

Flight muscle development and dispersal in the life cycle of carabid beetles: patterns and processes

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Abstract

Seasonal patterns of flight muscle development are documented for 27 carabid species, collected from different habitats. The phenology or timing of their life cycle is compared to the presence of a functional flight apparatus during complete year cycles. The majority of the investigated ground beetles have never been studied before in this respect. In most species there is a distinct seasonal pattern of flight muscle functionality. Some species, with similar life cycle timing and/or similar habitat requirements, show the same pattern of flight muscle development. Inter- and intraspecific variability in maximal proportions of beetles with functional flight muscles indicates flight muscle dimorphism. The reproductive state of females (obtained through dissection of the ovaries) is used to test the generality of an "oogenesis-flight syndrome" (trade-off between dispersal and reproduction), the null hypothesis being that functional flight musculature and ripe ovaries occur independently. Observed significant deviations towards a higher proportion of beetles with functional flight muscles in unripe as compared to ripe females indicate such a syndrome in most of the species studied. It is especially true for species emerging during late spring before their summer-autumn reproduction. The proportion of ripe females with functional flight muscles differs between species and can be used as a measure for a less deterministic version of an "oogenesis-flight" syndrome. A complex of factors must play a role in the expression of flight muscle development. Integration of all results suggests habitat choice, evolution of life cycle timing and other life history traits as ultimate factors responsible for the observed patterns of flight muscle functionality. Flight muscle development in ground beetles therefore seems to be part of a suite of coadapted traits.

Key words: Carabidae, dispersal power, life cycle, flight muscle development, oogenesis-flight syndrome, reproduction, wing dimorphism, adaptations, suite of coadapted traits

Résumé

Les profils saisonniers du développement des muscles alaires sont reportés pour 27 espèces de Carabidae, récoltées dans des habitats différents. Durant des cycles annuels complets, la phénologie ou la période du cycle vital est comparée pour chaque espèce à la présence d'un appareil de vol fonctionnel. La majorité des espèces de Carabidae concernées n'a jamais été étudiée sous cet angle avant ce travail. Chez la plupart des espèces, il y a un cycle saisonnier de la fonctionnalité des muscles alaires. Certaines espèces qui ont un cycle de vie et/ou des exigences environnementales similaires démontrent le même profil saisonnier au niveau des muscles de vol. Si l'on considère la période du cycle de vie où le développement des muscles de vol est le plus important, on constate une variabilité inter- et intraspécifique, ce qui suggère un dimorphisme de muscles alaires. L'état reproductif des femelles (obtenu après dissection des ovaires) est utilisé pour tester la présence d'un "oogenesis-flight syndrome" (balance entre dispersion et reproduction), l'hypothèse nulle étant qu'une musculature alaire fonctionnelle et la maturité des ovaires apparaissent indépendamment.

Les déviations significatives observées pour une proportion plus importante de coléoptères avec des muscles de vols fonctionnels chez des femelles non matures en comparaison avec celles matures indiquent un tel syndrome chez la plupart des espèces de Carabidae étudiées. Ceci s'applique surtout aux espèces qui émergent à la fin du printemps, juste avant leur période de reproduction en été-automne. Le pourcentage de femelles matures avec des muscles alaires fonctionnels diffère entre espèces et peut être utilisé comme une mesure d'un "oogenesis-flight syndrome" moins déterministe. L'analyse globale de tous les résultats suggère que les caractéristiques suivantes interviennent comme facteurs expliquants les profils observés au niveau des muscles de vol: choix de l'habitat, évolution du cycle de vie, ainsi que d'autres éléments de la vie de l'insecte. Le développement des muscles de vol des Carabidae semble dès lors faire partie d'un ensemble de caractères coadaptés.

Mots-clés: Carabidae, pouvoir de dispersion, cycle de vie, développement des muscles alaires, oogenesis-flight syndrome, reproduction, dimorphisme alaire, adaptations, caractères coadaptés

Introduction

In many insect groups, species are known to show polymorphisms affecting their flight ability. The most obvious examples are variations in wing and flight muscle development (HARRISON, 1980). Wing polymorphisms are under genetic and environmental control (HARRISON, 1980; ROFF, 1986).

Numerous observations indicate that in many insect species migration is limited to the post-teneral, pre-reproductive period. These observations have led to define the "oogenesis-flight syndrome" as a characteristic of insect migration (JOHNSON, 1969; for Coleoptera, see f.e. LINDERS et al., 1995, MUDA et al., 1981, RANKIN et al., 1994, TADA et al., 1991). The inherent assumption is that migration (through flight dispersal by means of functional flight muscles and developed hind wings) and reproduction are alternating physiological states. This view was strengthened by the fact that migration in many cases is associated with or induced by conditions promoting adult diapause (i.o.w. delaying reproduction), for example a shorter photoperiod, lower temperatures or poor food conditions (RANKIN et al., 1986). Migrating insects moreover often are physiologically comparable to diapausing insects in their possession of hypertrophic fat bodies and immature ovaries. Studies on the physio-

logy and endocrinology of flight muscle degeneration and regeneration, in a few insect species, have suggested a control by juvenile hormone (FAIRBAIRN & YADLOWSKI, 1997; ZERA et al., 1997). A strong negative correlation has commonly been observed between flight muscle mass and ovarian mass of insects (ROFF, 1986), suggesting that the construction and maintenance of the flight apparatus competes with egg production for a limited internal nutrient pool (ZERA & DENNO, 1997). The metabolic rates of flying insects can be 20-100 times that of resting animals and are among the highest known (RANKIN & BURCHSTED, 1991). Nevertheless, several authors (cf. GATEHOUSE & ZHANG, 1995) have challenged the assumption that the oogenesis-flight syndrome is a general phenomenon.

Ground beetles are well-known for their varying degree of hind wing development. Some species are constantly winged, others show a wing polymorphism or wing dimorphism and some species always possess reduced wings. Carabid beetles consequently exhibit a large amount of variation in their respective dispersal power. Wing development is largely under direct genetic control in the few ground beetle species studied so far (cf. AUKEMA, 1986; DESENDER, 1989a; LINDROTH, 1946). About three-quarters or as much as 280 carabid species from Belgium are known to be constantly macropterous or full-winged. Nevertheless wing development and, as a consequence, flight capacity are extremely variable between winged species too, as has been shown on the basis of a biometric approach (DEN BOER et al., 1980; DESENDER et al., 1986; DESENDER, 1989b). Many winged ground beetles moreover not necessarily possess functional flight muscles. Below a certain value of relative wing size, functional flight muscles apparently are only rarely observed (DEN BOER et al., 1980; DESENDER, 1989b).

