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# Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova*

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## Summary

On the basis of morphometric measurements of 69 Carabidae species, the dispersal power of beetles at different stages of their physiological development was estimated. As quantitative criteria for estimation of dispersal possibilities the indices of potential migrants (*Ipm*) and conventional load on the wing (*Pf*) were introduced. Among constantly macropterous carabids, three groups of beetles with different levels of wing muscles development were distinguished. Monomorphic macropterous (MMm) species are characterized by the highest flight activity of both sexes throughout imago stage. Though in many di(poly)morphic carabids (DPM species) a proportion of macropterous females in the populations is large, the wing muscles are better developed in macropterous males, which ensures similar migration possibilities of males and females. In populations of polymorphic macropterous (MPm) and DPM species dispersion is carried out mostly by teneral and immature beetles. The maximum loss in flight ability occurs in mature females with developed eggs in ovaries. Large species of ground beetles produce relatively large eggs, which are deposited in a single batch. After the development of gonads, body mass in these species increases sharply, while wing muscles decline. In small-sized carabid species gonads develop gradually and they lay relatively small eggs continuously. The changes in body mass in these species are usually small. Therefore, the temporal changes in the *Pf*-index are more pronounced in large- and medium-sized carabid species compared to small-sized beetles. The dispersal power of carabid beetles in different regions is discussed.

**Key words:** Carabidae, wing apparatus, polymorphism, dispersal power, flight ability

## Introduction

The level of development of the wing apparatus is very important for flight ability in insects. Wing polymorphism in carabid beetles is well studied; constantly macropterous, constantly brachypterous or apterous as well as di- and poly-morphic species are reported (Lindroth 1949; Haeck 1971; Den Boer 1977; Den Boer et al. 1980; Brandmayer 1983; Desender et al. 1986). Different criteria for a quantitative estimation of dispersal power in carabid beetles have been proposed. Lindroth (1949) systematized the available data on wing polymorphism of European carabids and suggested that migration ability depends on the proportion

*This paper was presented at the II (XII) All-Russian Conference on Soil Zoology (Moscow, 1999) of macropterous specimens in a given population. A higher dispersal power is characteristic for constantly macropterous species. However, Den Boer (1977) stressed that this is not necessarily true since some macropterous species have shorter wings. As a quantitative criterion of dispersal power, an index of relative wing surface (a ratio between the surface of wing and elytra) was suggested and three groups of beetles with low, high and uncertain dispersal power were distinguished (A, B and C species, respectively). However, the level of development of wing muscles was not reported, which limits the efficacy of Den Boer's (1977) classification, since the existence of well-developed wings is a necessary but not a sufficient condition for successful flight.

Having studied wing size and muscles in more than 300 species of European carabids, Desender (1989) has shown that in some species the level of development of wing muscles changes during the beetles' life. He distinguished three groups of species, i. e. with functional, undeveloped and degraded wing muscles. According to his data, in macropterous species with functional or degraded wing muscles the size of wings does not differ significantly. By contrast, in macropterous species with undeveloped wing muscles wings are considerably shorter.

Without doubt, polymorphism of both hind wings and wing muscles should be considered together to obtain a more comprehensive estimate of the dispersal power in carabid beetles. Moreover, for understanding of flight dispersal possibilities the sexual and age structure of populations has to be considered. A successful colonisation of new habitats and the search of sexual partners may vary strongly between sexes and depend on age.

The main goals of our study were: (1) to develop quantitative criteria for estimation of the flight dispersal power of carabids, on the basis of a complex study of polymorphism of both hind wings and wing muscles; (2) to compare the dispersal power of different constantly macropterous carabid species; (3) to estimate how the flying possibility differs in males and females, and how this difference changes with development of gonads.

## Materials and Methods

Carabids were collected in the south-western Moldova (flood plain of the Prut river near Kahul, 45°18' N, 28°12' E) in May–October 1990-1991, by means of light, window and pitfall traps and by soil hand-sorting (Matalin 1994) in 10 biotopes: alfalfa, potatoes and winter wheat fields, a vineyard, a walnut grove, a forest belt, reed stands, a flood plain forest and banks of the river Prut and Fundul Roshu brook. Length and width of elytra, maximal length and width of hind wings and live body mass were measured and the development of hind wings, wing muscles and gonads were determined in 69 constantly macropterous and di(poly)morphic carabid species. To estimate the degree of intraspecific variability, at least 30 specimens of each age and both sexes were examined. The conditions of gonads of both sexes were determined after Wallin (1987). The size groups were designated using elytra length after Desender (1989). After standardizing by means of frequency histograms, six size groups were distinguished: I – 1.0–2.99 mm; II – 3.0–4.99 mm; III – 5.0–6.99 mm; IV – 7.0–11.99 mm; V – 12.0–15.99 mm; VI – more than 16.0 mm. The development of hind wings and wing muscles was evaluated according to Den Boer (1977) and Tietze (1963) with modifications of Matalin (1994).

The following indexes were calculated:

(1) index of potential migrants: $Ipm = KI \times MI = Nm / N$;

(2) index of conventional load on the wing: $Pf = M / SW$;

(3) index of relative wing surface (Den Boer 1977): $So = SW / SE$

(KI – index of wing (=Nn/N); MI – index of wing muscle (=Nm/Nn); N – total number of specimens; Nn – number of macropterous specimens; Nm – number of macropterous specimens with functional wing muscles; M – live body mass of a specimen; SW – surface of hind wing, calculated as maximum length × maximum width; SE – surface of elytra, calculated as length × width).

The above indexes were calculated for all studied species and individuals, if applicable. Differences between mean values were tested using Tukey's HSD-test for unequal n (Borovikov 2001).

## Results

*So* of all the 69 species studied was higher than 1.5 (Appendix 1). According to Den Boer (1977), such species are potentially able to fly. During our study all these species were caught by window or light traps, except for *Broscus cephalotes*, which was present in pitfall traps only. This species may not be able to fly due to its small wing surface (*So* = 1.8). In the similar-sized *Pterostichus niger So* was 2.0, and even higher (2.8 – 3.1) in *Calathus halensis*, *Harpalus rufipes*, *Chlaenius spoliatus* and *C. festivus*, which were regularly collected by light or window traps. Hence, *B. cephalotes* was classified as a provisionally macropterous species.

