Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.)*
The importance of food during larval growth

M.N.E. Nelemans
Biological Station, Kampsweg 27 9418 PD WIJSTER, The Netherlands

**Summary.** The carabid beetle *Nebria brevicollis* (F.), despite being macropterous, has a very low flight potential. Only a few percent of the beetles has functional flight muscles, flight motivation is low, and the period favourable for flight is short. The inability to fly is caused mainly by arrested development of the flight muscles. Dispersers are formed only under favourable conditions in the larval stages as shown by laboratory experiments (much food, short day-length). In *N. brevicollis* dispersal by flight cannot be considered as a reaction to deteriorating conditions but just the other way round. Because of the usually low numbers of potential dispersers conditions during larval development are apparently suboptimal. However, *N. brevicollis* is widespread and abundant in our area. The "choice" of using energy for the metabolic costs of larval growth, and only secondarily for the building up of flight muscles does not prevent the species from fully exploiting the habitat.

**Key words:** Flight muscles – Dispersal – Food – Carabids – Larvae

Although most ground beetles (Carabidae) perform "normal" activities such as feeding, mating and egg laying by means of walking, many species are also capable of flight. Sometimes, as in *Amara plebeja* Gyll (van Huizen 1977), flight is indispensable to enable an obligatory habitat change (the hibernation- and reproduction habitats are quite different). For other species, it can be expected that the building up and supporting of a flight apparatus will be related to dispersal potential which would increase the chance to survive in an ever changing world (i.e. Lindroth 1945; Dingle 1972; Den Boer 1971). However, between individuals (and this is not restricted to carabid beetles) the capacity for flight can vary, which makes adaptive changes of dispersal possible (Johnson 1976; Harrison 1980; Den Boer et al. 1980). This variation can manifest itself both in wing-length (from macropterous to brachypterous), and in flight muscle development. Many adults with full grown alae either cannot fly at all, or can fly for a short period only. This is related to individual variation in the ability to build up or subsequently to histolyse the flight muscles (Smith 1964; Tietze 1963; Van Huizen 1977, 1979; Solbreck 1986).

The question then arises about what factors are respon-

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**Material and methods**

**Species**

*Nebria brevicollis* (F.) is a common species in Western Europe, and is abundant in woody areas, parks and meadows (Thiele 1977). Its distributional range extends from southern Scandinavia through central Europe as far as Turkey (Turin et al. 1977).

Young beetles hatch at the end of May, are very active during a short period and then enter summer diapause. Reproduction starts towards the end of August, peaks in the second part of September, and sometimes – but not in our area – seems to continue until February (Penney 1966). The species is virtually semelparous (Den Boer 1979). Although consistently macropterous, only a few flight observations have been reported (Lindroth 1945; Nelemans 1983, 1987).

**Study area**

A population of *N. brevicollis* from a small deciduous woodland near the Biological Station of the Agricultural University (Wijster, province of Drenthe, the Netherlands) was studied from 1979 until 1983. Additional data were collected in a woody area near Marum (province of Gron-
Food: have the potential to fly (flight muscles in class IV can withstand flight muscles in classes IV and V were assumed to be traceable fibers (class I). Beetles experimentally induced to fly (flight muscles in class V, some-what show just traceable fibers (class I). Beetles experimental in six classes: class 0 indicates flight muscles, means that there is no trace of any flight muscle at all, whereas class V indicates full grown flight muscles, that enable a beetle to fly. I adapted this classification to N. brevicollis, on the basis of the one hand on beetles that were experimentally induced to fly (flight muscles in class V, sometimes in IV) and on the other hand on newly emerged specimens, that always show just traceable fibers (class I). Beetles with flight muscles in class IV and V were assumed to have the potential to fly (flight muscles in class IV can reasonably be expected to develop into class V, or to be degenerated from class V). Sometimes complete reduction of flight muscles could be distinguished from no development by position and shape of fat bodies in the metathorax. During the reduction process flight muscles are transformed into fat that initially takes the same position and appearance.

