



To fly or not to fly: Factors influencing the flight capacity of carabid beetles (Coleoptera: Carabidae)

STEPHEN VENN

Department of Environmental Sciences, P.O. Box 65 (Viikinkaari 2a), University of Helsinki, FI-00014, Finland;
e-mail: stephen.venn@helsinki.fi

Key words. Coleoptera, Carabidae, aeroplankton, anemohydrochoric dispersal, autolysis, biogeography, brachyptery, colonization, dispersal, disturbance, flight muscle, flight wing, histolysis, macroptery, migration, oogenesis flight syndrome

Abstract. This review considers factors affecting the flight capacity of carabid beetles and the implications of flight for carabids. Studies from the Dutch polders in particular show that young populations of carabids consist predominantly of macropterous species and macropterous individuals of wing-dimorphic species. Also populations of wing-dimorphic carabid species at the periphery of their geographical range contain high proportions of macropterous individuals. However, studies from Baltic archipelagos show that older populations of even highly isolated island habitats contain considerable proportions of brachypterous species and individuals. This suggests that macroptery is primarily an adaptation for dispersal and that there exists a mechanism for subsequently reducing the ratio of macropterous to brachypterous species under stable conditions, due to the competitive advantage of brachyptery. Populations in isolated habitats, such as islands and mountains, have high proportions of brachypterous species. Many macropterous species do not possess functional flight muscles. Species of unstable habitats, such as tree canopies and wet habitats, are mostly macropterous. Brachypterous species tend to disappear from disturbed habitats. There is uncertainty regarding the extent to which carabid dispersal is directed and how much passive. Both Den Boer and Lindroth recognized that mostly macropterous individuals of macropterous and wing-dimorphic species disperse and found new populations, after which brachyptery tends to rapidly appear and proliferate in the newly founded population. It is most likely that the allele for brachyptery would arrive via the dispersal of gravid females which had mated with brachypterous males prior to emigration. Whilst many studies consider wing morphology traits of carabid beetles to be species-specific and permanent, a number of studies have shown that the oogenesis flight syndrome, whereby females undertake migration and subsequently lose their flight muscles by histolysis before eventually regenerating them after reproducing, has been reported for a growing number of carabid species. Wing morphology of carabid beetles clearly offers strong potential for the study of population dynamics. This field of study flourished during the 1940's to the late 1980's. Whilst a considerable amount of valuable research has been performed and published, the topic clearly holds considerable potential for future study.

1. WING MORPHOLOGY IN CARABID BEETLES

Carabid beetles are one of a number of insect taxa that exhibit variable patterns of wing morphology, as a result of which there are considerable differences in the dispersal potential of different species and even between different populations and individuals within the same species. Regarding wing morphology, the Carabidae include species that possess fully developed wings (macropterous), reduced wings (brachypterous) or vestigial wings (micropterous). As far as I am aware, there are no apterous species of Carabidae. A number of ecological studies (e.g. Kavanaugh, 1985; Aukema, 1995; Venn, 2007) consider the ecological implications of this phenomenon, and a broad and diverse literature and data on such traits of carabid beetles is generally available (Homburg et al., 2013). In this paper, I present a review of studies on the significance and implications of these differences in the trait of flight capac-

ity, with the aim of facilitating accurate consideration of the role of flight in ecological studies in particular.

The phenomenon of wing-dimorphism or polymorphism in insects was described already by Sahlberg in 1868 (fide Lindroth, 1992), and prior to this, Wollaston (1854) had observed that more than a third of the indigenous beetle species of the island of Madeira possessed reduced wings. Darwin (1872) considered the question of why island faunas generally contain much higher proportions of species with reduced wings. As an explanation, he suggested that flight capable beetle species “are blown away or straggle away from exposed environments” leading to a reduction in their number. Whilst Darwin’s suggestion is not very convincing, Lindroth (1949, 1953) has pointed out that flying constitutes reduced fitness of macropterous individuals in any locations surrounded by inhospitable environments.

Jackson (1933) reported that many beetle species, particularly in the families Curculionidae and Chrysomelidae, possess fully developed wings but non-functional flight muscles and it has been suggested (Darlington, 1943; Thiele, 1977), and confirmed (Tietze, 1963), that the same is also true of many carabid species. Darlington (1943) assumed that all Carabidae are descended from full-winged ancestors, as did Den Boer (1971), and that the majority of extant species are flight capable. Thiele (1977) suggested that these have subsequently evolved into polymorphic and dimorphic species. Whilst mountains and islands have been reported as having high proportions of brachypterous carabid species, there are also examples of areas with 100% full-winged species, such as the Barro Colorado wet lowland rainforest of Panama (Darlington, 1943). Darlington also found that arboreal and hygrophilic carabid species are almost invariably full-winged and suggested that this was due to the necessity of frequent dispersal in patchy and unstable habitats.

Application of the term wing-dimorphism to a species implies that it exhibits only two wing morphologies: brachypterous or macropterous, whereby Mendelian inheritance is likely to determine their proportions. However, Lindroth also observed that there are a considerable number of carabid species with more or less continuous variation in wing morphology between full-winged and reduced-winged (Lindroth, 1992), for which the term polymorphic would be appropriate. The Carabidae also include a number of species in which the wings are vestigial, being reduced to a small scale, such as *Trechus secalis* (Paykull, 1790), for instance. For these species, the term micropterous is more appropriate than brachypterous.

The study of wing morphology in carabid beetles by a number of eminent researchers during the period from the 1940's to the 1970's, led to intensive speculation about the ecological and evolutionary significance of dispersal, in which the main protagonists were Den Boer and Lindroth. In 1969, Den Boer hosted a symposium on the topic of "Dispersal and Dispersal Power in Carabid Beetles". Nine papers on the topic, as well as discussion sessions from the symposium, are reported and presented in Den Boer (1971b). Subsequent work on the topic resulted in a series of papers by Den Boer (e.g. 1977), a major volume by Lindroth (1992) that was collated and edited by Erwin and published posthumously in 1992, and a major contribution by Thiele (1977), as well as numerous papers by other workers in the field (e.g. Meijer, 1974; Van Huizen, 1979; Aukema, 1986).

My own studies of data on wing-length within species (Venn, 2007) and those of Desender (1989a) suggest that (1) the term wing-polymorphic is more appropriate than dimorphic as a general term for describing species containing macropterous and brachypterous individuals, though dimorphic is appropriate for any species that can be demonstrated as constantly producing two cohorts, without individuals of intermediate wing-length and (2) even if analysis of large datasets suggests a species is monomor-

phic, this does not exclude the possibility of subsequently generating individuals of an alternative wing morphology.

The second of these conclusions clearly has implications for the identification of species using keys, where a number of similar species are distinguished from each other primarily according to wing morphology. Examples from Lindroth's (1985, 1986) key for the Fennoscandian carabids include the macropterous species *Patrobis septentrionis* Dejean, 1828, which is distinguished according to wing morphology from the brachypterous *P. atrorufus* (Ström, 1768) and *P. assimilis* Chaudoir, 1844. Wing-length is also one of the more precise characters given for separating *Bembidion guttula* (Fabricius, 1792) from *B. mannerheimii* C.R. Sahlberg, 1827. This causes problems for research on the significance of wing-length in cases where wing-length has been used as a diagnostic character in species determination.

The degree of variation in wing-length within macropterous species is considerable (Desender, 1989a; Venn, 2007). This variation has been assessed by applying a biometric approach to produce an unbiased index of hind-wing development for a considerable number of constantly macropterous carabid beetle species by Desender (1989a). Desender (1989b) also pointed out that a considerable number of macropterous carabid species are in practice flightless due to their lack of functional flight musculature. His study included biometric analysis of more than 300 species of carabid beetle indigenous to Belgium, and revealed that species associated with temporal habitats tended to have high dispersal power in terms of wing-length and possession of functional flight muscles. Desender (1989b) did not however succeed in demonstrating any selective advantages of reduced wing development, though he concurred with the suggestion of Lindroth (1945, 1946, 1949) that these traits were often characteristic of old, stable populations.

2. THE INHERITANCE OF WING MORPHOLOGY

Lindroth studied the phenomenon of wing morphology extensively, and classified the carabid species described in his regional keys as macropterous, brachypterous or dimorphic (Lindroth, 1974, 1985, 1986). Lindroth noted that the proportions of the different wing morphs varied considerably between populations, even within the same species (Lindroth, 1992). Consequently he decided to investigate the inheritance pattern, to determine how the genetics of wing morphology influence the observed distribution patterns. In breeding studies, Lindroth performed crosses between different combinations of brachypterous and macropterous individuals of the dimorphic *Pterostichus anthracinus* (Panzer, 1795) and demonstrated that inheritance of wing morphology in that species follows a Mendelian pattern of inheritance, with the gene for macroptery being recessive. Thus the macropterous individuals were homozygous recessive and brachypterous individuals were heterozygous or homozygous dominant (Lindroth, 1946).

Darlington (1943) proposed a simple mechanism for the spread of brachyptery in a population, whereby after

the appearance of brachypterous individuals by mutation, there is subsequent positive selection in populations where flight does not confer a major fitness benefit, because the flightless individuals have a greater viability, simpler anatomy and physiology, and a lower energy requirement. This suggestion was based on the finding of Jackson (1928), that brachypterous individuals of the curculionid species *Sitona hispidula* (Fabricius, 1776) had higher viability than macropterous individuals. On the other hand, Lindroth (1949, 1953) was unable to support such a fitness benefit for carabids when he tried to experimentally test it.