**Table 1.** Means of elytra length (mm) and *Ipm*- and *Pf*-indexes (± SD) of four carabid species groups. Different letters in a row indicate significant difference (Tukey's HSD-test for unequal n, P < 0.05)

| | *MMm species* | *MDm species* | *MPm species* | DPM species |
|---|---|---|---|---|
| Elytra length | 3.48±1.32 a | 3.79±1.65 a | 7.19±2.64 b | 6.38±3.09 b |
| Ipm-index | 1.00±0.00 a | 0.79±0.06 b | 0.53±0.22 c | 0.14±0.14 d |
| Pf-index | 0.35±0.19 a | 1.06±0.10 ab | 1.44±0.78 b | 1.82±0.75 b |

Some other carabids (*Carabus granulatus*, *Poecilus crenuliger*, *Platynus assimile*, *Amara aenea* and *Harpalus picipennis*) also had relative low *So*-values (1.5–2.0). However, all these species were collected by window or light traps during our study.

Polymorphism of wing muscles was frequent in constantly macropterous species. In some of them a degradation of wing muscles was observed during the imago lifespan, and specimens with functional (+m), non-functional (±m) or undeveloped (-m) wing muscles were present in the population. Such species were classified as macropterous with polymorphic state of wing muscles (MPm). Other macropterous species had only two types of wing muscles, functional (+m) or undeveloped (-m). They were classified as macropterous with dimorphic state of wing muscles (MDm). Finally, many species always had functional wing muscles (+m) and are referred to as macropterous with monomorphic state of wing muscles (MMm). In fully-winged specimens of di(poly)morphic carabids polymorphism of wing muscles was also observed. However, there were only few di(poly)morphic species and therefore they were treated as single DPM group (Appendix 1).

The *Imp*-index indicates the proportion of specimens with the ability to fly. Among constantly macropterous carabids MMm species had the highest dispersal power (*Ipm* = 1). In populations of MDm species the abundance of potential migrants was smaller (range 0.7–0.9) and further decreased in MPm species (range 0.1–0.9). DPM species had the lowest migration potential (range 0.01–0.35). The differences

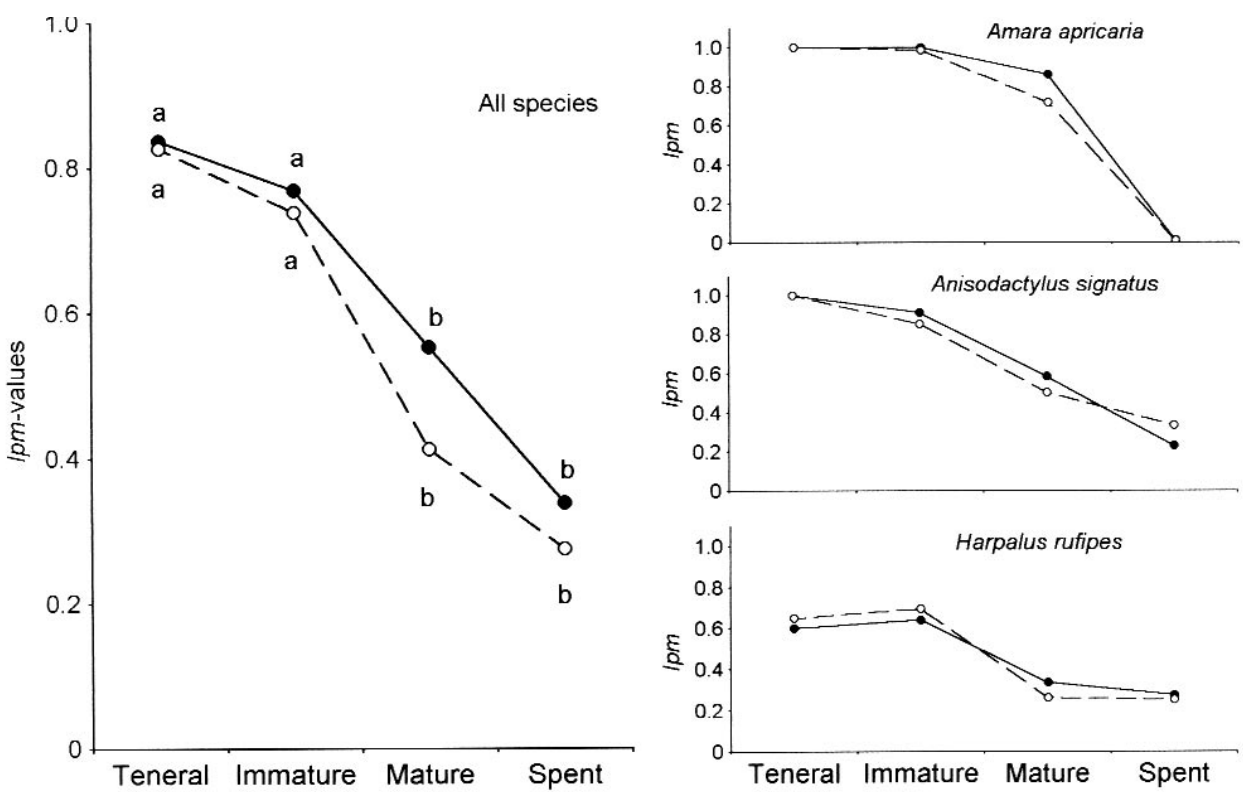


**Fig. 1.** Age changes of *Ipm*-values in MPm, MDm and DPM species. Black circles – males; white circles – females. Different letters indicate significant difference (Tukey's HSD-test for unequal n, P < 0.01). Three MPm species are given as examples

in *Ipm* values between all the groups were significant (Table 1).

The *Ipm*-index allows to estimate quantitatively the dispersal power of beetles of different sexes or ages. For DPM species, both *KI*- (wing development) and *MI*- (wing muscle development) indexes varied broadly. In *Poecilus crenuliger*, *Pterostichus longicollis*, *P. inquinatus*, *Patrobus atrorufus*, *Oxypselaphus obscurum* and *Harpalus picipennis* the *KI* index was larger in females (mean 0.52) than in males (0.45). However, wing muscles were better developed in macropterous males (*MI* male = 0.23; *MI* female = 0.18) that ensured similar migration possibilities of males and females. In MPm species the wing muscles were also better developed in males than in females (data not shown).