Dissections
Before dissecting beetles were kept in formalin. They were examined under a binocular microscope, and the following characteristics were noted: sex, size of the elytron and ala (at an enlargement of 7 x), relative gut content, relative amount of fat, size and maturity of the gonads and development state of the flight muscles, the latter according to Tietze (1963). He divided the musculature of the flight apparatus of insects into (1) flight muscles (direct and indirect ones, according to their functions) and (2) flight joint muscles. Flight muscles can atrophy; flight joint muscles may decrease in number, but still remain traceable, even in consistently brachypterous species. Besides, he mentions the so-called bifunction flight muscles that only are influenced by morphological changes caused by brachypterous degeneration. In this paper I refer to flight muscles of the first type. Tietze (1963) classified these in six classes: class 0 means that there is no trace of any flight muscle at all, whereas class V indicates full grown flight muscles, that enable a beetle to fly. I adapted this classification to N. brevicollis, based on the one hand on beetles that were experimentally induced to fly (flight muscles in class V, sometimes in IV) and on the other hand on newly emerged specimens, that always show just traceable fibers (class I). Beetles with flight muscles in classes IV and V were assumed to have the potential to fly (flight muscles in class IV can reasonably be expected to develop into class V, or to be degenerated from class V). Sometimes complete reduction of flight muscles could be distinguished from no development by position and shape of fat bodies in the metathorax. During the reduction process flight muscles are transformed into fat that initially takes the same position and appearance.

Rearing
In 1980, '81 and '82, beetles for rearing were collected in Wijster both by means of pitfalls and by hand. Experiments were carried out with these beetles and their offspring.

Adults and larvae were kept either in incubators with variable day-lengths or under outside conditions. Generally, feeding and checking occurred weekly, in some experiments more frequently. Larvae and adults were fed with maggots of different sizes, dependent on the size of the beetle or larva. When necessary (e.g. in the experiments with minimal feeding) larvae, maggots and adults were weighed weekly or daily.

More detailed information on the rearing conditions is given by Nelemans (1987). The following treatments were performed (see also Table 1):

1. Rearing from egg till adult (A-I). Food, temperature and day-length varied.
2. Rearing third instar larvae, field-collected by means of pitfalls (J).
3. Feeding experiments with teneral beetles from the breeding experiments, and with young beetles collected in the field as young as possible (only beetles with soft elytra were used).

Ad point 1 and 2. Young beetles were killed after six weeks and dissected.

Ad point 3. In 1981 and 1982 teneral beetles from experiments A and B were separated into two groups — for six

Table 1. Experimental conditions

<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>Food</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>Pupa</th>
<th>Adult</th>
<th>Day-length</th>
</tr>
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<tbody>
<tr>
<td>A</td>
<td>1980-81</td>
<td>+</td>
<td>12° C</td>
<td>12° C</td>
<td>5 w 5° C 12° C</td>
<td>12° C</td>
<td>15° C</td>
<td>same as outside</td>
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<td>B</td>
<td>1981/82</td>
<td>+</td>
<td>12° C</td>
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<td>C</td>
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<td>D</td>
<td>1981/82</td>
<td>+/-</td>
<td>12° C</td>
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<td>E</td>
<td>1981/82</td>
<td>+</td>
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<td>5 w 5° C 12° C</td>
<td>12° C</td>
<td>15° C</td>
<td>same as outside</td>
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<td>F</td>
<td>1981/82</td>
<td>+</td>
<td>8.5° C</td>
<td>9 w 5° C 12° C</td>
<td>12° C</td>
<td>15° C</td>
<td>same as outside</td>
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<td>G</td>
<td>1981/82</td>
<td>+</td>
<td>outside</td>
<td>outside</td>
<td>outside</td>
<td>outside</td>
<td>15° C</td>
<td>same as outside</td>
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<td>H</td>
<td>1981/82</td>
<td>+/-</td>
<td>outside</td>
<td>outside</td>
<td>outside</td>
<td>outside</td>
<td>15° C</td>
<td>same as outside</td>
</tr>
<tr>
<td>I</td>
<td>1982/83</td>
<td>+</td>
<td>12° C</td>
<td>12° C</td>
<td>5 w 5° C 12° C</td>
<td>12° C</td>
<td>15° C</td>
<td>14 L/10 D</td>
</tr>
<tr>
<td>J</td>
<td>1982/83</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>3-5 w 5° C 12° C</td>
<td>12° C</td>
<td>15° C</td>
<td>same as outside</td>
</tr>
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</table>

Food: + + food in excess, 6-9 maggots a week; + food, about 4 maggots a week; +/- minimal food, 1-2 maggots a week

Temperature: Groups F-H were held in an outdoor insectary, and experienced the same temperatures as outside

Day-length: Groups F-H the same as outdoors. In the other groups (except group I) the day-length changed once a week, corresponding with the outdoors situation. In group I from the third instar on larvae and pupae were placed in an incubator with 14 L/10 D. All young beetles were kept under a photoperiod of 16 hours light

Group J: Collected third instar larva with a weight of less than 30 mg were put at 5° C for a period of 5 weeks; larvae with a greater weight for 3 weeks only; thereafter both groups were transferred to 12° C