Genetic studies on flight muscle development have not yet been performed in ground beetles, with one exception: NELEMANS (1987) showed that there is no simple genetic basis for flight muscle development in *Nebria brevicollis*. However, genetic studies on other beetles (two species of Scarabaeidae; TADA et al., 1993, 1994, 1995) have demonstrated genetic flight muscle dimorphism, besides environmental control of flight muscle development. Seasonal changes in the proportions of carabid beetles with functional flight musculature for a given species could suggest phenotypic plasticity and point to environmental conditions possibly influencing flight muscle development. Some studies have shown that proportions of beetles with flight capability differ between species. Seasonal aspects, however, usually were not included. Such data could nevertheless suggest whether there is some kind of dimorphism or polymorphism in the determination of flight muscle functionality.

The current knowledge on seasonal variation in flight muscle development as compared to adult life cycle of ground beetles is limited to some five species only. *Amara plebeja*, reproducing during spring and hibernating as adult, showed a strict "oogenesis-flight" syndrome: migration occurs during autumn (post-teneral), but also during spring (after hibernation and before re-

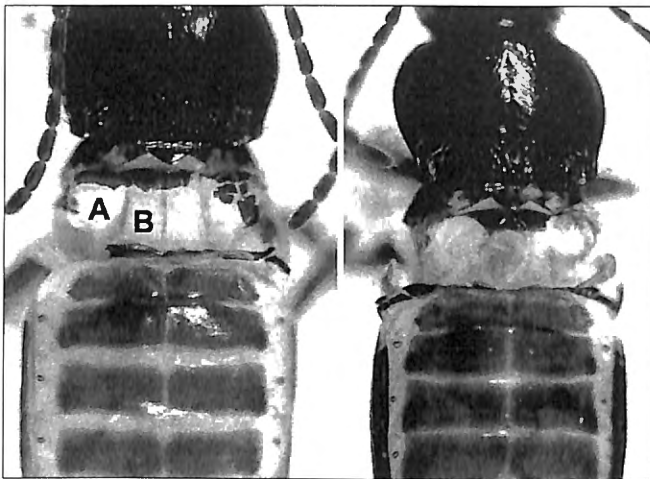
production) and is related to habitat change (TIETZE, 1963; VAN HUIZEN, 1977). Flying females were always unripe. According to DEN BOER et al. (1980) some species (*Amara familiaris*, *Anisodactylus binotatus*, *Calathus rotundicollis* and *Nebria brevicollis*) deviate more or less from an "oogenesis-flight" syndrome. In *Nebria brevicollis* developing flight muscles were found in immature beetles (i.e. in spring) more than in reproducing beetles (in autumn), while at least some flight activity was observed during autumn too (NELEMANS, 1987). MATALIN (1994, 1997) and ZHANG et al. (1997) studied *Harpalus rufipes* and came to the conclusion that flight was more prevalent in (but not limited to) young beetles before reproduction. MEIJER (1974) suggested variation in flight behaviour of the small *Bembidion varium* (always possessing functional flight muscles): in spring relatively more unripe females were recorded flying as compared to reproducing ones.

Clearly, there is a considerable lack of empirical data on most carabid beetles in this respect. To this end, we have dissected large numbers of ground beetles collected during complete year cycles in a multitude of habitats and belonging to 27 different species (20 constantly macropterous, seven wing dimorphic or polymorphic). These species can be roughly divided into spring breeders (adult hibernators) on the one hand and summer-autumn breeders (larval or larval/adult hibernators) on the other hand.

In this paper, we will first look at seasonal patterns of flight muscle development by comparing the phenology or timing of the life cycle in each species to the relative occurrence of a functional flight apparatus. Secondly, the reproductive state of females (obtained through dissection of the ovaries) will be used to test the generality of an "oogenesis-flight syndrome", the null hypothesis being that functional flight musculature and ripe ovaries occur independently. A significant deviation towards a higher proportion of beetles with functional flight muscles in unripe females as compared to ripe females would be an indication for such a syndrome. The percentage of ripe females with functional flight muscles can be used as a measure for a less deterministic version of an "oogenesis-flight" syndrome. Results for species with different life cycle timing will finally be compared in an attempt to give ultimate explanations or underlying evolutionary processes responsible for the observed variability and timing of the presence of functional flight musculature.

Material and Methods

Two groups of indirect flight muscles, situated in the metathorax of beetles, are essential for flight activity (Fig. 1). The medio-dorsal longitudinal muscles (Fig. 1B) bulge the metatergum outwards when contracting and provoke the downward stroke of the wings. The lateral dorso-ventral muscles (Fig. 1A) have an antagonistic effect and flatten the metatergum, in this way provoking the upward stroke of the wings.



Figs. 1-2 — Functional (Fig. 1) and degenerated indirect flight muscles (Fig. 2; muscle fibres replaced by adipose tissue) in the metathorax of *Pogonus chalcicus*; 1A: lateral dorso-ventral muscles, 1B: medio-dorsal longitudinal muscles

Dissection of carabid beetles reveals that these muscles can be reduced to different degrees or even totally be replaced by adipose tissue (Fig. 2). Intra-specific differences in the state of flight musculature are not necessarily restricted to different individuals, but may, in certain species, occur during the lifetime of even a single beetle. In such a case flight musculature can differentiate, be resorbed or autolysed and then regenerate.

We dissected the metathorax from about 10.000 field-collected beetles belonging to 27 different carabid species (nomenclature according to DESENDER et al., 1995), occurring in different habitats in Belgium, in order to define the state of their flight muscles. From 13 species, a high number of individuals could be checked: in these cases monthly fractions of beetles with functional flight muscles were plotted with their respective 95% confidence limits (WONNACOTT & WONNACOTT, 1977). In the remaining species only the obtained fractions were plotted. The timing of the life cycle was also illustrated for each species. Based on data from the same sampling sites (nearly always from pitfall year cycle series, interpolated per month), frequency distributions were given for adult and teneral (newly emerged) beetles (in some cases also for larvae; in one case based on seasonal occurrence of mean number of ripe eggs in females). Data from seven wing dimorphic or wing polymorphic species are included: here, proportions of beetles with functional flight muscles were calculated based on macropterous individuals only. For two high-density populations of *Bembidion properans* (a wing dimorphic species), the monthly proportion of observed macropterous beetles was also calculated and plotted in order to look for possible seasonal changes in these fractions too.

For the current paper we distinguished beetles with well-developed flight muscles from all states of flight

muscle reduction, i.o.w. individuals with a non-functional flight apparatus. When available, replicate year samples from different sites were studied. The ovaries of about 3000 females belonging to the same 27 species (except *Amara tibialis* and *Clivina fossor*) were dissected in order to define their reproductive state as compared to flight muscle functionality. The null hypothesis (functional flight muscles and ripe ovaries occur independently) was tested by means of a G-test of independence (SOKAL & ROHLF, 1981).

Results

1. Seasonal variation of flight muscle functionality in spring-reproducing ground beetles (adult hibernators)

Fig. 3 (A-Q) summarises data obtained for 10 carabid species, reproducing mainly during spring. *Amara aenea* was studied in 6 populations (Fig. 3, G-L), *Agonum muelleri* (Fig. 3, M-N) and *Pterostichus versicolor* (Fig. 3, P-Q) in 2 populations. The remaining species were studied in a single population year cycle (Fig. 3, A-F, O). These 10 species show their reproductive activity (expressed as numbers caught per month in pitfall traps) mainly during spring, resulting in larvae developing during summer and the emergence of the new beetle generation during autumn (teneral beetles, indicated by black columns). Table 1 summarises the results for females from the same spring-reproducing species, along with G-test results and sample sizes.