In MPm and DPM species the dispersal is mainly accomplished by teneral and immature specimens. As the beetles become older, the fraction of potential migrants decreases due to the development of gonads and reduction of wing muscles, which is faster in females. The fraction of potential migrants (*Ipm*) in mature and spent specimens was on average 60 % lower than in immature beetles (Fig. 1). Thus, in MPm (*Calosoma auropunctatum*, *Clivina fossor*, *C. ypsilon*, *Amara apricaria*, *Anisodactylus signatus*, *Harpalus rufipes*, *H. calceatus*, *Chlaenius vestitus* etc.) and DPM species (*Pterostichus melanarius*, *P. longicollis*, *P. inquinatus*, *Harpalus picipennis*) flight activity peaked in teneral and immature specimens. The activity of flying mature beetles was low, and males predominated among them. Mature and spent beetles were abundant in soil traps before or after flight activity. On the contrary, flight activity in MMm species (*Tachys micros*, *T. fulvicollis*, *Bembidion varium*, *B. minimum*, *Stenolophus discophorus*, *S. mixtus*, *S. proximus*, *Acupalpus luteatus* etc.) was high during the whole season. The activity of immature, mature and spent specimens of both sexes was similar. Moreover, the peaks of flight and ground activity coincided.

The existence of developed hind wings and wing muscles does not guarantee the possibility of active flight. As one of the possible criteria for quantitative estimates of flight activity, the *Pf* index was used, showing energetic cost of flying of a single specimen. The *Pf* indexes of all the species groups overlapped, and the difference was only significant between MMm species and other groups (Table 1). The *Pf* values were at a maximum in mature females due to the development of eggs and increase in body mass.

The MMm and in MDm species were small or medium-sized beetles (I–III size groups) and their *Pf*-values only slightly increased from immature to mature specimens: by 0.05–0.35 units in females and 0.01–0.1 units in males (Fig. 2). A large part (10–42 %) of flying mature MMm females had developed eggs in their ovaries (Table 2).

On the contrary, in medium- and large-sized MPm and DPM species (IV–VI size groups) the changes of Pf-values from immature to mature females were much larger, ranging from 0.1–0.4 (*Poecilus cupreus*, *Amara apricaria*, *Harpalus calceatus*, *Anisodactylus signatus*, *Chlaenius vestitus* etc.) to 0.5–0.8 (e.g. *Harpalus rufipes*, *Calosoma auropunctatum*, *Pterostichus melanarius*, *P. niger*). Females with developed eggs were rarely collected by light traps; the ones which were captured had smaller numbers of eggs than the females caught by pitfall traps (Table 2). The differences between *Pf*-values in immature and mature males were within 0.2–0.4 units (Fig. 3).

**Table 2.** Proportion of gravid females and numbers of eggs per female in dominant carabid species sampled by light and pitfall traps (flood plain and second terrace of Prut river, 1990)

| Species | Size group | Wing/Muscle groups | *Light traps* | | | *Pitfall traps* | | |
|---|---|---|---|---|---|---|---|---|
| | | | Total number of females | Females with eggs (%) | Eggs per female (mean ± SD) | Total number of females | Females with eggs (%) | Eggs per female (mean ± SD) |
| *Tachys micros* (F.-W.) | I | MMm | 1027 | 11.1 | 1.5±0.9 | 550 | 45.5 | 4.6±3.1 |
| *Stenolophus discophorus* (F.-W.) | II | MMm | 1356 | 40.1 | 2.4±1.8 | 159 | 48.7 | 4.1±2.3 |
| *Stenolophus mixtus* (Herbst) | II | MMm | 2738 | 38.0 | 2.0±1.2 | 630 | 46.8 | 4.1±2.1 |
| *Clivina fossor* (L.) | II | MPm | 179 | 11.2 | 1.2±0.4 | 31 | 47.1 | 2.7±1.4 |
| *Anisodactylus signatus* (Panz.) | III | MPm | 134 | 5.2 | 2.6±1.9 | 177 | 50.3 | 5.3±4.2 |
| *Harpalus calceatus* (Duft.) | III | MPm | 716 | 2.4 | 1.6±0.8 | 90 | 20.0 | 7.4±3.0 |
| *Harpalus rufipes* (Deg.) | IV | MPm | 589 | 1.7 | 1.1±0.3 | 1556 | 37.8 | 4.4±3.1 |
| *Calathus halensis* (Schall.) | IV | MPm | 90 | 1.1 | 2.5±2.1 | 91 | 27.5 | 10.2±5.5 |
| *Carabus granulatus* L. | V | DPM | 4 | 0 | – | 30 | 43.3 | 9.0±6.8 |
| *Calosoma auropunctatum* (Herbst) | VI | MPm | 12 | 0 | – | 24 | 62.5 | 9.9±6.5 |