3. THE INFLUENCE OF HABITAT ON WING MORPHOLOGY

Whilst it was proposed by Darlington (1943) that carabids are descended from full-winged ancestors, he also considered that currently flight capable carabid species have each retained their flight capacity for a purpose. In the case of arboreal species, this purpose is to disperse between patches of resources within the tree canopies. Brandmayr (1983) suggested that two factors primarily affect the proportions of brachypterous and macropterous species in assemblages: ecological stability and soil water balance, with brachyptery being favoured in homogenous environments with high levels of stability. Hygrophilic species retain flight capacity to escape inundation of habitats, though it has been shown by Thiele (1977) that riparian carabid species generally employ other strategies for dealing with inundation of their habitats, such as the capacity to survive long periods of submersion. On the other hand, Darlington (1943) considered that epigeic (terrestrial) carabids had little need for flight, as they do not generally rely on flight for hunting or escaping enemies. Despite this lack of any obvious benefit from flight, Darlington acknowledged that the majority of epigeic carabid species were macropterous and generally flight capable. However, he did not consider the influence of habitat specialization, as flight would certainly be advantageous for species that are restricted to scarce and isolated habitats in particular. Darlington did however acknowledge that whilst many such species had no apparent need for flight for predation or escaping predators, in species that occurred in isolated habitats under unstable conditions, the possibility to disperse by flight and recolonize habitat patches would be advantageous and enable such species to maintain their populations. This reasoning comes close to the principles of metapopulation dynamics, though without considering the implications for species' population dynamics. Indeed, Darlington (1943) proposed that the main virtue of flight for epigeic carabids is to maintain networks of scattered unstable populations in unstable habitats by the establishment and re-establishment of populations. He also reasoned that this would provide a selective mechanism for the retention of flight capability in wing-dimorphic species. Darlington (1943) also suggested that epigeic carabid species that did not occupy unstable habitats have no reason to fly, and therefore evolve brachypterous forms and become flightless. It has also been pointed out by Dingle (1974) that a diverse range

of other environmental factors can similarly influence the development of flight ability.

4. THE INFLUENCE OF DISTURBANCE

In an influential paper on the effects of disturbance on populations, Gray (1989) suggested that populations subjected to stress should contain species with smaller body size and greater dispersal ability. A number of studies have tested this phenomenon for carabid assemblages and whilst the results have not been unequivocal, there has been considerable support for Gray's hypotheses. In these studies, the proportion of macropterous or wing-dimorphic species or individuals of such species, have been the most generally used indicators. Venn & Rokala (2005) studied carabid assemblages in urban park grasslands under different mowing regimes and demonstrated that the assemblages from the most intensively managed treatments did indeed contain a greater proportion of small sized beetles and a greater proportion of macropterous species. In a subsequent paper on the same material, Venn (2007) showed that within the wing-polymorphic species, there was a greater proportion of brachypterous individuals in the populations of more disturbed sites, and the effect was considerably stronger in males. This is in keeping with the suggestions of Gray (1989) and Magura et al. (2010), that dispersal capacity should be well developed in species of disturbed environments, though the reasons for the sexual difference remain obscure.

A number of studies have suggested a relationship between habitat stability and the proportion of brachypterous species in wing-dimorphic taxa, such as water striders (Järvinen & Vepsäläinen, 1976; Vepsäläinen, 1978), seed bugs (Solbreck, 1978) and also carabids (Ranta & Ås, 1982; Bonn et al., 2002).

Carabid beetles inhabit a broad range of terrestrial and marginal (temporarily inundated, riparian) habitats, and in temperate regions there are assemblages of carabid species associated with practically every discernible terrestrial habitat. As increasingly vast areas have been subjected to management regimes of varying intensity during recent centuries, traits that enhance a species' capacity to persist in a disturbed or stressed environment are likely to affect assemblage composition.

The assignment of specialist or generalist status to the species in an assemblage depends on reliable knowledge of food sources, habitat preferences and specificity, as well as dispersal ability. For carabid species, the literature contains information on habitat affinity at a coarse level (forest type, open habitat, moisture level preferences), though only scanty and vague information on feeding preferences. Dispersal ability for carabids is generally equated to flight ability in the literature, and whilst comprehensive information is available regarding wing morphology, the reality is more complicated. Firstly, some flightless species are considered by some authors (Den Boer, 1971a; Lindroth, 1992) to be very efficient dispersers. For example, *Carabus problematicus* Herbst, 1786 was amongst the first species to colonize the E-Flevoland polder in the Nether-

lands (Den Boer, 1970). Secondly, whilst some consistently macropterous species fly readily, there are also many macropterous species that are either incapable of flight or do not readily fly. In addition, there are also a large number of wing-dimorphic species, for which a variable proportion of each population is flight capable. So for dispersal ability in carabids, whilst some species can be unequivocally considered to be good dispersers, there are many intermediate species which are difficult to categorize with confidence as either effective or poor dispersers. It is also clearly possible that a species might be a poor disperser under one set of conditions and an efficient disperser, possibly in response to disturbance, under an alternative set of conditions.

It has been suggested that individuals that invest more in dispersal incur a cost in fecundity (Roff, 1986). If this is so, then brachypterous individuals would be expected to have a higher reproductive rate than macropterous. Whilst this has been supported in the majority of cases, there are also a small number of instances reported in which macropterous females have greater fecundity than brachypterous ones (Desender, 1989b; Aukema, 1991).

Finally, Kotze & O'Hara (2003) found that wing-dimorphic carabid species have been less prone to decline over recent decades than either macropterous or brachypterous species, and suggested that wing-dimorphic species are better adapted to disturbed environments, as the long-winged individuals are adapted for dispersal, and the short-winged individuals are adapted for reproduction. Thus in unstable environments, macropterous individuals can rapidly re-colonize habitats, and as brachypterous individuals become more numerous, then their superior fecundity will lead to a high rate of population growth.

5. FLIGHT MUSCLES

Flight muscles have also been found to exhibit similar patterns of reduction to that described for flight wings. It has been suggested by Tietze (1963) that species that exhibit a varying degree of reduction of the flight muscles represent an intermediate evolutionary stage in the development of brachyptery and the condition can also be considered to be associated with wing-dimorphism (Carter, 1976). This has been observed in a large proportion of the carabid species that colonized newly exposed habitats in the Lauweszepolder in the Netherlands (Meijer, 1974), adding further support to the suggestion that such a condition is prevalent in highly dispersive species.

In a study of species of the genus *Pogonus* from salt marsh habitats, Matalin & Makarov (2008) observed that all specimens were macropterous, though their dispersal potential in terms of flight muscle development varied considerably. The proportion of dispersive individuals in the populations decreased during the main reproductive period of this species, with the increasing proportion of mature and spent (post-reproductive) individuals. A number of previous studies have suggested that egg production is lower in old females than young ones.

It has been shown by Van Schaick Zillesen & Brunsting (1984) that flight muscle development in *Pterostichus*

oblongopunctatus (Fabricius, 1787) is dependent on environmental conditions during the larval development phase. When deprived of food and light, there is an increase in the proportion of adults with conspicuous flight muscles. Nelemans (1983 & 1987) and Bommarco (1998) have also studied the effect of food provision on flight muscle development in *Nebria brevicollis* and *Poecilus cupreus*, respectively. Their results for these species, however, contradicted the results of Van Schaick Zillesen & Brunsting (1984), as increased provision of food resulted in larger flight muscles and a larger proportion of individuals with flight muscles. Nilsson et al. (1993) suggest that this could be a mechanism for a climate change effect on the proportions of macropterous individuals in populations, though these results suggest that it could be a response to either declining or improving environmental conditions.

6. FLIGHT ACTIVITY

There are a considerable number of carabid species that are known to be macropterous and even to possess flight muscles but for which there are no records of flight activity (Lindroth, 1985, 1986). It has been suggested that the majority of carabids are either morphologically or behaviourally flightless (Lindroth, 1949). Matalin (2003) addressed this issue by calculating values of wing-load (surface area of flight wing / mass), which revealed that there are a number of species for which this value is simply too small to facilitate flight, and in many instances this threshold was exceeded by the mass of reproductive females.

Whilst Matalin (2003) was able to show that there is a considerable difference in the flight activity of monomorphic macropterous and dimorphic macropterous carabid species, Den Boer (1970) has shown that both are equally efficient in colonizing new habitat. In studies of the colonization of the E-Flevoland polder, macropterous individuals (of both monomorphic and dimorphic species) occurred frequently amongst the species to first colonize these newly available habitats. Den Boer noted also that, in addition to species of unstable habitats, also some sparsely occurring species of stable habitats, such as *Pterostichus strenuus* (Panzer, 1796), also invest in dispersal. This led Den Boer (1970) to suggest that “populations of species facing a high risk of extinction generally will have a sufficient chance of founding populations (high turnover) when investing extensively in dispersal”. In addition to Den Boer (1970) and Lindroth (1946, 1953, 1992), also Kataev (2001) reports that there are generally high proportions of macropterous individuals in the populations of wing-dimorphic species at the edge of their distributional range, whereas brachypterous individuals tend to be more prevalent in more central parts of their distributional range. This principle was the basis for Lindroth's (1949, 1992) reconstruction of the routes of post-glacial recolonization of Fennoscandia by carabid beetles.

Matalin (1994) also looked at the propensities of various species for movement by flight as opposed to walking. He found that species of the hygrophilic genus *Stenolophus* resort primarily to flight, and suggested that this was an

adaptation to inhabiting unstable habitats with a propensity for rapid inundation. Whilst in many flight capable species breeding or spent specimens lose their flight capacity, these too were flight capable in *Anisodactylus signatus* (Panzer, 1797).