The percentage of beetles with functional flight muscles shows no clear pattern of seasonal variation in *Amara familiaris* (Fig. 3 A) and *Asaphidion curtum* (Fig. 3 B). Both are characterised by well-developed hind wings (DESENDER, 1989b). At any time during the adult life cycle of *Amara familiaris* about 25 to 50% of the individuals show functionality of the flight apparatus (cf. DEN BOER et al., 1980). This carabid is known to occur in rather ephemeral habitats, for example on open, recently created, sandy sites (our sampling site was a recent motorway verge on sandy soil). *Asaphidion curtum* is particularly common in light forest and forest clearings. The continuous possession (at least in a number of individuals) of a functional flight apparatus in these species thus can be interpreted as an adaptation to unpredictable changes in their habitat. There is no statistical deviation from independence between reproductive state and flight muscle functionality (Table 1), i.o.w. we do not observe a significant oogenesis-flight syndrome.

Most other spring breeders, on the other hand, show a significant oogenesis-flight syndrome (Table 1), although somewhat less deterministic. In each species we observe at least some reproducing females with functional flight muscles, but the reproductive period overlaps only partly with the period of functional flight muscles. *Anisodactylus binotatus* and *Acupalpus flavicollis* individuals all possess flight muscles during early spring (at the onset

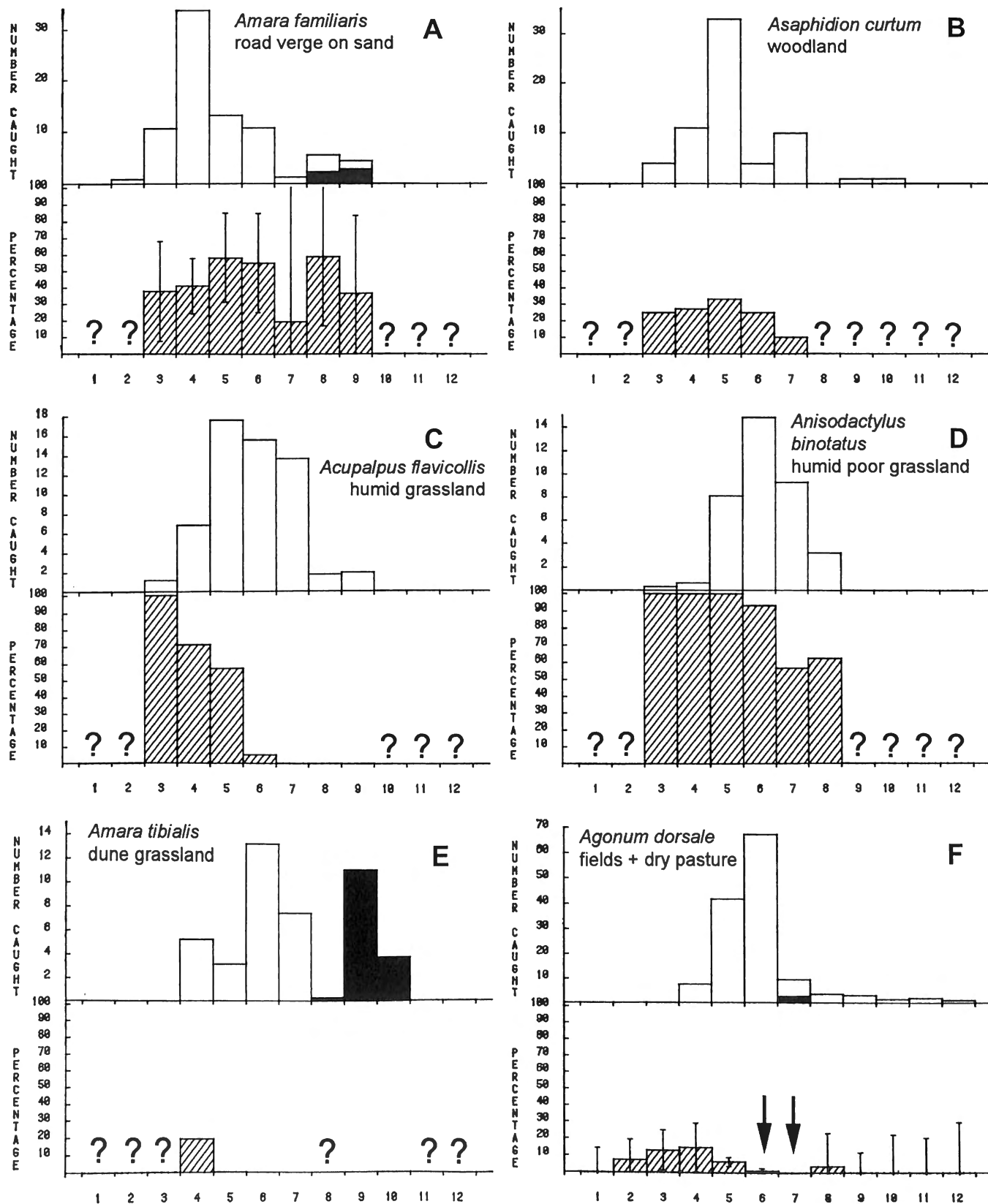


Fig. 3 (A-Q) — Phenology of the life cycle in spring breeding ground beetles (upper figure; black columns: teneral beetles), compared to the seasonal occurrence of monthly proportions of beetles with functional flight muscles (lower figure; with 95% c.i. for large samples,?: months without data, arrows indicate zero-values based on large sample sizes). A: *Amara familiaris* (recent motorway verge on sandy soil), B: *Asaphidion curtum* (woodland site), C: *Acupalpus flavicollis* (humid grassland), D: *Anisodactylus binotatus* (humid poor grassland), E: *Amara tibialis* (dune grassland), F: *Agonum dorsale* (cultivated fields and dry pasture).