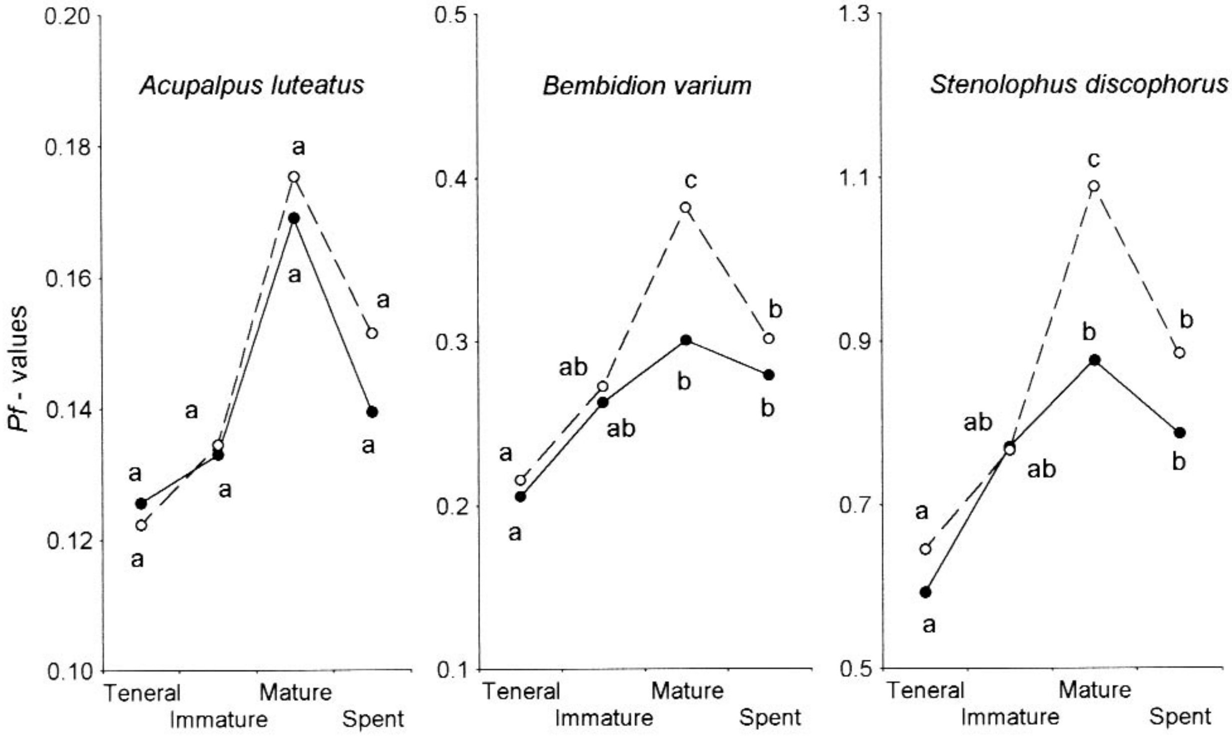


**Fig. 2.** Age changes of *Pf*-values MMm species. Black circles – males; white circles – females. Different letters indicate significant difference (Tukey's HSD-test for unequal n, $P < 0.01$)

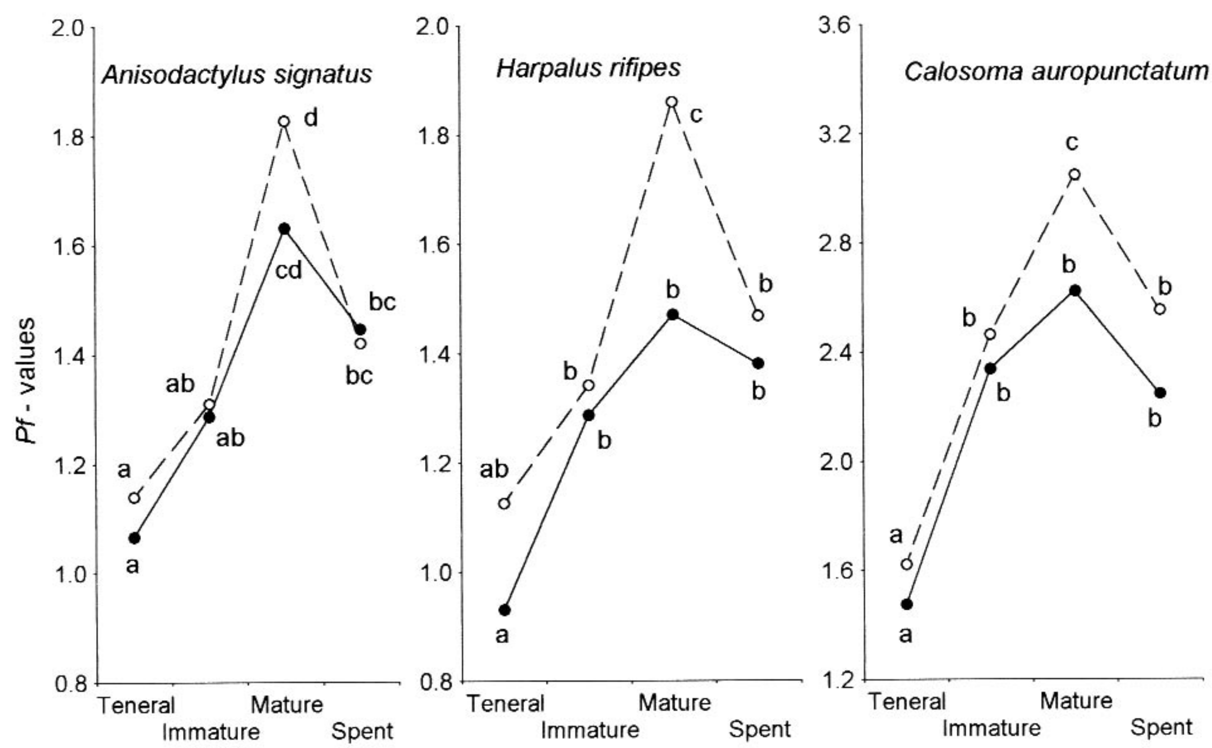


**Fig. 3.** Age changes of *Pf*-values MPm species. Black circles – males; white circles – females. Different letters indicate significant difference (Tukey's HSD-test for unequal n, $P < 0.01$)

## Discussion

Our study confirms the occurrence of polymorphism of wing muscles in carabid beetles (Meijer 1974; Den Boer et al. 1980; Desender et al. 1986; Desender 1989). Wing muscles are known to degrade with increase in body mass (Den Boer 1971). Meijer (1974) and Van Huizen (1977) assumed that eggs are developing at the cost of wing muscles. On the other side, the development of wing muscles may result in a 20 % reduction of the size of gonads (Dixon et al. 1993). Females of large and some medium-sized carabid species produce relatively large eggs, which are deposited in a single batch (Brandmayer & Zetto Brandmayer 1979; Fazekas et al. 1999). After the development of gonads, body mass in these species increases sharply and wing muscles decline. Hence, in these species the abundance of flying mature specimens is low. Our data suggest that mature females of larger carabids (V and VI size groups) have very limited flight possibilities (high *Pf*-index). Presumably, they do not fly at all since no mature females were caught in light traps (Table 2). It is known that there is a threshold of body mass above which active flight in insects becomes energetically disadvantageous or even impossible (Casey 1981; Gorodnitskiy 1996).