7. DISPERSAL

In studies of dispersal in carabid beetles, distinction has been made between active dispersal, involving directed flight, and passive dispersal, in which either air currents or water currents are instrumental in transporting individuals to new locations (Feng et al., 2007; Kotze 2008). This also implies intermediate situations, with varying proportions of intentional, directed motion and subsequent passive transport. The term anemohydrochoric dispersal has been applied to such a combination of active and passive dispersal, whereby insects fly out over the sea, fall into the water and are subsequently carried passively by ocean currents to other shores. Such a phenomenon has been reported for a considerable number of carabid species by Palmén (1944). It has also been suggested that high-altitude flight may be a significant dispersal mode even in species that are considered to be poor flyers, such as *Notiophilus biguttatus* Fabricius, 1779 (Chapman et al., 2005).

It also seems highly likely that different carabid species respond to a variety of different stimuli to fly at different stages in their life cycles. *Pterostichus angustatus* (Duftschmid, 1812), for instance, has been observed to swarm during a period of approximately two months during the autumn, whereafter the species does not fly (Paarmann, 1966). Lindroth (1992) also observed that the harpaline species *Oodes gracilis* A. Villa & G.B. Villa, 1833 has a strong inclination to fly during spring but does not fly during the summer. In a study of flight activity in carabid beetles of the steppe region, Matalin (1998) reported that migratory activity tends to be seasonal. Whilst migratory activity was associated with the period of atmospheric drought, Matalin considered that the main factors determining migratory activity were physiological. It has been suggested that in general, the majority of individuals in macropterous carabid populations make only minimal use of their potential for flight (Ås, 1984). It has also been reported that atmospheric electromagnetic disturbances can be a stimulus for beetles to fly (Palmén, 1944: 126; Glick, 1939: 129). Studies of other macropterous insect taxa have shown that flight activity can be correlated with such phenomena as temperature (Taylor, 1963) or the phase of the lunar cycle in some lepidopteran taxa (Nowinszky et al., 2009).

The variety of potential wing phenotypes has been associated with selective advantages. Macropterous, flight-capable individuals are better adapted to systems of isolated habitat patches with frequent disturbance, as they are well adapted for colonization. Such species have been characterized as pioneer (T) species by Den Boer (1987). Brachypterous species which are incapable of flight, and referred to as (L) species (Den Boer, 1987), are generally able to invest more in reproduction and have a selective

advantage in stable environments where reproduction is more beneficial than dispersal. Kotze & O'Hara (2003) suggested that wing-polymorphism also confers a major advantage in colonization, as macropterous individuals can disperse efficiently and the brachypterous individuals amongst their progeny can then reproduce efficiently. The one phenotype for which it is difficult to conceive of a selective benefit are those which are macropterous but incapable of flight.

8. BIOGEOGRAPHY

A number of early studies reported that there are high proportions of brachypterous species on isolated habitats, such as islands (Wollaston, 1854) and mountains (Darlington, 1943). Subsequently Lindroth (1969, 1992) noted that there were considerable differences in the proportions of brachypterous to macropterous individuals at a regional level. Data on the incidences of wing morphologies in populations of dimorphic species in the region of Fennoscandia constituted much of the basis for Lindroth's studies on biogeography, particularly regarding the post-glacial recolonization of Fennoscandia (Lindroth, 1969, 1992).

In a study of insular carabid populations from the Galapagos Islands, Desender (1984) found that species of the genus *Pterostichus* were invariably flightless. In addition, there was a significant effect of altitude on wing-length, with a gradual decrease in wing-length from lowland to highland populations, both within and between species. Desender (1984) interpreted this as indicating increasing isolation with increasing altitude, corresponding to a higher chance of previous unidirectional gene flow. This interpretation is supported to an extent by the observation of greater variation in relative wing-length at lower altitudes, constituting wing-polymorphism.

The carabid fauna of mountain habitats has been summarized by Darlington (1943) as comprising small numbers of predominantly epigeic and brachypterous species. When trying to identify potential reasons for the high proportion of brachypterous species in mountain faunas, Darlington (1943) suggested the possibility of a temperature gradient effect. Tropical carabid faunas are predominantly macropterous, whereas faunas of lowland temperate regions contain a considerable number of brachypterous species and in mountain faunas, brachypterous species are prevalent. One suggested reason for this is that flight requires a considerable amount of energy, which might be more costly to provide in cooler climates (Darlington, 1943). This suggestion is in keeping with Darlington's report of 100% macroptery in the Barro Colorado wet lowland rainforest of Panama. In addition to this potential disadvantage of flight from the perspective of energy budget, it is also likely that habitat conditions are more stable, with little risk of inundation on mountains, thereby reducing the potential benefits of flight (Darlington, 1943). However, whilst Darlington reported a general trend of montane assemblages containing high proportions of brachypterous species, which has also been supported by a study of the fauna of the Italian Alps (Brandmayr, 1983), Nilsson (1993) found that the fauna

of habitat specialist species of Scandinavian alpine regions was dominated by macropterous species. One of the reasons for this was that many of the genera which account for the brachypterous species of other montane regions are absent or poorly represented in Scandinavia. Nilsson (1993), however, whilst looking for an explanation for the low proportion of brachypterous species in montane regions of Scandinavia, did not consider the possibility of a latitudinal gradient. It has also been reported that the carabid fauna of dry meadow habitats in Finland (Venn et al., 2013) contains surprisingly few brachypterous species when compared to assemblages of similar habitats in central Europe (Gobbi et al., 2010). An explanation of this trend is that the regional carabid fauna of dry meadows includes only three brachypterous species, so there is no possibility of their comprising a substantial element of the fauna of those habitats in Finland (Venn et al., 2013). It is quite possible that this latitudinal decrease in brachypterous species also applies to the montane fauna.

The fauna of the northern arctic region has been suggested to comprise both a migratory component, primarily on islands since the last glaciation, and a stable component. The migratory component comprises mainly macropterous species, whereas the stable component comprises mainly brachypterous species and predominantly brachypterous morphs of dimorphic species (Chernov & Makarova, 2008).

Studies of the carabid assemblages of islands have addressed the question as to whether the species-area relationship, possibly in combination with habitat heterogeneity (Ås, 1984; Ås et al., 1997), or the principle of island biogeography (MacArthur & Wilson, 1967), are the major determinants of species richness. Kotze (2008) found that for carabid populations of islands in the Baltic, there was a significant effect of area, though considerably less than that predicted. Contrary to their expectation of a greater proportion of flight-capable than flightless species on islands, they found that there was a considerable component of flightless species (Ås, 1984; Kotze, 2008), as had been previously reported by Wollaston (1854), Desender (1984) and Lindroth (1992).

A latitudinal trend has also been noted in carabid wing morphology, with brachypterous species being more numerous in temperate regions and macropterous species in the tropics (Darlington, 1943). Suggested reasons for this include competition with ants and high levels of population isolation or niche differentiation in tropical regions. It has also been shown that in Europe, there is a general increase in the proportion of brachypterous species from north to south (Homburg et al., 2013). The mechanism behind this could be a secondary response to aridity, which increases towards the equator. As energy economics have been suggested as a disadvantage of flight (Goodwyn & Fujisaki, 2007), it is also possible that higher levels of heat energy and primary productivity in the tropics mean that expenditure of energy to maintain and use flight apparatus are less disadvantageous in tropical than in temperate regions. Another factor which may contribute to the greater

importance of flight to tropical carabids is that they are predominantly arboreal, and as Darlington (1943) also pointed out, arboreal species are one of two major groups for which flight is important.

Both Lindroth and Den Boer used data on the proportions of macropterous and brachypterous individuals in local populations of wing-dimorphic species to test hypotheses on biogeographical phenomena over very different time-scales. Den Boer (1970, 1971a, 1977) investigated populations of beetles that became established on novel habitat after land reclamation on the polders of the North Sea coast of the Netherlands. He suggested that stable populations of wing-dimorphic species were predominantly composed of brachypterous individuals but produced a small number of macropterous individuals assumed to be capable of flight (Den Boer considered these to be dispersive individuals). His dataset from these studies also included brachypterous species that colonized novel habitats, so macroptery is not essential for dispersal, though is advantageous. If functional macroptery thus constitutes high dispersal power, then the difference in dispersal power between macropterous and brachypterous individuals should determine whether the founder population is likely to be exclusively macropterous or to include also brachypterous individuals. Increasing distance between the colonizing population and the founder population should increase the certainty that the new population is founded by exclusively macropterous individuals. In practice, if the distance is sufficiently short for the brachypterous individuals, then the process is population expansion rather than colonization.

Den Boer (1970) found that over time the proportion of macropterous individuals in the population decreased. These results are in keeping with the hypothesis, that homozygous macropterous individuals colonize new habitats and breed to establish a population in which the proportion of macropterous individuals will gradually decrease by selection (Den Boer, 1970). By the time the community stabilizes, the population will achieve an equilibrium state, with a small minority of macropterous and a majority of brachypterous individuals. A proportion of these macropterous individuals will be able to disperse and possibly establish new populations. However, study of the genetics of the wing-dimorphic species *Pterostichus anthracinus* by Lindroth (1946) had shown that macropterous individuals are homozygous. Therefore a mechanism had to be proposed to account for the arrival of the allele for brachyptery in the population.

9. POPULATION DYNAMICS

The adoption of a strategy of active dispersal by a population of a species also has major implications for the dynamics of the source population through turnover (Den Boer, 1970). A strategy of high investment in dispersal seems intuitively appropriate for populations that have a high risk of extinction. This would result in a high rate of turnover (Den Boer, 1970).