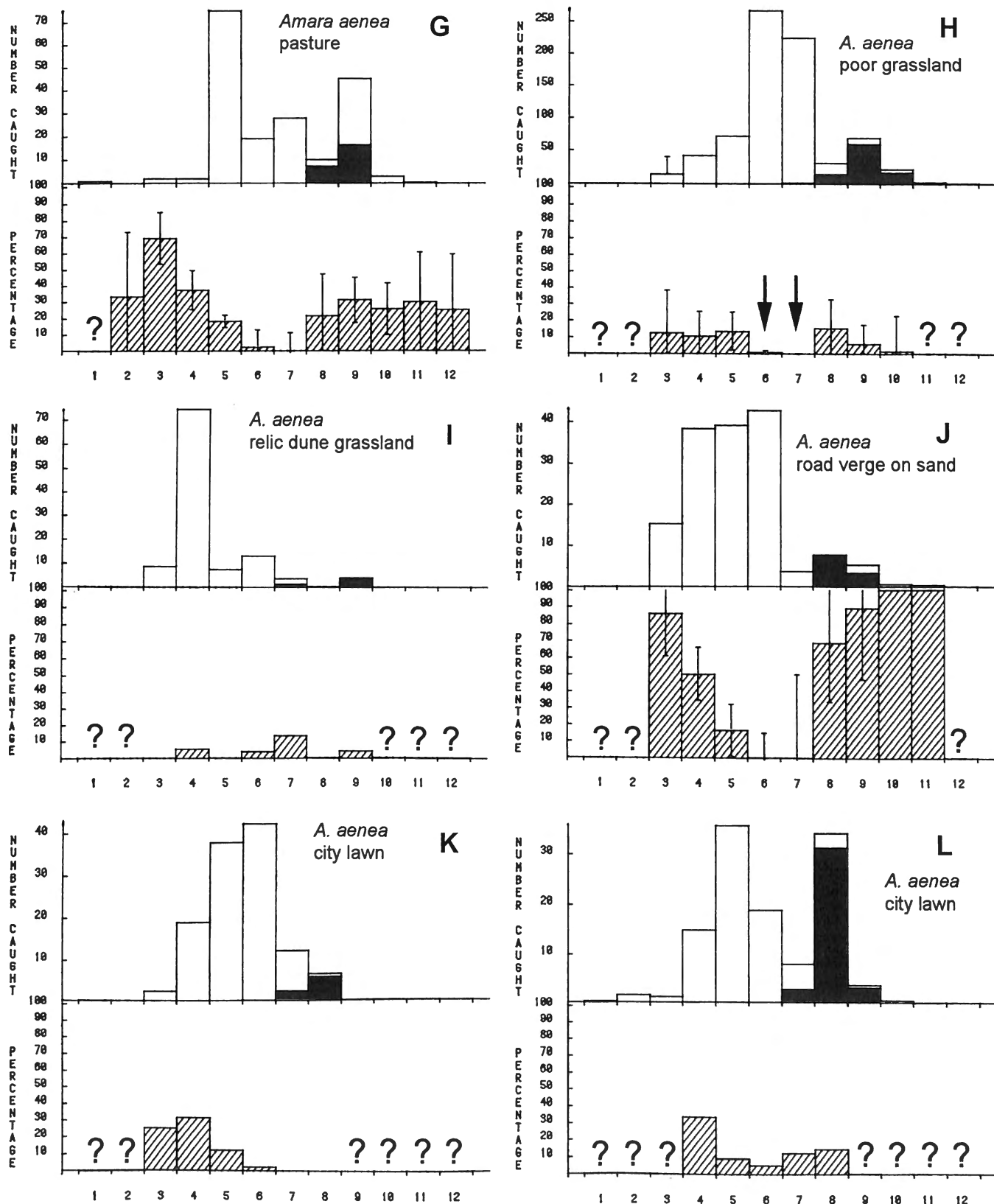


Fig. 3 (continued) — G-L: *Amara aenea* (G: pasture, H: dry poor grassland, I: relic dune grassland, J: recent motorway verge on sandy soil, K-L: lawns in city of Ghent).

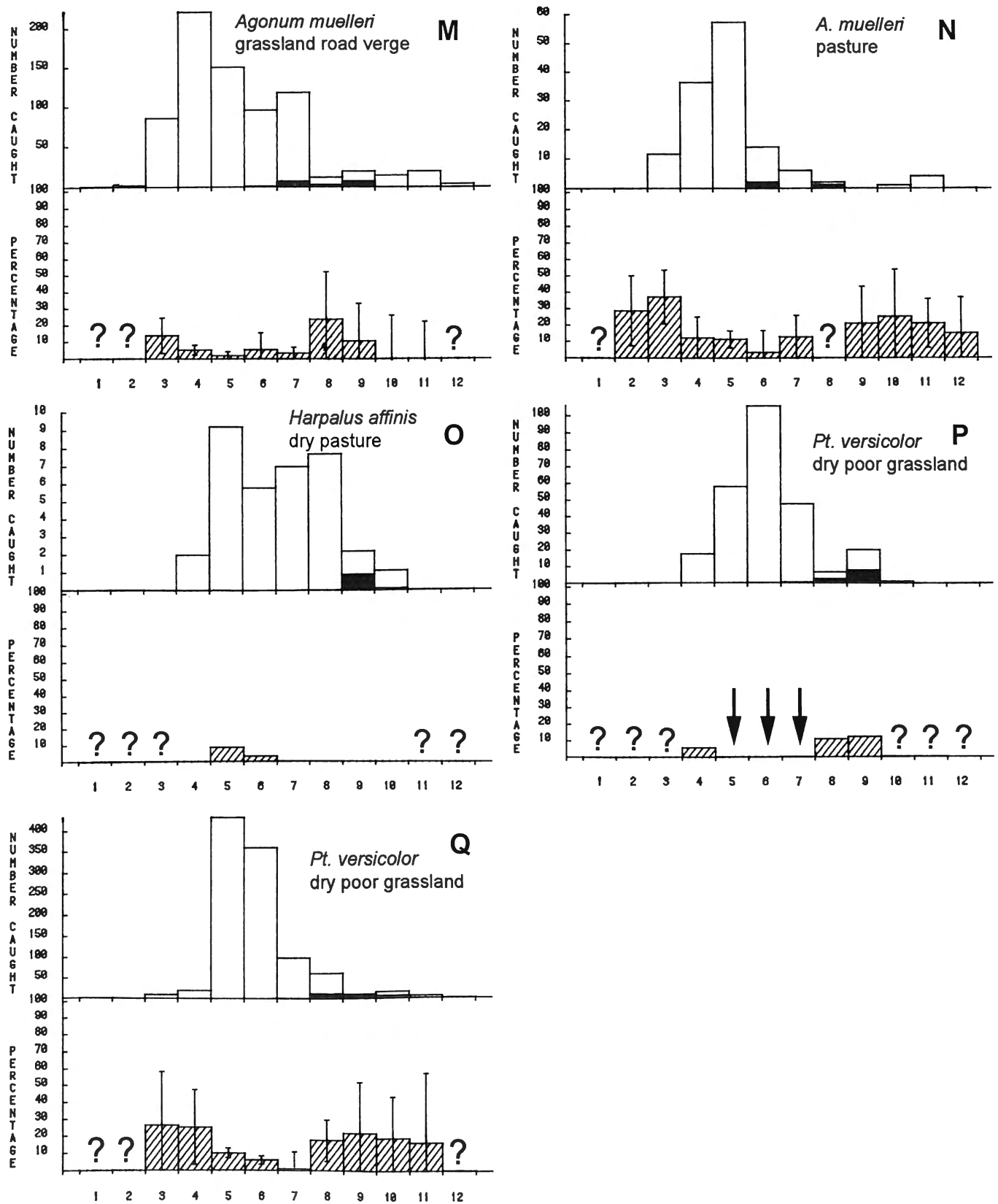


Fig. 3 (continued) — M-N: *Agonum muelleri* (M: grassland on motorway verge, N: pasture), O: *Harpalus affinis* (dry pasture); P-Q: *Pterostichus versicolor* (dry-poor grasslands).