Females of small and some medium-sized species (*Brachinus*, *Bembidion*, *Acupalpus*, *Stenolophus*, several *Calathus* and *Pterostichus*) produce relatively small eggs. Their gonads develop gradually and eggs are laid continuously in small batches or one by one (Van Dijk 1979; Heessen 1980); the changes in body mass of those beetles are small. Therefore, in mature females of smaller species (I and II size groups) the reduction of flight ability was low. Their catches in light traps were high and the number of developed eggs in the females from pitfall and light traps was similar. In medium-sized beetles (III and IV size groups) the reduction of flight ability was more pronounced. Mature females of these species were rare in light traps and had low numbers of developed eggs in their ovaries. On the contrary, in pitfall traps the abundance of mature females and the number of eggs in their ovaries was high (Table 2).

*So*-, *Ipm*- and *Pf*-values may vary in the different climatic zones or habitats, which may be explained by variability of environmental conditions (Den Boer et al. 1980; Desender 1989). For example, *Bembidion tetracolum* is known to be wing-polymorphic in Holland (Den Boer et al. 1980), Belgium (Desender 1989) and Mordovia (P. Budilov, pers. comm.), while in south-western Moldova it is constantly apterous. In Holland (Den Boer 1977; Den Boer et al. 1980), Belgium (Desender & Pollet 1985) and southern Quebec (Levesque & Levesque 1994) *Clivina fossor* is wing-polymorphic, but in south-western Moldova it is constantly macropterous with wing muscles degrading during the beetles' life (Matalin 1994). The relative wing surface (*So*) of *C. fossor* is 2.7 in Holland (Den Boer 1977; Den Boer et al. 1980), but reaches 4.5 in Moldova. Similarly, *Platynus assimile* (*So* = 1.5) were collected by window and light traps in Moscow region and Moldova (Samkov & Belov 1988; Karpova & Matalin 1992; this study), while in Holland *So*-value for *P. assimile* was only 1.3 and no specimens were collected by window traps (Den Boer 1977; Den Boer et al. 1980). In *Pterostichus niger So*-value was 2.0 in this study, but only 1.2 in Holland (Den Boer 1977; Den Boer et al. 1980). On the contrary, in *Harpalus rufipes* and *Anchomenus dorsalis* the average *So*-values were similar both in Holland (Den Boer et al. 1980) and in Moldova (2.8–2.9 and 2.1, respectively).

Lindroth (1949) suggested that the regions with predominantly brachypterous populations of ground beetles were colonised first. This may also be true for species with polymorphic state of wing muscles. Thus, in oldest populations of MPm carabid species the values of *IPM* index should be low. On the contrary, the high values are expected in marginal populations.

It can be concluded that in macropterous beetles with monomorphic wing muscles (MMm species) flying ability is at a maximum. In these species beetles of both sexes and all ages participate in dispersion. In other constantly macropterous and di(poly)morphic species many specimens do not fly because their wing muscles degrade during the beetles' life, or due to the increase in body mass as a result of gonad development. Dispersal in these species is carried out by teneral and immature beetles of both sexes, but predominately by males. *Ipm*- and *Pf*-indices allowed to measure and classify the dispersal power of ground beetles and to elucidate changes in flight ability in carabid species in different climatic zones.

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**Appendix 1.** Morphometric data, body mass and indexes characterizing flight ability (means ± SD) in 69 carabid species. SG – Size group; W/M – wing/muscle group; MMm – MMm species; MDm – MDm species; MPm – MPm species; (pm) – provisionally macropterous species; DPM – DPM species; *KI* – index of wing; *MI* – index of wing muscle; *Ipm* – index of potential migrants; *Pf* – index of conventional load on the wing; *So* – index of relative wing surface