In terms of successful dispersal to new habitats, studies of species colonizing the E-Flevoland polder in the

Netherlands suggest that there is no difference between the dispersal power of monomorphic macropterous versus dimorphic species (Den Boer, 1970). Because older populations of dimorphic species are considered to contain lower proportions of macropterous individuals (Lindroth, 1949), this implies that in a region with a high level of stability, the whole metapopulation evolves a reduced potential to benefit from dispersal as a strategy for persistence should the conditions become unstable and less favourable. Thus, as conditions become more favourable for a population of a wing-dimorphic species over time and with increasing stability (Lindroth, 1949; Den Boer, 1970; Roff, 1990), the proportion of macropterous individuals in the population will decline and fecundity will increase. If this increased stability is associated with increased survival, then the population density should approach its carrying capacity. This in turn would mean that there is increasing incentive for the dwindling proportion of macropterous individuals to emigrate from the population, thereby further exacerbating this trend of decreasing macroptery under stable conditions. If the conditions subsequently become unfavourable for the population, then Den Boer (1970) suggests that such a population would have reduced potential to respond to the decline by dispersing. However, if dispersal is density driven, as is assumed by Den Boer (1970), then any population decline due, for instance, to instability or adverse conditions, would be expected to result in a reduction in dispersal by macropterous individuals. If prior to this decline in conditions there is an ongoing increase in the proportion of homozygous brachypterous individuals, then such a change would lead to an increase in the proportion of heterozygotes and accordingly enhance the potential to generate macropterous individuals. If there would, on the contrary, be a rapid increase in the frequency of macropterous individuals, and increased dispersal in response to the onset of adverse conditions, then that would be likely to result in rapid population decline and the loss of individuals with the gene for macroptery, which would further increase the vulnerability of the population in question. In theory, such a strategy could increase the possibility of establishing new satellite populations, from which dispersive individuals could potentially subsequently re-establish the original population. On the other hand, if there is reasonably frequent dispersal from such populations of dimorphic species anyway, then it would be highly likely that all adjacent and potentially suitable habitats would be occupied anyway. If a high frequency of inoculation is necessary to establish a new population in a habitat, then it is unlikely that such a population would be very stable but would rather constitute a sink (Pullam, 1988), and the further influx of macropterous individuals would do little to enhance the persistence of either the source or sink populations. However, it remains uncertain as to whether dispersal in carabids is driven by density, as studies of the species *Harpalus rufipes* (Duftschmid, 1812) and *Pterostichus niger* (Schaller, 1873) suggest that dispersal is unaffected by density (Midtgaard, 1999).

If the gene for macroptery is indeed recessive, then the founder individuals of a new population will consist of homozygous macropterous individuals, and the subsequent f1 and f2 generations would also consist of homozygous macropterous individuals. So this presents a puzzle as to how brachyptery arises and subsequently proliferates in such populations. Both Den Boer (1970, 1971a, 1977) and Lindroth (1992) considered how the successional development of a population of a wing-dimorphic species founded by a small number of macropterous individuals could arise from the arrival of a small number of reproductive individuals that subsequently breed, so that the newly founded population is derived entirely from the gene-pool of the colonizing individuals. The solution that the founder individuals could include gravid females, which might have previously mated with brachypterous males from the source population, was proposed by Haeck (1971). Thus the founder population could give rise to a small number of heterozygous individuals. If these individuals have greater fitness and high fecundity, then brachyptery would be expected to proliferate in the population.

In a study of 69 species of macropterous and dimorphic carabid species, Matalin (2003) examined the status of individuals participating in migration and determined that dispersal was predominantly undertaken by teneral and immature individuals. The proportion of macropterous individuals in older cohorts was, on average, 60% smaller, presumably because many of the females in particular undergo reduction of their flight muscles prior to the onset of gonadal development. In males the change was less remarkable, and they were predominant amongst flying mature carabids. In monomorphic macropterous species, there was a high level of flight activity throughout the season and by individuals at all stages of maturity and reproductivity. This suggests that there is a major difference between the use of flight between these two groups of species, with monomorphic macropterous species flying frequently and macropterous individuals of wing-dimorphic species utilizing flight primarily for the purpose of dispersal and just at an early stage of their life cycle.

10. POST-GLACIAL COLONIZATION OF SCANDINAVIA BY CARABID BEETLES

Lindroth (1949, 1992) used the proportions of brachypterous and macropterous morphs as the basis for conjecture about the routes of colonization of the Fennoscandian region, subsequent to the end of the last (Würms) ice age. The alternative routes were (1) from the southeast, via land bridges such as the Karelian Isthmus, (2) from the southwest, via the archipelago and (3) from the northwest, from glacial refugia. There are a number of species, such as *Calathus mollis* (Marsham, 1802), of which the populations in northern Central Europe contain high proportions of macropterous individuals, whereas populations on the Scandinavian Peninsula are entirely brachypterous. Lindroth considered this to be evidence that these species, predominantly of the alpine and subalpine fauna, which were

present close to the edge of the glacial ice sheet, had colonized Scandinavia post-glacially from a southern route, via Denmark and Skåne. Other species of this group include *Pterostichus adstrictus* Eschscholtz, 1823, *Nebria gyllen-hali* (Schönherr, 1806) and *Patrobis assimilis*. A second group of species, comprising the majority of the alpine and subalpine fauna of Central Sweden and Finland, was considered by Lindroth to have colonized Fennoscandia from the east. He also considered that most of the current Finnish flora and fauna arrived via post-glacial immigration from the east, partly via the southernmost Karelian immigration route, and others via a more northerly Kuusamo-Salla route. Evidence for this supposition comes from the proportion of brachypterous individuals in populations of dimorphic carabid species towards the north. He considered that some of these colonizers from the east subsequently expanded their range from the north into southern Norway and Sweden. In addition to these groups of species which Lindroth considered to have re-colonized Scandinavia from the south and east, there was a further group of species that Lindroth considered to have persisted in refugia within the region during the glacial period or to have hibernated. These species included *Amara interstitialis* Dejean, 1828, *A. lunicollis* Schiödt, 1837, *Bembidion grapei* Gyllenhal, 1827, *B. saxatile* Gyllenhal, 1827 and *Notiophilus biguttatus* (Fabricius 1779), amongst others.

However, evidence that macropterous morphs may disappear from populations within a century or so, which was considerably faster than was assumed by Lindroth (Den Boer et al., 1980; Honek, 1981; Aukema 1986), have given rise to doubts about the validity of Lindroth's conclusions on the post-glacial re-colonization of Scandinavia. Recent study of the genetic basis of flight capacity in the species *Pogonus chalceus* (Marshall, 1802) in response to habitat stability has shown that such traits can spread very rapidly in populations (Van Belleghem et al., 2015). In the light of current understanding of the rate of loss of macroptery, then the brachypterous populations of western Scandinavia should be interpreted as suggesting that the region has undergone a long duration of habitat stability, but not as far back as the Würms glaciation. With the benefit of hindsight, Lindroth's (1969) interpretation of the significance of a high proportion of brachypterous individuals in a population was somewhat subjective and was not based on objective consideration of potential alternative hypotheses, such as the effects of such factors as altitude, latitude or proportion of shoreline habitats (Nilsson et al., 1983). If Lindroth's (1949, 1992) hypothesis about post-glacial colonization was correct, then one would have expected that more stenotopic montane species would have become brachypterous during their period of isolation in glacial refugia, rather than the more widely distributed species considered by Lindroth (Nilsson et al., 1983).

11. SEASONAL VARIATION IN FLIGHT CAPACITY – OOGENESIS-FLIGHT

When considering the factors that influence dispersal and consequently the distribution of species, Lindroth (1992)

divided these into species traits and environmental characteristics. Studies of a variety of insect taxa have shown that many species are flight capable for only a short period of their life cycle, with subsequent histolysis of the flight muscles after migration and prior to reproduction. Such changes have been reported, e.g., for aphids (Aphididae) (Johnson, 1953), bark beetles (Scolytidae) (Atkins & Harris, 1962), crickets (*Gryllus*) (Zera et al., 1999) and water striders (Gerridae) (Andersen, 1973, 2000). A number of carabids are also capable of histolyzing their flight muscles (Van Huizen, 1979; Desender, 1989a, 2000).

Aphids (Johnson, 1953) and water striders (Spence, 2000) exhibit wing polymorphism, in which certain environmental factors result in the maturation of predominantly apterous or brachypterous morphs, and an alternate set of conditions results in the maturation of macropterous individuals (Dingle, 1974). Dingle suggested that reproduction and flight are inextricably linked, as a combination of internal and external stimuli determines whether an individual will begin reproducing upon maturity or migrate first. For many insect species that exhibit wing-dimorphism, it has been shown that the macropterous individuals are capable of losing their wings and flight muscles at stages of their life cycle when they confer hindrance rather than advantage. Spence (2000) reports that water striders use flight to migrate between overwintering, feeding and reproduction habitats, with brachypterous individuals overwintering in close proximity to their feeding habitats. Such migration is essential in the boreal region for species inhabiting water surfaces due to their freezing over during the winter. Strategies used by water striders include diapause adjacent to their reproduction site, macroptery, migration and flight muscle histolysis. In the latter case, flight is used to disperse to a habitat suitable for reproduction, after which the flight muscles are histolyzed, with a consequent enhancement of fecundity. The oogenesis-flight syndrome (Johnson, 1969) has been coined to describe the trade-off between investing resources in reproduction or flight in insects, whereby those species that invest in reproduction benefit from increased fecundity and faster onset of reproductive maturity (Zera & Denno, 1997; Zera & Brink, 2000).