Table 1 — The oogenesis-flight syndrome in ground beetles: flight muscle development and reproductive state of ovaries in females of the investigated ground beetles; **n** = number of dissected females; **R** = ovaries with ripe eggs, **O** = ovaries immature or only with corpora lutea (spent, after egg-laying), + = functional flight muscles, - = degenerated flight muscles; **G-test**-statistic: test of independence after comparing [number with flight muscles and unripe or spent ovaries to the total with unripe or spent ovaries] with [number with flight muscles and ripe ovaries to the total with ripe ovaries]; number of specimens with or without flight muscles within some species not comparable (indicated with an asterisk); data only used to test independence between the occurrence of reproduction and functional flight musculature; **species** ordered in three groups as in results (spring breeders, autumn breeders and dimorphic/polymorphic species) and in alphabetic order within each group.

Species	n	O+	O-	R+	R-	G-test	significance
<i>Acupalpus flavicollis</i>	33	19	6	5	3	0.53	n.s.
<i>Agonum dorsale</i> *	118	6	16	11	85	3.17	n.s.
<i>Agonum muelleri</i> *	78	19	12	9	38	14.55	p<0.001
<i>Amara aenea</i>	324	24	59	27	214	13.21	p<0.001
<i>Amara familiaris</i>	48	7	7	18	16	0.03	n.s.
<i>Amara tibialis</i>	-						
<i>Anisodactylus binotatus</i>	14	9		3	2	4.20	p<0.05
<i>Asaphidion curtum</i>	117	8	18	30	61	0.04	n.s.
<i>Harpalus affinis</i>	33	9	5	8	11	1.60	n.s.
<i>Pterostichus versicolor</i>	92	26	28	9	29	5.84	p<0.05
<i>Amara bifrons</i>	26	3		1	22	17.23	p<0.001
<i>Harpalus attenuatus</i>	96	19	11		66	51.13	p<0.001
<i>Harpalus rubripes</i> *	31	10	4	2	15	12.31	p<0.001
<i>Harpalus rufipes</i> *	30	3	18		9	1.42	n.s.
<i>Harpalus rufipalpis</i> *	15	10	1	2	2	2.76	n.s.
<i>Harpalus tardus</i> *	45	5	1		39	34.23	p<0.001
<i>Leistus fulvibarbis</i> *	22	5	7		10	5.39	p<0.05
<i>Leistus rufomarginatus</i>	106	14	4		88	75.44	p<0.001
<i>Nebria brevicollis</i>	349	9	99	1	240	15.83	p<0.001
<i>Trechus quadristriatus</i> *	95	34	4	21	36	28.72	p<0.001
<i>Bembidion properans</i> *	219	28	11	44	136	30.77	p<0.001
<i>Bradycellus harpalinus</i>	130	12	9	1	108	44.47	p<0.001
<i>Calathus rotundicollis</i>	63	2	7		54	10.39	p<0.01
<i>Clivina fossor</i>	-						
<i>Pogonus chalceus</i>	407	4	87	16	300	0.07	n.s.
<i>Pterostichus minor</i>	59	1	18		40	2.07	n.s.
<i>Pterostichus vernalis</i> *	390	21	108	15	246	10.68	p<0.005

of their reproductive period) (Fig. 3, C-D). Later on, this percentage decreases. These carabids also possess well-developed hind wings (DESENDER, 1989b). Both species can be found in moderately to very humid sites, which regularly inundate during winter. The remaining species to some degree show two periods a year with a more elevated fraction of beetles with functional flight muscles (*Amara tibialis* and *Harpalus affinis* show one such period, but the number of individuals studied was low in these species). In nearly all species the periods with a higher incidence of functional flight musculature are clearly complementary to the reproductive period (Fig. 3, E-Q). Without exception, these carabids live in open habitat types, ranging from dune grasslands (*Amara*

tibialis), poor grasslands (*Pterostichus versicolor*) to pastures and cultivated fields (*Agonum dorsale*, *Agonum muelleri*, *Amara aenea*, *Harpalus affinis*). Some of these species are known to hibernate in edges of fields, hedges or woodland edges. The obtained patterns therefore can be interpreted in terms of habitat change performed by beetles, though not necessarily in many individuals by means of flight dispersal.

Species studied from multiple populations show comparable patterns. The different populations of *Amara aenea*, for example, show a clear alternation of the period of reproduction and periods with a higher proportion of individuals with functional flight muscles. The maximal proportion of beetles with functional flight muscles how-

ever shows a large interpopulation variability. These differences can nevertheless at least partly be interpreted when comparing the sampling site characteristics. High percentages of beetles with functional flight muscles are observed on a recently created motorway verge (Fig. 3, J), whereas very low values are found in a population occurring in a relic site from an old, highly decalcified, dune grassland area (Fig. 3, I). These results indicate that a complex of factors plays a role in the expression of flight muscle development (not only habitat characteristics, but also age of the population since initial colonisation, mean individual body size influenced by environmental conditions during ontogeny, etc.; cf. DESENDER, 1989a).

In *Agonum dorsale* and *Agonum muelleri* (two species available in sufficiently large numbers), the number of individuals with flight muscles is reduced to zero during winter. This suggests that a number of specimens must develop and subsequently autolyse or resorb their flight muscles at least two or three times during their lifetime. They first develop their flight muscles after emergence during autumn in order to fly in search of a convenient hibernation quarter. Then, they autolyse their muscles, followed by regeneration during early spring in order to search for a suitable reproductive site and, once again, resorption at the onset of reproduction.

Comparison of the observed maximal proportion of beetles with flight muscles and the species-specific hind wing development (DESENDER, 1989b), shows that those species with smallest relative wing size (*Agonum dorsale*, *Amara tibialis*) show very low percentages of beetles with flight muscles.

2. Seasonal variation of flight muscle functionality in summer-autumn-reproducing ground beetles (larval or larval/adult hibernators)

Data on 10 species are shown in Fig. 4 (A-P). For *Nebria brevicollis*, *Harpalus tardus* and *Harpalus attenuatus*, data are given on respectively 4, 3 and 2 year cycle series. These species can be grouped into different categories: (1) *Amara bifrons*, a species with summer reproduction (short adult period), (2) species belonging to the genus *Harpalus*, probably with summer reproduction, some species in an annual (larval hibernation) to biennial cycle (larval and adult hibernation), (3) *Leistus fulvibarbis*, *Leistus rufomarginatus* and *Nebria brevicollis*, all known to emerge in spring, followed by an adult aestivation dormancy and reproduction during autumn, (4) *Trechus quadristriatus*, with its new generation appearing in summer, reproducing in autumn till early next spring. The number of beetles with functional flight muscles in non-reproductive as compared to reproductive females is given in Table 1, along with the results of G-tests of independence, as well as sample sizes.