| Species | W/M | SG | Morphometric data (mm) | | | | Body mass (mg) | Indexes | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Wing length | Wing width | Elytral length | Elytral width | | *KI* | *MI* | *Ipm* | *Pf* | *So* |
| *Tachys micros* (F.-W.) | MMm | I | 2.7±0.1 | 1.1±0.1 | 1.5±0.1 | 0.4±0.1 | 0.5±0.1 | 1.00 | 1.00 | 1.00 | 0.17±0.03 | 4.8±0.1 |
| *Tachys fulvicollis* (Dej.) | MMm | I | 2.6±0.1 | 1.1±0.1 | 1.5±0.1 | 0.4±0.1 | 0.5±0.1 | 1.00 | 1.00 | 1.00 | 0.16±0.03 | 4.4±0.6 |
| *Bembidion minimum* (F.) | MMm | I | 3.2±0.1 | 1.3±0.1 | 1.8±0.1 | 0.6±0.1 | 1.1±0.2 | 1.00 | 1.00 | 1.00 | 0.26±0.03 | 3.7±0.2 |
| *Bembidion varium* (Ol.) | MMm | I | 5.5±0.2 | 1.9±0.1 | 2.8±0.1 | 1.0±0.1 | 3.3±0.7 | 1.00 | 1.00 | 1.00 | 0.31±0.05 | 3.8±0.2 |
| *Bembidion fumigatum* (Duft.) | MMm | I | 5.2±0.1 | 1.9±0.1 | 2.4±0.1 | 0.8±0.1 | 1.9±0.1 | 1.00 | 1.00 | 1.00 | 0.23±0.01 | 5.1±0.1 |
| *Bembidion tenellum* Ěr. | MMm | I | 3.3±0.1 | 1.3±0.1 | 1.7±0.1 | 0.7±0.1 | 0.9±0.2 | 1.00 | 1.00 | 1.00 | 0.21±0.04 | 3.6±0.2 |
| *Bembidion latiplaga* Chaud. | MMm | I | 3.2±0.1 | 1.3±0.1 | 1.8±0.01 | 0.6±0.1 | 1.2±0.3 | 1.00 | 1.00 | 1.00 | 0.29±0.06 | 3.9±0.1 |
| *Acupalpus luteatus* (Duft.) | MMm | I | 3.3±0.1 | 1.5±0.1 | 1.7±0.1 | 0.6±0.1 | 0.8±0.2 | 1.00 | 1.00 | 1.00 | 0.16±0.05 | 4.8±0.4 |
| *Acupalpus suturalis* Dej. | MMm | I | 4.1±0.1 | 1.6±0.1 | 2.2±0.1 | 0.7±0.1 | 1.6±0.2 | 1.00 | 1.00 | 1.00 | 0.24±0.02 | 4.1±0.4 |
| *Acupalpus parvulus* (Sturm) | MMm | I | 4.8±0.1 | 1.9±0.1 | 2.7±0.1 | 0.9±0.1 | 2.4±0.2 | 1.00 | 1.00 | 1.00 | 0.26±0.02 | 4.1±0.3 |
| *Anthracus consputus* (Duft.) | MMm | I | 5.3±0.1 | 2.2±0.1 | 3.0±0.1 | 1.0±0.1 | 2.3±0.5 | 1.00 | 1.00 | 1.00 | 0.21±0.04 | 4.0±0.3 |
| *Clivina fossor* (L.) | MPm | II | 6.6±0.3 | 2.4±0.2 | 3.6±0.2 | 1.0±0.1 | 5.6±1.4 | 1.00 | 0.62±0.41 | 0.62±0.41 | 0.42±0.07 | 4.5±0.4 |
| *Clivina ypsilon* Dej. | MPm | II | 6.7±0.1 | 2.3±0.1 | 3.8±0.1 | 0.8±0.1 | 7.0±1.4 | 1.00 | 0.81±0.12 | 0.81±0.12 | 0.45±0.08 | 4.7±0.3 |
| *Clivina laevifrons* Chaud. | MMm | II | 6.5±0.1 | 2.4±0.1 | 3.5±0.1 | 0.8±0.1 | 4.8±0.5 | 1.00 | 1.00 | 1.00 | 0.31±0.03 | 5.9±0.5 |
| *Omophron limbatum* (F.) | MDm | II | 6.7±0.2 | 2.9±0.1 | 3.8±0.4 | 2.2±0.1 | 19.6±3.3 | 1.00 | 0.82±0.21 | 0.82±0.21 | 1.02±0.12 | 2.3±0.1 |
| *Bembidion dentellum* (Thungb.) | MMm | II | 6.8±0.2 | 2.5±0.1 | 3.5±0.2 | 1.3±0.1 | 4.8±0.9 | 1.00 | 1.00 | 1.00 | 0.28±0.05 | 4.0±0.2 |
| *Pterostichus longicollis* (Duft.) | DPM | II | 6.9±0.1 | 2.5±0.1 | 4.0±0.1 | 1.2±0.1 | 9.5±0.3 | 0.63±0.13 | 0.18±0.17 | 0.11±0.02 | 0.55±0.01 | 3.5±0.1 |
| *Anchomenus dorsalis* (Pontop.) | MPm | II | 5.9±0.2 | 2.3±0.2 | 4.3±0.1 | 1.5±0.1 | 13.9±3.9 | 1.00 | 0.57±0.09 | 0.57±0.09 | 1.01±0.21 | 2.1±0.1 |