A number of studies have demonstrated a negative relationship between dispersal and fecundity. Thus an individual can be well adapted for flight, or well adapted for reproduction (Meijer, 1974; Van Huizen, 1977). It has accordingly been demonstrated for *Anisodactylus signatus*, for instance, that for females caught in window traps (and therefore demonstrably capable of flight) the number of ova was never more than two. However, females caught at the same site in pitfall traps contained up to 18 ova with an average of eight (Matalin, 1994). A similar trend was also recorded for other species.

A number of insect taxa that are capable of histolyzing their indirect flight musculature are also capable of subsequently regenerating them. This phenomenon has been reported for coleopteran taxa, including the Colorado beetle *Leptinotarsa decemlineata* (Say, 1824) (De Kort, 1969; Stegwee et al., 1963), the Douglas fir beetle *Dendroctonus*

pseudotsugae Hopkins, 1905 (Ryan, 1959), and *Ips paraconfusus* Lanier, 1970 (Unnithan & Nair, 1977). The phenomenon was first reported in Carabidae by Van Huizen (1977), who found that *Amara plebeja* (Gyllenhal, 1810) uses flight to migrate from an overwintering habitat to its reproductive habitat and subsequently to return to the overwintering habitat. For this species, studies of the ovaries of females confirmed that reproduction occurred in ruderal habitats and overwintering in deciduous woodland, with a seasonal migration by flight between the two. In both male and female specimens collected from the woodland during the winter, the flight muscles were completely reduced. Also the females included both immature and spent females. This circumstantial evidence was interpreted by Van Huizen (1979) as suggesting that the species migrates both from the overwintering habitat to the reproduction habitat and subsequently back to the overwintering habitat, and that the flight muscles are histolyzed subsequent to the migration to the overwintering habitat and regenerated prior to the spring migration to the reproduction habitat. This report of histolysis of flight muscles at the overwintering habitat subsequent to reproduction is remarkable, as the primary benefit of histolysis of the flight musculature has previously been assumed to be the enhancement of fecundity. Examination of individuals of *A. plebeja* from its overwintering habitat showed that the anatomical space vacated by histolysis of the flight muscles was occupied with fat, suggesting that this post-reproductive histolysis represents an adaptation for overwintering. However, Van Huizen also reported that macropterous individuals during the period of the autumn migration to the overwintering habitat had a considerable fat supply. This suggests that accumulation of fat occurs at the reproduction habitat prior to the regeneration of the flight muscles for the autumn migration, which is contrary to the suggestion that the benefit of the subsequent histolysis of the flight muscles is to vacate space for the accumulation of fat prior to diapause, unless there is also an intensive accumulation of fat also subsequent to the autumn migration.

After the spring migration to the reproduction habitat, the flight muscles become completely reduced. Once the female has laid all of her eggs, then the flight muscles regenerate. As females with dark *corpora lutea*, indicating that they had previously reproduced, were recorded from window traps during the spring migration, it can be assumed that some individuals undergo this cycle of histolysis and regeneration of their flight muscles at least twice (Van Huizen, 1979).

Lindroth too considered that flight in carabids is “often associated with hibernation” and primarily for the purpose of migration, or in Lindroth’s terms, “to bring about a rapid, occasionally major change of quarters” (Lindroth 1992).

Van Huizen (1977) suggested that the histolysis of the flight muscles occurs soon after the spring migration and that this might prevent individuals that migrate to secondary heathland habitats from undertaking a subsequent migration from such secondary habitat to more favourable habitat for reproduction. This suggests that the mechanism

involves generation of flight muscles during the spring, migration immediately upon the occurrence of suitably hot and sunny weather conditions, and subsequent histolysis of the flight muscles shortly after termination of the migratory flight. Whilst this mechanism is consistent with the results of pitfall and window trapping, and anatomical analyses of samples of the trapped individuals, it is unsubstantiated and requires further investigation, such as records of mass migration and observations of flight muscle changes over a period of time subsequent to migration. It has also been suggested by Van Huizen (1977) that far from being unique amongst the Carabidae, the oogenesis-flight syndrome may occur in the species *Amara anthobia* Villa & Villa, 1833, *A. aenea* (DeGeer, 1774), *A. familiaris* (Duftschmid, 1812), *Anisodactylus binotatus* (Fabricius, 1787), *Pterostichus vernalis* (Panzer, 1795) and *Bradycellus harpalinus* (Audinet-Serville, 1821). *Amara lunicollis* has also been recorded as demonstrating oogenesis-flight, though in that species only 16% of adults show developed flight muscles, compared to 90% in *A. plebeja* (Van Huizen, 1977).

Tietze (1963) suggested that reduction of flight muscles in macropterous carabid species might be the first stage along the evolutionary path towards brachyptery. However, whilst the oogenesis-flight syndrome provides a mechanism for the introduction of brachyptery into an otherwise macropterous population, which could be favoured by natural selection, at least in the case of *A. plebeja*, macropterous migration appears to be an essential element of the life cycle. On the other hand, in the case of suitable overwintering habitat occurring in close proximity to the reproduction habitat, it is likely that selection would be directed against the oogenesis-flight syndrome, and instead favour entirely brachypterous individuals. Whilst in *A. plebeja*, oogenesis-flight seems to be important for the population, as evidenced by the presence of functional flight muscles in 90% of individuals caught in pitfalls during the migratory period, *A. lunicollis* has, in the same region, a much lower incidence of individuals with functional flight muscles. Presumably in that species, oogenesis-flight is beneficial for the population though not essential, as flightlessness is clearly also a generally successful strategy.

Whilst other studies have also supported the existence of such a trade-off between fecundity and flight, it is clear that the relationship between the two is in terms of potential rather than absolute. It is highly unlikely that there is a statistical relationship between the two factors, with the amount of flight capacity, represented by the physical volume of the flight muscle, being offset by an equivalent decrease in fecundity. In Matalin’s (1994) study, whilst we can be relatively confident that individuals caught in a window trap were flight capable, there is no such certainty that the individuals caught in the pitfall traps were incapable of flight. It would have been interesting to know whether there was a relationship between the number of ova present and the volume of flight muscle, though that is not reported in Matalin’s paper (1994). The significance of this trade-off between fecundity and dispersal capacity also has significance for the population dynamics of wing-dimorphic

species. It is clear that individuals with functional flight muscles and full wings are better adapted for colonization than individuals without such resources, whilst those with higher fecundity are better adapted to establish a population at a newly colonized site.

So far we have only considered this trade-off in carabids from the perspective of the female. It may seem unlikely that the space given over to flight muscles might affect the fecundity of male individuals, so the most obvious disadvantage of possessing functional flight apparatus is the presumably higher metabolic rate. Clearly it is possible that the proportion of brachypterous individuals (both male and female) in a population may be entirely dependent on inheritance from the female (Roff & Fairbairn, 1991), though it is also highly likely that selection also acts on the males (Denno et al., 1991; Ott, 1994). In those studies of wing-dimorphic insects in which possible trade-off benefits for males have been considered, these include greater success in male-male competition (Ichikawa, 1982), faster development (Novotny, 1995), more frequent success in mating (Crespi, 1988; Fujisaki, 1992; Kaitala & Dingle, 1993; Novotny, 1995), earlier reproduction (Utida, 1972; Fujisaki, 1992) and extended lifespan (Roderick, 1987). It has also been suggested that such trade-offs are more difficult to detect in males because the costs of reproduction are considerably less in males than females (Trivers, 1972). In addition to these intrinsic benefits, Langellotto et al. (2000) determined that brachypterous female planthoppers exhibited positive selection of brachypterous males and rejection of macropters, though this behaviour was reported as not statistically significant. It has also been reported in the planthopper *Nilaparvata lugens* (Stål, 1854), that both macropterous and brachypterous males prefer to mate with brachypterous females (Takeda, 1974), which have greater fecundity (Denno et al., 1989). However, in another species of planthopper, assertive mating has been reported, whereby macropterous males prefer to mate with macropterous females, and brachypterous males prefer to mate with brachypterous females (Langellotto et al., 2000). This study also showed that brachypterous males of the planthopper *Prokelisia dolus* Wilson, 1982 had greater fecundity than macropterous males. It can therefore be concluded that there are also inherent fitness advantages of brachyptery for males in at least some insect taxa.

12. ESTIMATING FLIGHT-CAPACITY

A considerable number of studies have considered the issue of how to quantify the dispersal capacity of carabids. At its simplest, the estimate may consist of the proportion of macropterous specimens in a population (Lindroth, 1949). The problem with this approach is that it fails to account for differences in flight-capacity between macropterous individuals, such as differences in wing-length (Den Boer, 1977). To address this issue, Den Boer (1977) developed an index of dispersal power, derived from the ratio of the surface area of the flight wing and the length of the elytron. On the basis of this index, he divided carabid species into

those with high, low or uncertain dispersal power. It was subsequently determined by Desender (1989b, 2000) that both variation in the shape of flight wings and the developmental status of the flight muscles affects their capacity for flight. Desender (1989a) consequently divided species into three groups, those possessing functional flight muscles, those possessing undeveloped flight muscles and those possessing degraded flight muscles. On the basis of a study of the flight apparatus of 300 species of European carabids, Desender (1989a) concluded that there was a correlation between wing size and flight muscle development.