Amara bifrons prefers dry sandy habitats with poor vegetation. Our results (Fig. 4 A) show no clear difference between the seasonal activity peak and the monthly proportions of beetles with flight muscles. Nevertheless,

there is a significant deviation from independence between reproduction and the occurrence of functional flight muscles, but the number of dissected beetles is low. A similar result is obtained for *Harpalus rufipes* (Fig. 4 E), but here the percentages of beetles with flight muscles are higher, while the G-test is not significant (but low sample size). *Harpalus rufipes*, known as a weed seed predator, prefers fields with a more or less developed herb layer (its larvae mainly feeding on small plant seeds), thus possibly requiring regular (re)colonisation.

The remaining *Harpalus* species (Fig. 4, B-I) show a higher proportion of beetles with functional flight muscles at the beginning of their phenology curve (coinciding with the appearance of the new generation), followed by a sharp decline. Dissection of females reveals that those with ripe eggs in the ovaries never possess functional flight muscles, demonstrating a complete (highly significant) oogenesis-flight syndrome (Table 1). All these *Harpalus* species are more or less bound to sandy soil, usually with poor grassy vegetation. Differences between maximal proportions of beetles with flight muscles are relatively large between species, but somewhat less reliable due to relatively low sample sizes. *Harpalus tardus* (Fig. 4, G-I), with low fractions of beetles with functional flight muscles, shows some variability between populations. The differences between the two populations of *Harpalus attenuatus* can be in part the consequence of a possible detection problem: proportions with functional flight muscles in the dune grassland (Fig. 4, B-C) could have been biased to lower values because of the very high proportion of newly emerged tenerals in this sample. In such beetles flight muscle development is sometimes difficult to describe. If such individuals develop post-teneral functional flight muscles, flight muscle development would need at least some days to some weeks after the beetles have emerged and already could have been active on the soil surface (cf. SMITH, 1964).

Leistus fulvibarbis, *Leistus rufomarginatus* and *Nebria brevicollis* (Fig. 4, J-O), three species with a high number of dissected specimens, show strong similarities in their patterns of seasonal flight muscle development. Again, beetles with functional flight muscles are largely restricted to the non-reproductive period, i.e. the emergence period during late spring, before the summer aestivation. These species suggest the occurrence of a distinct (significant) oogenesis-flight syndrome (Table 1). Differences in the fractions of beetles with flight muscles can be interpreted in terms of the habitats preferred by the different species. Both *Leistus* species occur in woodlands, especially in moderately humid to wet sites. *Nebria brevicollis*, on the other hand, is a very eurytopic species from forests, parkland and grasslands.

Trechus quadristriatus (Fig. 4 P), a common species on certain types of cultivated fields, is an example of an autumn breeder emerging during summer (July-August) and reproducing from autumn till early next spring. Once again, immature beetles from the new generation show a much more elevated proportion (nearly 100%) of indivi-

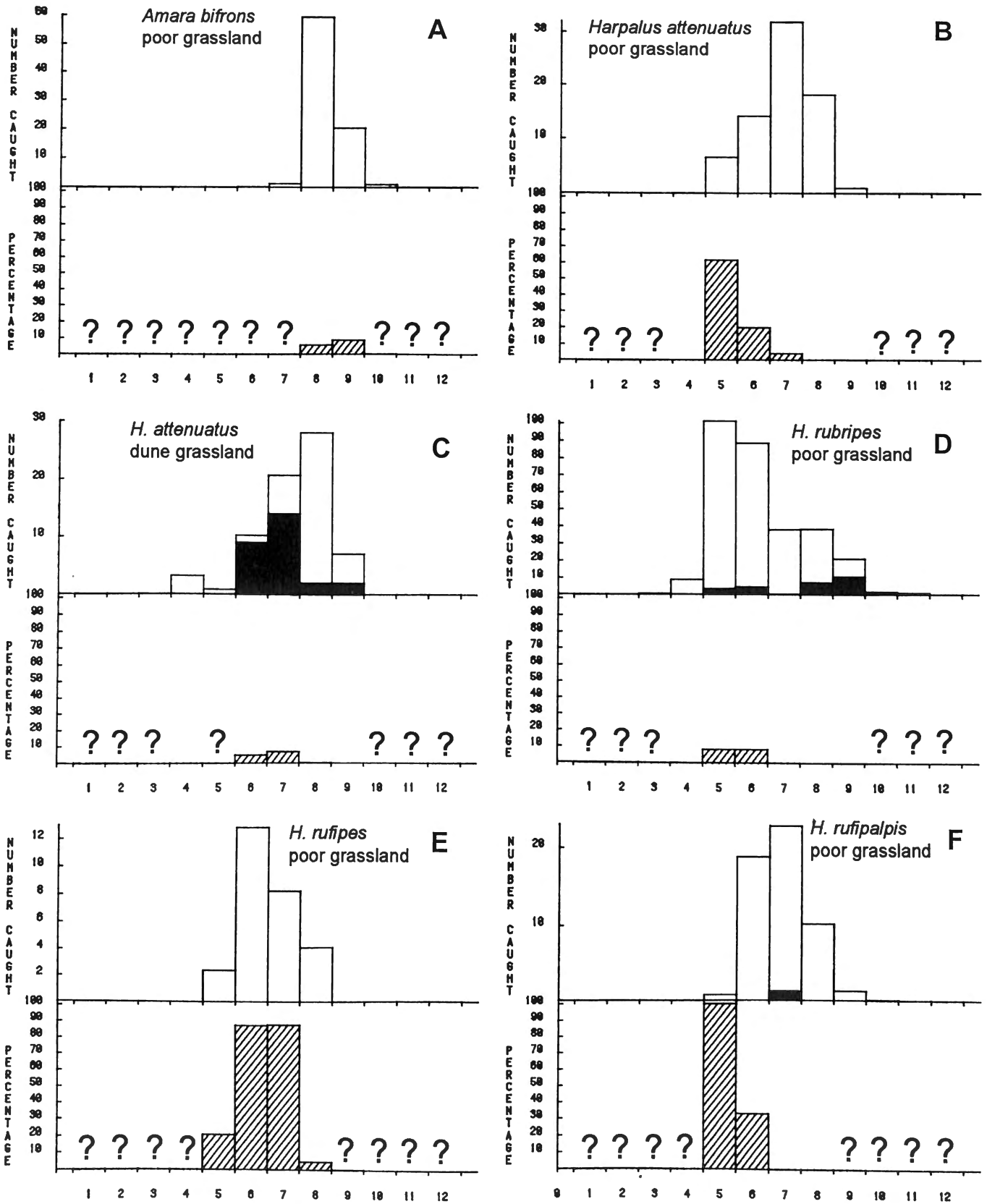


Fig. 4 (A-F) — Phenology of the life cycle in summer-autumn breeding ground beetles (upper figure; black columns: teneral beetles), compared to the seasonal occurrence of monthly proportions of beetles with functional flight muscles (lower figure; with 95% c.i. for large samples,?: months without data, arrows indicate zero-values based on large sample sizes). A: *Amara bifrons* (poor grassland on sandy soil), B-C: *Harpalus attenuatus* (B: poor grassland on motorway verge on sandy soil; C: dune grassland), D: *Harpalus rubripes* (poor grassland), E: *Harpalus rufipes* (poor grassland), F: *Harpalus rufipalpis* (poor grassland on motorway verge on sandy soil).

