*, 2nd Ed., 11 (3): i-xiv, 1-105.

Pulpán, J. & K. Hůrka, 1984. Verzeichnis der Tsechoslowakischen Laufkäfer (Coleoptera, Carabidae).- *Zpravodaj* 1: 1-28.

Serrano, A. R. M. & P. A. V. Borges, 1986. A new Calathus Bonelli from the Azores (Coleoptera, Carabidae).- *Boletim de Sociedade Portuguesa de Entomologia* 78: 1-6.

Serrano, J., 1981. Chromosome numbers and karyotypic evolution of Caraboidea.- *Genetica* 55: 51-60.

Taglianti, A. V., F. Comandini, P. Bonavite, S. Felici & A. de Ciceroni, 1988. Primi dati sulle communita di coleotteri carabidi dei Quercetea ilicis nel Lazio.- *Atti XV Congresso Nazionale Italiano di Entomologia, L'Aquila* 1988: 415-422.

Thiele, H.-U., 1977. *Carabid beetles in their environments.* A study on habitat selection by adaptations in physiology and behaviour: i- xvii, 1-369. Berlin.

Trautner, J. & K. Geigenmüller, 1987. *Tiger Beetles - Groundbeetles.* Illustrated key to the Cicindelidae and Carabidae of Europe: 1-488. Margraf, Aichtal, Germany.

Turin, H., J. Haeck & R. Hengeveld, 1977. Atlas of the carabid beetles of The Netherlands.- *Verhandelingen der Koninklijke Nederlandse Academie van Wetenschappen, afdeling Natuurkunde* (2) 68: 1-228.

Turin, H., 1981. Provisional checklist of the European groundbeetles (Coleoptera: Cicindelidae & Carabidae).- *Monografieën Nederlandse Entomologische Vereniging* 9: 1-249.

Vereshchagina, T. N., 1985. The genus Calathus Bon. (Coleoptera, Carabidae) in the USSR.- *Entomological Review* 63: 75-94.

Whitehead, P. F., 1989. An inland record of Calathus mollis (Marsham) (Col., Carabidae) in Worcestershire.- *Entomologist's Monthly Magazine* 125: 198.

APPENDIX C

CARABUS MOLLIS MARSHAM, 1802 (CURRENTLY *CALATHUS MOLLIS*; INSECTA, COLEOPTERA): SPECIFIC NAME CONSERVED *

RULING

(1) Under the plenary powers the specific name *mollis* Ström, 1768, as published in the binomen *Carabus mollis*, and all uses of the name *Carabus mollis* prior to that by Marsham, 1802, are hereby suppressed for the purpose of both the Principle of Priority and the Principle of Homonymy.
(2) The name *mollis* Marsham, 1802, as published in the binomen *Carabus mollis* and as defined by the lectotype designated by Aukema & Luff (1992), is hereby placed on the Official List of Specific Names in Zoology.
(3) The name *mollis* Ström, 1768, as published in the binomen *Carabus mollis* and as suppressed in (1) above, is hereby placed on the Official Index of Rejected and Invalid Specific Names in Zoology.

HISTORY OF CASE 2782

An application for the conservation of the specific name of Carabus mollis Marsham, 1802 was received from Drs B. Aukema (plant Protection Service, Wageningen, The Netherlands) and M. L. Luff (University of Newcastle upon Tyne, U.K.) on 9 July 1990. After correspondence the case was published in BZN 49: 28-29 (March 1992). Notice of the case was sent to appropriate journals.

It was noted on the voting paper that the lectotype designation for *Calathus mollis* (Marsham, 1802) dated from its publication by Aukema & Luff (1992) in BZN 49: 28 and not from 'Aukema 1990' as recorded on the specimen label (para. 2 of the application).

DECISION OF THE COMMISSION

On 1 December 1992 the members of the Commission were invited to vote on the proposals published in BZN 49: 28-29. At the close of the voting period on 1 March 1993 the votes were as follows:

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* Published in Bulletin of Zoological Nomenclature 50: 166-167 as Opinion 1723

Affirmative votes - 29: Bayer, Bock, Bouchet, Cocks, Cogger, Corliss, Dupuis, Hahn, Halvorsen, Heppell, Holthuis, Kabata, Kraus, Lehtinen, MacPherson, Mahnert, Martins de Souza, Minelli, Nielsen, Nye, Ride, Savage, Schuster, Starobogatov, Štys, Thompson, Trjapitzin, Uéno, Willink.

Negative votes - none.

ORIGINAL REFERENCES

The following are the original references to the names placed on an Official List and an Official Index by the ruling given in the present Opinion:
mollis, *Carabus*, Marsham, 1802, Coleoptera Britannica ....., vol. 2, p. 456.
mollis, *Carabus*, Ström, 1768, Kongelige Norske Videnskabers Selskabs Skrifter, 4: 330.

The following is the reference for the designation of the lectotype of Carabus mollis Marsham, 1802: **Aukema, B. & Luff, M. L.** 1992. BZN 49: 28.