13. ORIENTATION AND STIMULATION OF CARABID FLIGHT

Whilst much attention has been given to the study of carabid morphology regarding their potential for flight, relatively little study has been made regarding the purpose, timing of and conditions for flight in carabids. The general assumption is that flight is generally infrequent and seasonal (Chapman et al., 2005). Distinction has been made between long-range and short-range migratory flight and vegetative flight, with vegetative flight referring to flights associated with feeding and reproduction (Chapman et al., 2005). It has been suggested that *Amara plebeja*, for instance, undergoes seasonal migrations between overwintering sites and habitats where it reproduces (Van Huizen, 1977). A small number of studies using aerial sampling and more recently also radar techniques have shown that a considerable number of carabid species fly at high altitudes and seem to undergo long-range, windborne migrations (Glick, 1939; Chapman et al., 2005, 2010). There has been considerable discussion about whether carabid beetles are able to exercise control over their direction of flight and destination, or whether they simply rise into the air and are subsequently carried passively by air currents (Lindroth, 1992). Lindroth considered passive dispersal to be more significant than active dispersal. Sampling of aeroplankton from aircraft has produced records of 470 individuals from 30 species of carabid beetles from altitudes of up to 3000 m (Glick, 1939). Lindroth's (1992) explanation of this phenomenon is that carabid beetles with only a weak capacity of flight are passively born upwards by convectional air currents. Clearly this kind of flight is unlikely to be directed, though it may serve the purpose of facilitating long-distance dispersal. Lindroth argued that this might constitute a purposeful dispersal strategy, particularly in species which exhibit mass generation, such as parthenogenic organisms, though its significance for carabids is likely to be minor, at most.

One study in South-East England suggested that *Notiophilus biguttatus* undertakes a mass migration at an altitude of ca. 200m during the second half of July. The earlier study of Glick recorded more than 30 species of carabids flying at altitudes of up to 3000m in Tallulah, Louisiana, USA and Mexico during August 1926–October 1931. The majority of carabids from Glick's (1939) study, including the abundant *Micratopus fusciceps* Casey, 1914, *Harpalus*

nitidulus Chaudoir, 1843, *Agonoderus pallipes* (Fabricius, 1792) and all the carabids from the Chapman et al. (2005) study, flew during the daytime.

Another environmental factor which is known to have a major influence on flight by carabids is light. A number of studies have shown that in many regions there is also a considerable amount of nocturnal flight by carabids (Glick, 1939; Šustek, 1999). Night-flying beetles in particular are well known to be attracted to bright lights. Lindroth (1992) tested the influence of sunlight on the flight of six species of carabid beetles and found that they all flew towards the sun. In addition to a simple attraction/repulsion effect of light sources as a primary cue, light polarization is known to influence the movement of some insect taxa (Kirschfeld, 1986; Dacke et al., 2004), though this has not been studied for carabids. Studies using light sources in the city of Bratislava, Slovakia (Šustek, 1999) have shown that the *Harpalus* species *H. griseus* and *H. rufipes*, as well as such species as *Amara apricaria* (Paykull, 1790), *A. consularis* (Duftschmid, 1812), *Dolichus halensis* (Schaller, 1783) and *Trechus quadristriatus* (Schränk, 1781), were all nocturnally highly abundant at light traps in an urban area. The activity commenced 12–20 minutes prior to nightfall and continued for two to three hours. Šustek (1999) reported that there were three major peaks of flight activity for different groups of species during the period 7th August to 6th November, and that these represented a migration, mainly of species typical of agricultural fields, though also some hygrophilous species from outside the city, to urban habitats, attracted by light sources in the city.

As heat is also an acknowledged prerequisite for flight, Lindroth (1992) argues that diurnally flying species are likely to fly late in the day, when it is sufficiently warm and the sun sufficiently low in the sky to influence the direction of flight. For nocturnally flying species, he argues that flight is likely to be predominantly during the first hours of darkness for the same reasons. Therefore, sunlight directed flight is likely to be predominantly in the same direction, i.e., towards the west. In a number of insect taxa, including carabids, it has been reported that air temperature constitutes a stimulus to fly (Thiele, 1977). For both *Amara plebeja* and *Notiophilus biguttatus*, it has been reported that 17°C is a minimum threshold below which little or no flight occurs and above which the species fly actively (Chapman, 2010; Van Huizen, 1979). However, Matalin (1998) has reported nocturnal flight by carabids in September when temperatures were as low as 1.3–3.5°C, though he also reports temperatures of 12–17°C as minimum threshold temperatures for flight by carabids in July. Other suggested criteria for flight in *A. plebeja* were listed as sunny conditions, rain ≤ 0.01 mm d⁻¹ and wind speed ≤ 4 ms⁻¹. Wind direction also seems to have an influence on carabid flight. In the Drenthe region of The Netherlands, winds from the east and southeast resulted in the greatest flight activity in carabid beetles (Van Huizen, 1984) during the spring time, a period during which winds from the north, northeast and east are most prevalent. This gives rise to the question of whether there is a correlation between

the incidences of these wind directions and the previously mentioned favourable conditions for flight, or whether the beetles choose to fly when the wind is in a particular direction. Particularly in the case of *A. plebeja*, which has been suggested to migrate backwards and forwards between two habitat types, it would be interesting to know whether the beetles utilize winds in opposite directions to migrate between the same patches of overwintering and reproduction habitat or not, or if the stimuli that initiate their flight direct them to winds in opposite directions in autumn than in spring. If not, then it would be highly likely that the population of this species would drift across the landscape in the direction of the wind that they predominantly utilized, though this question appears not to have been researched for the species.

In his studies of *A. plebeja*, Van Huizen (1977) concluded that a second migration during the reproductive period is highly unlikely. As the species also occurs on heathlands during the summer season, though with no records of sexually mature males or females being present there, this suggests that such habitats are either secondary with inadequate resources to support reproduction or fulfil an as yet undetermined role in the life cycle of the species, probably unconnected with reproduction. In the former case, such habitats may simply constitute sink habitats (Pulliam, 1988) into which individuals migrate but which do not have sufficient resources for a population to become successfully established. Using a time series analysis approach, it has been shown that the effects of climate conditions on flight activity vary not only according to annual climatic variation but also according to species microclimatic preferences. An increase in the incidence of drought conditions was associated with increased flight activity in the hygrophilic species *Clivina fossor* (Linnaeus, 1758), though the flight activity of the xerophilic species *Harpalus griseus* (Panzer, 1797) and *H. froelichii* Sturm, 1818 declined (Kadar & Szentkiralyi, 1997).

These studies show that there is a considerable amount of migratory activity by carabids, some of which is driven by changes in the availability of resources but also with meteorological conditions providing stimuli for flight activity. Light pollution also seems to affect the behaviour of night-flying carabids. It also seems evident that window traps close to ground level are not effective for intercepting carabids embarking on high altitude, long-range migration. In order to develop a better understanding of the factors that stimulate, direct and influence flight by carabids, there is clearly a need for long-term research on flight by carabids in different climatic regions.

14. SYNTHESIS

The aim of this paper was to provide a comprehensive overview of the role of flight capacity or its absence in carabid species and populations in the temperate region from the perspective of ecological studies. Much of the material on this topic is presented in papers that are not easily accessible to all. To accurately consider the ecological implications of flight, it is necessary to appreciate that it is not

simply a trait of certain individuals in certain populations but may also vary temporally in the same individual. Accordingly I have not attempted to go deeply into the genetic or molecular basis of the phenomenon of flight, which are both fields in which more work is necessary to complete the picture.

ACKNOWLEDGEMENTS. The author gratefully acknowledges the comments of Petr Svacha, which greatly improved the content of this paper.