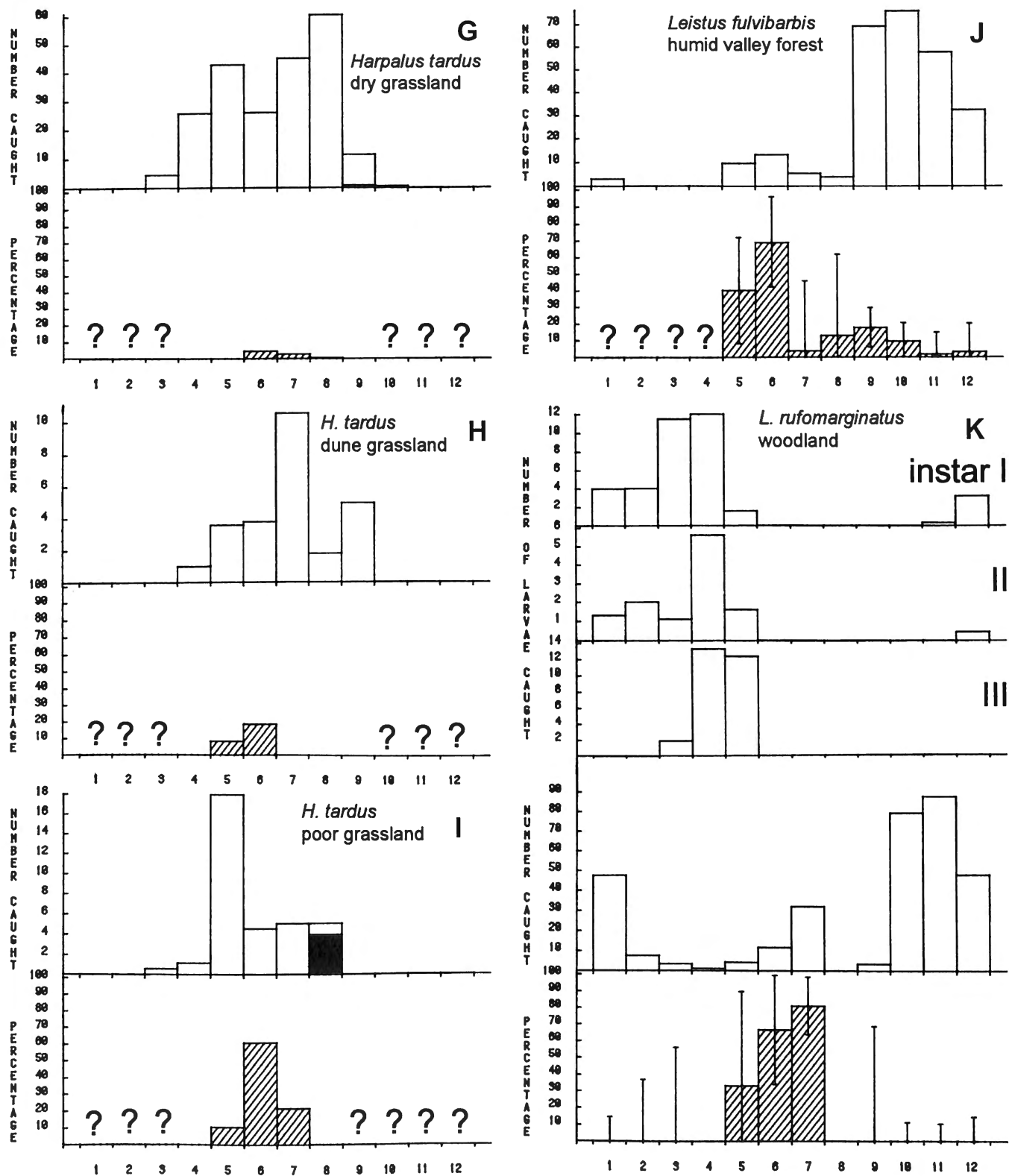


Fig. 4 (continued) — G-K: G-I: *Harpalus tardus* (G: dry grassland, H: dune grassland, I: poor grassland), J: *Leistus fulvibarbis* (humid valley forest), K: *Leistus rufomarginatus* (woodland site; phenology of the three larval instars added).