| *Oxypselaphus obscurum* (Herbst) | DPM | II | 5.6±0.1 | 2.3±0.1 | 3.5±0.1 | 1.4±0.1 | 12.0±1.1 | 0.02±0.01 | 0.07±0.03 | 0.002±0.001 | 0.93±0.03 | 2.6±0.1 |
| *Agonum thorey* (Dej.) | MMm | II | 7.5±0.1 | 2.7±0.1 | 4.5±0.1 | 1.3±0.1 | 9.2±0.2 | 1.00 | 1.00 | 1.00 | 0.45±0.03 | 3.4±0.1 |
| *Amara bifrons* (Gyll.) | MPm | II | 6.9±0.3 | 2.6±0.1 | 4.1±0.2 | 1.3±0.1 | 12.8±1.1 | 1.00 | 0.72±0.17 | 0.72±0.17 | 0.71±0.01 | 3.5±0.1 |
| *Ophonus azureus* (F.) | MMm | II | 8.3±0.4 | 3.1±0.1 | 4.5±0.4 | 1.5±0.1 | 14.8±0.3 | 1.00 | 1.00 | 1.00 | 0.58±0.04 | 3.8±0.4 |
| *Ophonus rupicola* (Sturm) | MMm | II | 9.5±0.1 | 3.6±0.1 | 4.8±0.3 | 1.7±0.1 | 18.5±0.1 | 1.00 | 1.00 | 1.00 | 0.54±0.03 | 4.3±0.2 |
| *Stenolophus discophorus* (F.-W.) | MMm | II | 7.5±0.5 | 2.7±0.2 | 4.2±0.2 | 1.2±0.1 | 10.6±2.5 | 1.00 | 1.00 | 1.00 | 0.52±0.08 | 4.1±0.1 |
| *Stenolophus proximus* Dej. | MMm | II | 7.1±0.2 | 2.8±0.1 | 3.9±0.2 | 1.2±0.1 | 7.0±2.0 | 1.00 | 1.00 | 1.00 | 0.35±0.08 | 4.2±0.2 |
| *Stenolophus mixtus* (Herbst) | MMm | II | 7.2±0.1 | 2.8±0.1 | 3.7±0.1 | 1.2±0.1 | 6.7±1.6 | 1.00 | 1.00 | 1.00 | 0.34±0.07 | 4.3±0.2 |
| *Stenolophus skrimshiranus* Steph. | MMm | II | 7.3±0.3 | 2.7±0.1 | 4.2±0.1 | 1.4±0.1 | 9.7±2.2 | 1.00 | 1.00 | 1.00 | 0.48±0.08 | 3.5±0.1 |
| *Stenolophus persicus* Mnnh. | MMm | II | 6.9±0.1 | 2.6±0.1 | 4.4±0.2 | 1.4±0.1 | 10.6±0.2 | 1.00 | 1.00 | 1.00 | 0.58±0.01 | 2.9±0.1 |
| *Badister dilatatus* (Chaud.) | MMm | II | 5.6±0.1 | 2.1±0.1 | 3.2±0.1 | 1.1±0.1 | 2.3±0.4 | 1.00 | 1.00 | 1.00 | 0.19±0.03 | 3.3±0.1 |
| *Badister unipustulatus* Bon. | MMm | II | 7.6±0.1 | 2.8±0.1 | 4.4±0.1 | 1.5±0.1 | 6.6±0.1 | 1.00 | 1.00 | 1.00 | 0.31±0.01 | 3.3±0.1 |
| *Polystichus connexus* (Fourcr.) | MMm | II | 8.2±0.2 | 3.1±0.1 | 4.8±0.1 | 1.5±0.1 | 14.6±1.4 | 1.00 | 1.00 | 1.00 | 0.58±0.08 | 3.4±0.1 |
| *Cicindela germanica* L. | MDm | III | 9.9±0.3 | 3.7±0.3 | 6.5±0.4 | 2.2±0.1 | 41.8±7.4 | 1.00 | 0.85±0.05 | 0.85±0.05 | 1.12±0.08 | 2.6±0.1 |
| *Poecilus cupreus* (L.) | MPm | III | 11.3±0.4 | 4.6±0.1 | 7.8±0.2 | 2.9±0.1 | 89.1±6.8 | 1.00 | 0.53±0.25 | 0.53±0.25 | 1.71±0.07 | 2.3±0.1 |
| *Poecilus crenuliger* Chaud. | DPM | III | 10.1±0.5 | 3.9±0.2 | 8.0±0.2 | 2.5±0.1 | 78.8±8.0 | 0.51±0.02 | 0.14±0.05 | 0.07±0.03 | 2.03±0.01 | 1.9±0.1 |
| *Pterostichus inquinatus* (Sturm) | DPM | III | 9.3±0.1 | 3.6±0.1 | 5.7±0.1 | 1.6±0.1 | 24.6±1.1 | 0.81±0.05 | 0.21±0.06 | 0.17±0.04 | 0.73±0.02 | 3.6±0.1 |
| *Pterostichus anthracinus* (Ill.) | MDm | III | 10.3±0.4 | 3.6±0.2 | 6.7±0.2 | 2.0±0.1 | 60.0±6.6 | 1.00 | 0.87±0.07 | 0.87±0.07 | 1.65±0.03 | 2.7±0.2 |