REFERENCES

- ANDERSEN N.M. 1973: Seasonal polymorphism and developmental changes in organs of flight and reproduction in bivoltine pondskaters (Hem. Gerridae). — *Entomol. Scand.* **4**: 1–20.
- ANDERSEN N.M. 2000: The evolution of dispersal dimorphism and other life history traits in water striders (Hem. Gerridae). — *Entomol. Sci.* **3**: 187–199.
- ATKINS M.D. & HARRIS S.H. 1962: A contribution to the knowledge of flight muscle changes in the *Scolytidae* (Coleoptera). — *Can. Entomol.* **94**: 25–32.
- AUKEMA B. 1986: Winglength determination in relation to dispersal by flight in two wing dimorphic species of *Calathus* Bonelli (Coleoptera, Carabidae). In Den Boer P.J., Luff M.L., Mossakowski D. & Weber F. (eds): *Carabid Beetles*. Gustav Fischer, Stuttgart, pp. 91–99.
- 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.
- AUKEMA B. 1995: The evolutionary significance of wing dimorphism in carabid beetles (Coleoptera: Carabidae). — *Res. Popul. Ecol.* **37**: 105–110.
- ÅS S. 1984: To fly or not to fly? Colonization of Baltic islands by winged and wingless carabid beetles. — *J. Biogeogr.* **11**: 413–426.
- ÅS S., BENGTTSSON J. & EBENHARD T. 1997: Archipelagos and theories of insularity. — *Ecol. Bull.* **46**: 88–116.
- BONN A., HAGEN K. & REICHE D.W.-V. 2002: The significance of flood regimes for carabid beetle and spider communities in riparian habitats – a comparison of three major rivers in Germany. — *River Res. Appl.* **18**: 43–64.
- BRANDMAYR P. 1983: The main axes of the coenoclineal continuum from macroptery to brachyptery in carabid communities of the temperate zone Ecology of carabids: the synthesis of field study and laboratory experiment. The main axes of the coenoclineal continuum from macroptery to brachyptery in carabid communities of the temperate zone. In Brandmayr P., den Boer P.J. & Weber F. (eds): *Ecology of Carabids: The Synthesis of Field Study and Laboratory Experiment. Report of the Fourth Meeting of European Carabidologists*. PUDOC, Wageningen pp. 147–169.
- CARTER A. 1976: Wing polymorphism in the insect species *Agonum retractum* Leconte (Coleoptera, Carabidae). — *Can. J. Zool.* **54**: 1375–1382.
- CHAPMAN J.W., REYNOLDS D.R., SMITH A.D., RILEY J.R., TELFER M.G. & WOJWOOD I.P. 2005: Mass aerial migration in the carabid beetle *Notiophilus biguttatus*. — *Ecol. Entomol.* **30**: 264–272.
- CHAPMAN, J., REYNOLDS, D. & SMITH, A. 2010: Migratory and foraging movements in beneficial insects: A review of radar monitoring and tracking methods. — *Int. J. Pest Manage.* **50**: 225–232.
- CHEKHOV Y.I. & MAKAROVA O.L. 2008: Beetles (Coleoptera) in High Arctic. In Penev L., Erwin T. & Assmann T. (eds): *Back to the Roots and Back to the Future. Towards a Synthesis amongst Taxonomic, Ecological and Biogeographical Approaches in Carabidology. Proc. of the XIII European Carabidologists Meeting, Blagoevgrad, August 20–24, 2007*. Pensoft, Sofia, pp. 213–246.
- CRESPI B.J. 1988: Adaptation, compromise, and constraint: the development, morphometrics, and behavioural basis on a fighter-flier polymorphism in male *Hoplothrips karnyi* (Insecta: Thysanoptera). — *Behav. Ecol. Sociobiol.* **23**: 93–104.
- DACKE M., BYRNE M.J., SCHOLTZ C.H. & WARRANT E.J. 2004: Lunar orientation in a beetle. — *Proc. R. Soc. Lond. (B)* **271**: 361–365.
- DARLINGTON P.J. 1943: Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. — *Ecol. Monogr.* **13**: 39–61.
- DARWIN C. 1872: *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. 6th London ed. John Murray, London, 504 pp.
- DE KORT C.A.D. 1969: Hormones and the structural and biochemical properties of the flight muscles in the Colorado beetle. — *Med. Landb. Hogeschool* **69**: 1–63.
- DEN BOER P.J. 1970: On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). — *Oecologia* **4**: 1–28.
- DEN BOER P.J. 1971a: On the dispersal power of carabid beetles and its possible significance. In Den Boer P.J. (ed.): *Dispersal and Dispersal Power of Carabid Beetles*. — *Miscellaneous Papers (Landbouwhogeschool, Wageningen)* **8**: 119–138.
- DEN BOER P.J. (ED.) 1971b: *Dispersal and Dispersal Power of Carabid Beetles*. — *Miscellaneous Papers (Landbouwhogeschool, Wageningen)* **8**: 1–151.
- DEN BOER P.J. 1977: Dispersal power and survival. Carabids in a cultivated countryside. — *Miscellaneous Papers (Landbouwhogeschool, Wageningen)* **14**: 1–190.
- DEN BOER P.J., VAN HUIZEN T.H.P., DEN BOER-DAANJE W., AUKEMA B. & DEN BIEMAN C.F.M. 1980: Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). — *Entomol. Gener.* **6**: 107–134.
- DENNO R.F., OLMSTEAD K.L. & MCCLOUD E.S. 1989: Reproductive cost of flight capability: a comparison of life history traits in wing dimorphic planthoppers. — *Ecol. Entomol.* **14**: 31–44.
- DENNO R.F., RODERICK G.K., OLMSTEAD K.L. & DÖBEL H.G. 1991: Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. — *Am. Nat.* **138**: 1513–1541.
- DESENDER K. 1984: Evolutionary ecology of carabids in Galapagos. In Stork N. (ed.): *The Role of Ground Beetles in Ecological and Environmental Studies*. Intercept, Andover, pp. 13–20.
- DESENDER K. 1989a: [Dispersal forms in the ecology of carabid beetles (Coleoptera, Carabidae).] *Doc. Trav. Inst. R. Sci. Nat. Belge (Gent)* **54**: 1–136 [in Dutch].
- 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.
- DESENDER K. 2000: Flight muscle development and dispersal in the life history of carabid beetles: patterns and processes. — *Bull. Inst. R. Sci. Nat. Belg. (Entomologie)* **70**: 13–31.
- DINGLE H. 1974: The experimental analysis of migration and life-history strategies in insects. In Browne L.B. (ed.): *Experimental Analysis of Insect Behaviour*. Springer, Berlin, Heidelberg, New York, pp. 329–342.
- FENG H.Q., ZHANG Y.H., WU K.M., CHENG D.F. & GOU Y.-Y. 2007: Nocturnal windborne migration of ground beetles, particularly

- Pseudoophonus griseus* (Coleoptera: Carabidae), in China. — *Agric. Forest Entomol.* **9**: 103–113.
- FUJISAKI K. 1992: A male fitness advantage to wing reduction in the oriental chinch bug, *Calvelerius saccharivorus* Okajima (Heteroptera: Lygaeidae). — *Res. Popul. Ecol.* **34**: 173–183.
- GLICK P.A. 1939: *The Distribution of Insects, Spiders and Mites in the Air*. U.S. Department of Agriculture, Technical Bulletins 673, Washington, 150 pp.
- GOBBI M., CACCIANIGA M., CERABOLINI B., DE BERNARDI F., LUZZARO A. & PIERCE S. 2010: Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. — *Commun. Ecol.* **11**: 223–231.
- GOODWYN P.P. & FUJISAKI K. 2007: Sexual conflicts, loss of flight, and fitness gains in locomotion of polymorphic water striders. — *Entomol. Exp. Appl.* **124**: 249–259.
- GRAY J.S. 1989: Effects of environmental stress on species rich assemblages. — *Biol. J. Linn. Soc.* **37**: 19–32.
- HAECK J. 1971: The immigration and settlement of carabids in the new IJsselmeer-polders. In Den Boer P.J. (ed.): *Dispersal and Dispersal Power of Carabid Beetles*. — *Miscellaneous Papers (Landbouwhogeschool, Wageningen)* **8**: 33–51.
- HOMBURG K., HOMBURG N., SCHÄFER F., SCHULDT A. & ASSMANN T. 2013: Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). — *Insect Conserv. Diver.* **7**: 195–205.
- HONEK A. 1981: Wing polymorphism in *Notiophilus biguttatus* in Bohemia. — *Vest. Cs. Spol. Zool.* **45**: 81–86.
- ICHIKAWA T. 1982: Density related changes in male-male competitive behavior in the rice brown planthopper, *Nilaparvata lugens* (Stal) (Homoptera: Delphacidae). — *Appl. Entomol. Zool.* **17**: 439–452.
- JACKSON D.J. 1928: The inheritance of long and short wings in the weevil, *Sitona hispidula*, with a discussion of wing reduction among beetles. — *Trans. R. Soc. Edinburgh* **55**: 665–735.
- JACKSON D.J. 1933: Observations on the flight muscles of *Sitona* weevils. — *Ann. Appl. Biol.* **20**: 731–770.
- JOHNSON B. 1953: Flight muscle autolysis and reproduction in aphids. — *Nature* **4383**: 813.
- JOHNSON C.G. 1969: *Migration and Dispersal of Insects by Flight*. Methuen, London 763 pp.
- JÄRVINEN O. & VEPSÄLAINEN K. 1976: Wing dimorphism as an adaptive strategy in water-striders (*Gerris*). — *Hereditas* **84**: 61–68.
- KADAR F. & SZENTKIRALYI F. 1997: Effects of climatic variations on long-term fluctuation patterns of ground beetles (Coleoptera, Carabidae) collected by light trapping in Hungary. — *Acta Phytopathol. Entomol. Hungar.* **32**: 185–203.
- KAITALA A. & DINGLE H. 1993: Wing dimorphism, territoriality and mating frequency of the water strider *Aquarius remigis* (Say). — *Ann. Zool. Fenn.* **30**: 163–168.
- KATAEV B.M. 2001: On some, mostly East European and Asian species of the genus *Ophonus* (Coleoptera: Carabidae). — *Zoosyst. Rossica* **99**[2000]: 161–187.
- KAVANAUGH D.H. 1985: On wing atrophy in carabid beetles (Coleoptera: Carabidae), with special reference to Nearctic *Nebria*. In Ball G.E. (ed.): *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. A Volume Dedicated to the Memory of Philip Jackson Darlington, Jr. (1904–1983). Series Entomologica 33*. Dr. W. Junk, Dordrecht, Boston, Lancaster, pp. 408–431.
- KIRSCHFELD K. 1988: Navigation and compass orientation by insects according to the polarization pattern of the sky. — *Z. Naturforsch. (C)* **43**: 467–469.
- KOTZE D.J. 2008: The occurrence and distribution of carabid beetles (Carabidae) on islands in the Baltic Sea: a review. — *J. Insect Conserv.* **12**: 265–276.
- KOTZE D.J. & O'HARA R.B. 2003: Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. — *Oecologia* **135**: 138–148.
- LANGELLOTTO G.A., DENNO R.F. & OTT J.R. 2000: A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. — *Ecology* **81**: 865–875.
- LINDROTH C.H. 1945: Die Fennoskandischen Carabidae. Eine tiergeographische Studie. I. Spezieller Teil. — *Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar (B. 4)*: 1–709.
- LINDROTH C.H. 1946: Inheritance of wing dimorphism in *Pterostichus anthracinus* Ill. — *Hereditas* **32**: 37–40.
- LINDROTH C.H. 1949: Die Fennoskandischen Carabidae. III. Allgemeiner Teil. — *Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar (B. 4)*: 1–911.
- LINDROTH C.H. 1953: Some attempts towards experimental zoogeography. — *Ecology* **34**: 657–666.
- LINDROTH C.H. 1969: The theory of glacial refugia in Scandinavia – comments on present opinions. — *Notul. Entomol.* **39**: 178–192.
- LINDROTH C.H. 1974: *Handbooks for the Identification of British Insects. Vol. IV, Part 2*. Royal Entomological Society, London, 148 pp.
- LINDROTH C.H. 1985: *The Carabidae (Coleoptera) of Fennoscandia and Denmark. Vol. 15, Part 1*. Scandinavian Press, Leiden, 225 pp.
- LINDROTH C.H. 1986: *The Carabidae (Coleoptera) of Fennoscandia and Denmark. Vol. 15, Part 2*. Scandinavian Press, Leiden, 497 pp.
- LINDROTH C.H. 1992: *Ground Beetles (Carabidae) of Fennoscandia – A Zoogeographic Study. Part III, General Analysis With a Discussion on Biogeographic Principles*. Smithsonian Institution Libraries and The National Science Foundation, Washington D.C., 814 pp.
- MACARTHUR R.H. & WILSON E.O. 1967: *The Theory of Island Biogeography*. Princeton University Press, Princeton, 205 pp.
- MAGURA T., LÖVEI G. & TÓTHMÉRÉSZ B. 2010: Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? — *Global Ecol. Biogeogr.* **19**: 16–26.
- MATALIN A.V. 1994: The strategy of dispersal behaviour in some Carabidae species of southeastern Europe. In Desender K., Dufrière M., Loreau M., Luff M.L. & Maelfait J.-P. (eds): *Carabid Beetles – Ecology and Evolution*. Kluwer Academic Publishers, Dordrecht, pp. 183–188.
- MATALIN A.V. 1998: Influence of weather conditions on migratory activity of ground beetles (Coleoptera, Carabidae) in the steppe zone. — *Biol. Bull.* **25**: 485–494.
- MATALIN A.V. 2003: Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. — *Pedobiologia* **47**: 311–319.
- MATALIN A.V. & MAKAROV K.V. 2008: Life cycles in the ground beetle tribe Pogonini (Coleoptera, Carabidae) from the Lake Elton region, Russia. In Penev L., Erwin T. & Assmann T. (eds): *Back to the Roots and Back to the Future. Towards a Synthesis amongst Taxonomic, Ecological and Biogeographical Approaches in Carabidology. Proc. of the XIII European Carabidologists Meeting, Blagoevgrad, August 20–24, 2007*. Pensoft, Sofia, pp. 305–338.
- MEIJER J. 1974: A comparative study of the immigration of carabids (Coleoptera, Carabidae) into a new polder. — *Oecologia* **16**: 185–208.

- MIDTGAARD F. 1999: Is dispersal density-dependent in carabid beetles? A field experiment with *Harpalus rufipes* (Degeer) and *Pterostichus niger* (Schaller) (Col., Carabidae). — *J. Appl. Entomol.* **123**: 9–12.
- NILSSON A.N., PETERSSON R.B. & LEMDAHL G. 1993: Macroptery in altitudinal specialists versus brachyptery in generalists – a paradox of alpine Scandinavian carabid beetles (Coleoptera: Carabidae). — *J. Biogeogr.* **20**: 227–234.
- NOVOTNY V. 1995: Adaptive significance of wing dimorphism in males of *Nilaparvata lugens*. — *Entomol. Exp. Appl.* **76**: 233–239.
- OTT J.R. 1994: An ecological framework for the study of planthopper mating systems. In Denno R.F. & Perfect T.J. (eds): *Planthoppers: Their Ecology and Management*. Chapman and Hall, New York, pp. 234–254.
- PAARMANN W. 1966: Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*Pterostichus angustatus* Dft. und *P. oblongopunctatus* F.) an ihre verschiedenen Lebensräume. — *Z. Wiss. Zool.* **174**: 83–176.
- PALMÉN E. 1944: Die anemohydrochore Ausbreitung der insekten als zoogeographischer Faktor. — *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo* **10**: 1–262.
- PULLIAM H.R. 1988: Sources, sinks, and population regulation. — *Am. Nat.* **132**: 652–661.
- RANTA E. & ÅS S. 1982: Non-random colonization of habitat islands by carabid beetles. — *Ann. Zool. Fenn.* **19**: 175–181.
- RODERICK G.K. 1987: *Ecology and Evolution of Dispersal in California Populations of a Salt Marsh Insect, Prokelisia marginata*. PhD Thesis, University of California, Berkeley, CA.
- 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. — *Ecol. Monogr.* **60**: 389–421.
- ROFF D.A. & FAIRBAIRN D.J. 1991: Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. — *Am. Zool.* **31**: 243–251.
- RYAN R.B. 1959: Termination of diapause in the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopkins, as an aid to continuous laboratory rearing. — *Can. Entomol.* **91**: 520–525.
- SAHLBERG J. 1868: Bidrag till kännedomen om Finlands Dimorpha Insekt-arter (Contribution to the knowledge of Finland's Dimorpha insect species). — *Notiser ur Sällskapet pro Fauna et Flora Fennica* **9** (1867), Helsinki [quoted in Lindroth, C.H. 1992].
- SOLBRECK C. 1978: Migration, diapause, and direct development as alternative life histories in a seed bug, *Neocoryphus bicrucis*. In Dingle H. (ed.): *Evolution of Insect Migration and Diapause*. Springer, New York, pp. 195–217.
- SPENCE J.R. 2000: Seasonal aspects of flight in water striders (Hemiptera: Gerridae). — *Entomol. Sci.* **3**: 399–417.
- STEGWEE D., KIMMEL E.C., DEN BOER J.A. & HENSTRA S. 1963: Hormonal control of reversible degeneration of flight muscle in the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera). — *J. Cell Biol.* **19**: 519–527.
- ŠUSTEK, Z. 1999: Light attraction of carabid beetles and their survival in the city centre. — *Biologia (Bratislava)* **54**: 539–551.
- THIELE H.-U. 1977: *Carabid Beetles in their Environments – A study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer, Berlin, 369 pp.
- TIETZE F. 1963: Untersuchungen über die Beziehungen zwischen Flügelreduktion und Ausbildung des Metathorax bei Carabiden. — *Beitr. Entomol.* **13**: 88–167.
- TRIVERS R.L. 1972: Parental investment and sexual selection In Campbell B. (ed.): *Sexual Selection and the Descent of Man*. Aldine, Chicago, pp. 136–179.
- UNNITHAN G.C. & NAIR K.K. 1977: Ultrastructure of juvenile hormone-induced degenerating flight muscles in a bark beetle, *Ips paraconfusus*. — *Cell Tissue Res.* **185**: 481–490.
- UTIDA S. 1972: Density dependent polymorphism in the adult of *Callosobruchus maculatus* (Coleoptera: Bruchidae). — *J. Stor. Prod. Res.* **9**: 111–126.
- VAN BELLEGHEM S.M., ROELOFS D. & HENDRICKX F. 2015: Evolutionary history of a dispersal associated locus across sympatric and allopatric divergent populations of a wing polymorphic beetle across Atlantic Europe. — *Mol. Ecol.* **24**: 890–908.
- VAN HUIZEN T.H.P. 1977: The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). — *Oecologia (Berlin)* **29**: 27–41.
- VAN HUIZEN T.H.P. 1979: Individual and environmental factors determining flight in carabid beetles. — *Miscellaneous Papers (Landbouwhogeschool, Wageningen)* **8**: 71–74.
- VAN HUIZEN T.H.P. 1984: 'Gone with the wind': Flight activity of carabid beetles in relation to wind direction and to the reproductive state of females in flight. In Stork N. (ed.): *The Role of Ground Beetles in Ecological and Environmental Studies*. Intercept, Andover, pp. 289–293.
- VAN SCHAICK ZILLESSEN P.G. & BRUNSTING A.M.H. 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). — *Entomol. Gener.* **9**: 143–147.
- VENN S. & ROKALA K. 2005: Effects of grassland management strategy on the carabid fauna of urban parks. In Skłodowski J., Huruk S., Barsevskis A. & Tarasiuk S. (eds): *Protection of Coleoptera in the Baltic Sea Region*. Warsaw Agricultural University Press, Warsaw, pp. 65–75.
- VENN S.J., KOTZE D.J., LASSILA T. & NIEMELÄ J. 2013: Urban dry meadows provide valuable habitat for granivorous and xerophilic carabid beetles. — *J. Insect Conserv.* **17**: 747–764.
- VENN S. 2007: Morphological responses to disturbance in wing-polymorphic carabid species (Coleoptera, Carabidae) of managed urban grasslands. — *Baltic J. Coleopterol.* **7**: 51–60.
- VEPSÄLAINEN K. 1978: Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In Dingle H. (ed.): *Evolution of Insect Migration and Diapause*. Springer, New York, pp. 218–253.
- WOLLASTON T.V. 1854: *Insecta Maderensia, Being an Account of the Insects of the Islands of the Madeiran Group*. J. Van Voorst, London, 634 pp.
- ZERA A.J. & BRINK T. 2000: Nutrient absorption and utilization by wing and flight muscle morphs of the cricket *Gryllus firmus*: implications for the trade-off between flight capability and early reproduction. — *J. Insect Behav.* **46**: 1207–1218.
- ZERA A.J. DENNO R.F. 1997: Physiology and ecology of dispersal polymorphism in insects. — *Annu. Rev. Entomol.* **42**: 207–230.
- ZERA A.J., SALL J. & OTTO K. 1999: Biochemical aspects of flight and flightlessness in *Gryllus*: flight fuels, enzyme activities and electrophoretic profiles of flight muscles from flight-capable and flightless morphs. — *J. Insect Physiol.* **45**: 275–285.

Received March 11, 2015; revised and accepted December 2, 2015
Published online December 30, 2016