**Appendix 1 continued (i)**

| Species | W/M | SG | Morphometric data (mm) | | | | Body mass (mg) | Indexes | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Wing length | Wing width | Elytral length | Elytral width | | *KI* | *MI* | *Ipm* | *Pf* | *So* |
| *Pathrobus athrorufus* (Ström) | DPM | III | 8.6±0.1 | 3.1±0.1 | 5.9±0.1 | 1.9±0.1 | 35.9±4.1 | 0.31±0.04 | 0.12±0.03 | 0.04±0.001 | 1.36±0.11 | 2.3±0.1 |
| *Platynus assimile* (Payk.) | MPm | III | 8.1±0.2 | 3.1±0.1 | 6.8±0.3 | 2.5±0.1 | 57.6±1.2 | 1.00 | 0.36±0.07 | 0.36±0.07 | 2.32±0.11 | 1.5±0.1 |
| *Agonum lugens* (Duft.) | MPm | III | 9.2±0.2 | 3.5±0.2 | 6.3±0.1 | 2.0±0.1 | 30.0±2.5 | 1.00 | 0.83±0.09 | 0.83±0.09 | 0.91±0.05 | 2.5±0.2 |
| *Agonum gracilipes* (Duft.) | MMm | III | 8.8±0.1 | 3.4±0.1 | 5.2±0.1 | 1.7±0.1 | 15.5±2.7 | 1.00 | 1.00 | 1.00 | 0.52±0.08 | 3.5±0.2 |
| *Amara aenea* (Deg.) | MPm | III | 5.8±0.1 | 2.6±0.1 | 5.0±0.2 | 1.5±0.1 | 26.5±1.3 | 1.00 | 0.37±0.03 | 0.37±0.03 | 1.81±0.01 | 2.0±0.1 |
| *Amara similata* (Gyll.) | MPm | III | 8.8±0.1 | 3.5±0.1 | 6.0±0.1 | 2.1±0.1 | 43.2±0.9 | 1.00 | 0.68±0.17 | 0.68±0.17 | 1.41±0.02 | 2.5±0.1 |
| *Amara ovata* (F.) | MPm | III | 8.6±0.1 | 3.6±0.1 | 5.9±0.1 | 2.1±0.01 | 41.9±2.6 | 1.00 | 0.61±0.06 | 0.61±0.06 | 1.38±0.05 | 2.5±0.1 |
| *Amara apricaria* (Payk.) | MPm | III | 8.9±0.5 | 3.4±0.1 | 5.1±0.1 | 1.7±0.1 | 24.3±3.3 | 1.00 | 0.71±0.43 | 0.71±0.43 | 0.81±0.09 | 3.6±0.2 |
| *Amara consularis* (Duft.) | MPm | III | 10.3±0.2 | 4.3±0.2 | 5.3±0.1 | 2.3±0.1 | 35.5±4.2 | 1.00 | 0.75±0.06 | 0.75±0.06 | 0.81±0.04 | 3.7±0.1 |
| *Curtonotus convexiusculus* (Marsh.) | MPm | III | 12.3±0.6 | 4.6±0.2 | 7.2±0.2 | 2.3±0.1 | 56.6±4.7 | 1.00 | 0.84±0.21 | 0.84±0.21 | 0.99±0.08 | 3.6±0.3 |
| *Anisodactylus signatus* (Panz.) | MPm | III | 12.8±0.6 | 4.7±0.2 | 7.9±0.1 | 3.2±0.1 | 85.8±14.2 | 1.00 | 0.84±0.15 | 0.84±0.15 | 1.42±0.27 | 2.4±0.2 |
| *Harpalus calceatus* (Duft.) | MPm | III | 14.3±0.6 | 5.3±0.3 | 8.2±0.4 | 2.4±0.1 | 84.5±12.1 | 1.00 | 0.72±0.14 | 0.72±0.14 | 1.11±0.08 | 3.9±0.1 |
| *Harpalus griseus* (Panz.) | MPm | III | 10.6±0.5 | 4.4±0.1 | 6.3±0.1 | 2.1±0.2 | 39.0±2.8 | 1.00 | 0.52±0.18 | 0.52±0.18 | 0.83±0.07 | 3.6±0.2 |
| *Harpalus serripes* (Quens.) | MPm | III | 10.8±0.4 | 4.5±0.1 | 6.6±0.2 | 2.2±0.1 | 68.4±8.2 | 1.00 | 0.26±0.02 | 0.26±0.02 | 1.42±0.12 | 3.4±0.1 |
| *Harpalus picipennis* Duft. | DPM | III | 5.2±0.1 | 2.1±0.1 | 5.1±0.1 | 1.1±0.1 | 26.3±3.0 | 0.51±0.07 | 0.71±0.1 | 0.36±0.01 | 2.38±0.31 | 2.0±0.1 |
| *Harpalus froelichi* Sturm | MMm | III | 8.9±0.4 | 3.4±0.1 | 5.5±0.3 | 1.7±0.1 | 34.7±0.6 | 1.00 | 1.00 | 1.00 | 1.15±0.11 | 3.3±0.1 |
| *Harpalus affinis* (Schrank) | MPm | III | 9.3±0.1 | 3.4±0.1 | 6.1±0.1 | 2.3±0.1 | 52.3±3.6 | 1.00 | 0.62±0.14 | 0.62±0.14 | 1.66±0.13 | 2.3±0.1 |
| *Harpalus distinguendus* (Duft.) | MPm | III | 9.3±0.1 | 3.4±0.1 | 5.9±0.2 | 2.1±0.1 | 43.4±8.2 | 1.00 | 0.35±0.24 | 0.35±0.24 | 1.36±0.26 | 2.5±0.2 |
| *Chlaenius nigricornis* (F.) | MPm | III | 9.3±0.1 | 3.5±0.1 | 6.9±0.1 | 2.2±0.1 | 59.2±7.6 | 1.00 | 0.41±0.05 | 0.41±0.05 | 1.81±0.21 | 2.2±0.1 |
| *Chlaenius nitidulus* (Schrank) | MPm | III | 9.3±0.1 | 3.5±0.1 | 6.8±0.2 | 2.3±0.1 | 56.7±0.9 | 1.00 | 0.43±0.04 | 0.43±0.04 | 1.75±0.02 | 2.1±0.1 |
| *Chlaenius vestitus* (Payk.) | MPm | III | 10.3±0.6 | 4.0±0.2 | 6.4±0.2 | 2.3±0.1 | 39.7±7.4 | 1.00 | 0.43±0.24 | 0.43±0.24 | 0.97±0.17 | 2.7±0.1 |
| *Brachinus elegans* Chaud. | MPm | III | 8.3±0.1 | 3.3±0.1 | 5.3±0.2 | 1.9±0.1 | 25.6±2.7 | 1.00 | 0.65±0.28 | 0.65±0.28 | 0.93±0.08 | 2.8±0.1 |
| *Brachinus plagiatus* Reiche | MMm | III | 10.3±0.1 | 3.8±0.1 | 6.1±0.1 | 2.1±0.1 | 35.1±4.8 | 1.00 | 1.00 | 1.00 | 0.91±0.11 | 3.0±0.1 |
| *Broscus cephalotes* (L.) | (pm) | IV | 14.9±0.8 | 5.3±0.4 | 11.6±1.0 | 3.7±0.3 | 295.9±53.1 | 1.00 | 0.13±0.15 | 0.13±0.15 | 3.72±0.47 | 1.8±0.1 |
| *Pterostichus macer* (Marsh.) | MPm | IV | 12.6±0.2 | 4.7±0.2 | 8.1±0.2 | 2.4±0.1 | 89.5±9.0 | 1.00 | 0.13±0.15 | 0.13±0.15 | 1.51±0.17 | 3.0±0.1 |
| *Pterostichus melanarius* (Ill.) | DPM | IV | 15.6±0.1 | 5.5±0.1 | 9.8±0.6 | 3.3±0.1 | 185.1±22.3 | 0.42±0.13 | 0.14±0.06 | 0.06±0.02 | 2.17±0.24 | 2.6±0.2 |
| *Pterostichus niger* (Schall.) | MPm | IV | 16.5±0.3 | 5.6±0.3 | 11.1±0.7 | 4.2±0.2 | 239.9±53.8 | 1.00 | 0.25±0.09 | 0.25±0.09 | 2.58±0.56 | 2.0±0.1 |
| *Calathus halensis* (Schall.) | MPm | IV | 15.7±0.5 | 5.5±0.1 | 10.1±0.1 | 3.1±0.1 | 134.1±1.2 | 1.00 | 0.33±0.11 | 0.33±0.11 | 1.56±0.04 | 2.8±0.1 |
| *Harpalus rufipes* (Deg.) | MPm | IV | 15.0±0.2 | 5.3±0.2 | 8.6±0.3 | 3.1±0.1 | 122.2±15.8 | 1.00 | 0.43±0.12 | 0.43±0.17 | 1.53±0.18 | 2.9±0.2 |
| *Chlaenius spoliatus* (Rossi) | MPm | IV | 16.3±0.8 | 6.1±0.4 | 10.1±0.1 | 3.1±0.3 | 156.7±3.6 | 1.00 | 0.42±0.09 | 0.42±0.09 | 1.59±0.13 | 3.1±0.1 |
| *Chlaenius festivus* (Panz.) | MPm | IV | 16.9±0.8 | 6.5±0.2 | 9.6±0.5 | 3.7±0.3 | 142.4±37.9 | 1.00 | 0.35±0.09 | 0.35±0.09 | 1.31±0.24 | 3.1±0.2 |
| *Carabus granulatus* L. | DPM | V | 16.9±0.1 | 6.5±0.1 | 12.9±0.9 | 4.8±0.1 | 341.9±49.0 | 0.82±0.05 | 0.41±0.03 | 0.32±0.05 | 3.11±0.46 | 1.8±0.1 |
| *Calosoma auropunctatum* (Herbst) | MPm | VI | 26.8±1.1 | 10.5±0.6 | 16.6±0.8 | 6.0±0.2 | 684.6±147.6 | 1.00 | 0.82±0.21 | 0.82±0.21 | 2.41±0.45 | 2.8±0.1 |