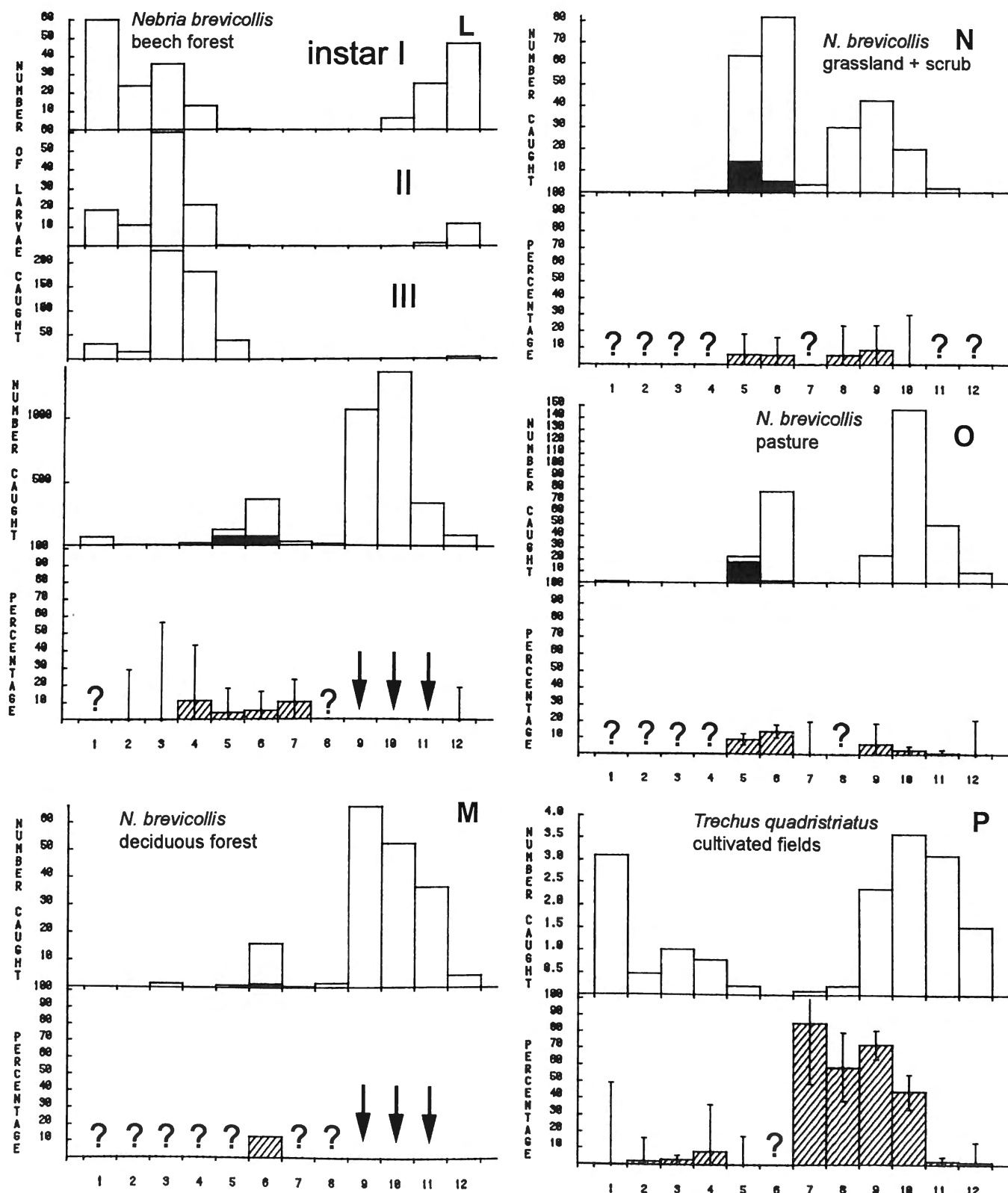


Fig. 4 (continued) — L-P: L-O: *Nebria brevicollis* (L: beech forest; phenology of the three larval instars added; M: deciduous forest; N: grassland with scrub; O: pasture), P: *Trechus quadristriatus* (cultivated fields).

duals with functional flight muscles as compared to beetles at a later stage of their life cycle. The flight period of this species is indeed restricted to a short period between July and September. Dispersal by flight is probably an adaptation to the temporary characteristics of the reproduction habitat (e.g. due to crop rotation, ploughing and other management practices). Although several females have ripe ovaries and at the same time functional flight muscles, a significant oogenesis-flight syndrome is observed (Table 1).

3. Seasonal variation of wing morph frequencies and flight muscle functionality in wing dimorphic and polymorphic ground beetles

Data on seven wing dimorphic or polymorphic carabid species are summarised in Fig. 5 (A-H) and in Table 1 (dissected females). Three populations were studied of the wing dimorphic *Bembidion properans*, two populations of the wing dimorphic *Bradycellus harpalinus*, one population of the wing dimorphic *Clivina fossor* and *Calathus rotundicollis*, and one population of the wing polymorphic *Pogonus chalceus*, *Pterostichus minor* and *Pterostichus vernalis*. Most of these species are reproducing during spring (adult hibernators), with the exception of *Calathus rotundicollis* (summer reproduction; larval hibernator) and *Bradycellus harpalinus* (reproduction during autumn till next spring).

Bembidion properans (Fig. 5 A-C) does not show much differences between observed wing morph frequencies per month (two populations) as opposed to the clear seasonal changes in functional flight muscle frequencies in all populations studied. The results suggest the occurrence of an oogenesis-flight syndrome during spring (see also Table 1), while only very few beetles with functional flight muscles are observed during autumn.

A higher incidence of beetles with flight muscles in spring and in autumn is observed in *Pterostichus vernalis* and *Pterostichus minor*, again suggesting the occurrence of a seasonal shift in habitat (migration towards or away from an overwintering habitat, cf. DESENDER et al., 1981). In the case of *Pterostichus vernalis*, however, maximal proportions of beetles with functional flight muscles are quite low. Obviously these numbers are further reduced not only during reproduction but also during hibernation diapause.

Clivina fossor (only limited data and no macropterous females available) shows a low maximal proportion of beetles with flight muscles, which seems to coincide with the reproductive period. Interestingly, this species has a largely subterranean way of life and does not seem to perform habitat change in the pasture studied (cf. DESENDER, 1983; DESENDER & POLLET, 1985).

The saltmarsh inhabiting *Pogonus chalceus* does not show an oogenesis-flight syndrome, although high numbers of beetles were investigated (Table 1). Despite being low, the yearly peak of beetles with functional flight muscles (DESENDER, 1985), coincides with the moment

of highest number of ripe eggs carried by the females in their ovaries (Fig. 5 G).

Calathus rotundicollis, a species from light forest and woodland edges, again seems to show an oogenesis-flight syndrome. Only at the onset of the seasonal activity cycle, at most 20% of the beetles possessed functional flight muscles.

Finally, *Bradycellus harpalinus* shows a pronounced oogenesis-flight syndrome: functional flight muscles and possible dispersal by flight are limited to the post-teneral and pre-reproductive period. Dry grassland, heathland as well as wetland are the preferred habitats of this rather eurytopic species.

Discussion

Because we did not study actual flight behaviour in ground beetles, our results give indirect evidence only for seasonal variation in the occurrence of dispersal by flight. Studies based on flight observations only, on the other hand, suffer from other shortcomings, because such observations are highly influenced by meteorological variation. In addition, flight observations, especially if gathered by light trapping, are much more difficult to quantify in terms of local population sizes. Data on flight muscle development (as in our study) give an idea of the maximal proportion of individuals in a population that might be able to fly.

Proximate factors influencing the onset and duration of flight in carabid beetles predominantly act as strong inhibitors for flight. VAN HUIZEN (1979) showed that most ground beetles show no flight activity below 17°C (see also HONEK & PULPAN, 1983), during precipitation and at wind speed exceeding about 5 m/s. Day-active species appear to require strong insolation prior to flight behaviour. For many carabids from our regions, these imposed physiological constraints reduce the number of days per year, suitable for flight, to a few days to some weeks, with extreme variation between years and sites. This has been confirmed by long term series of flight observations in ground beetles (e.g.: light traps: HONEK & PULPAN, 1983; window traps: VAN HUIZEN, 1979; DEN BOER et al., 1980). Published data on the flight periods in the species from our study (compiled in Table 2) largely correspond to our observed seasonal pattern of flight muscle functionality. Species which are known occasionally to perform mass flights also show nearly complete flight muscle functionality during such periods (e.g. *Bradycellus harpalinus*, cf. KERSTENS, 1961; *Trechus quadristriatus*, cf. LACMAN, in press).

If the species that we have investigated are grouped into spring breeders (short larval cycle in summer, adult hibernation) and summer-autumn breeders (long larval cycle till next spring or summer), the latter contain more species with functional flight muscles in the post-teneral and pre-reproductive period than the former. Such species fly during a short time span of the year (sometimes a few days only with mass flight, cf. HONEK & PULPAN, 1983).

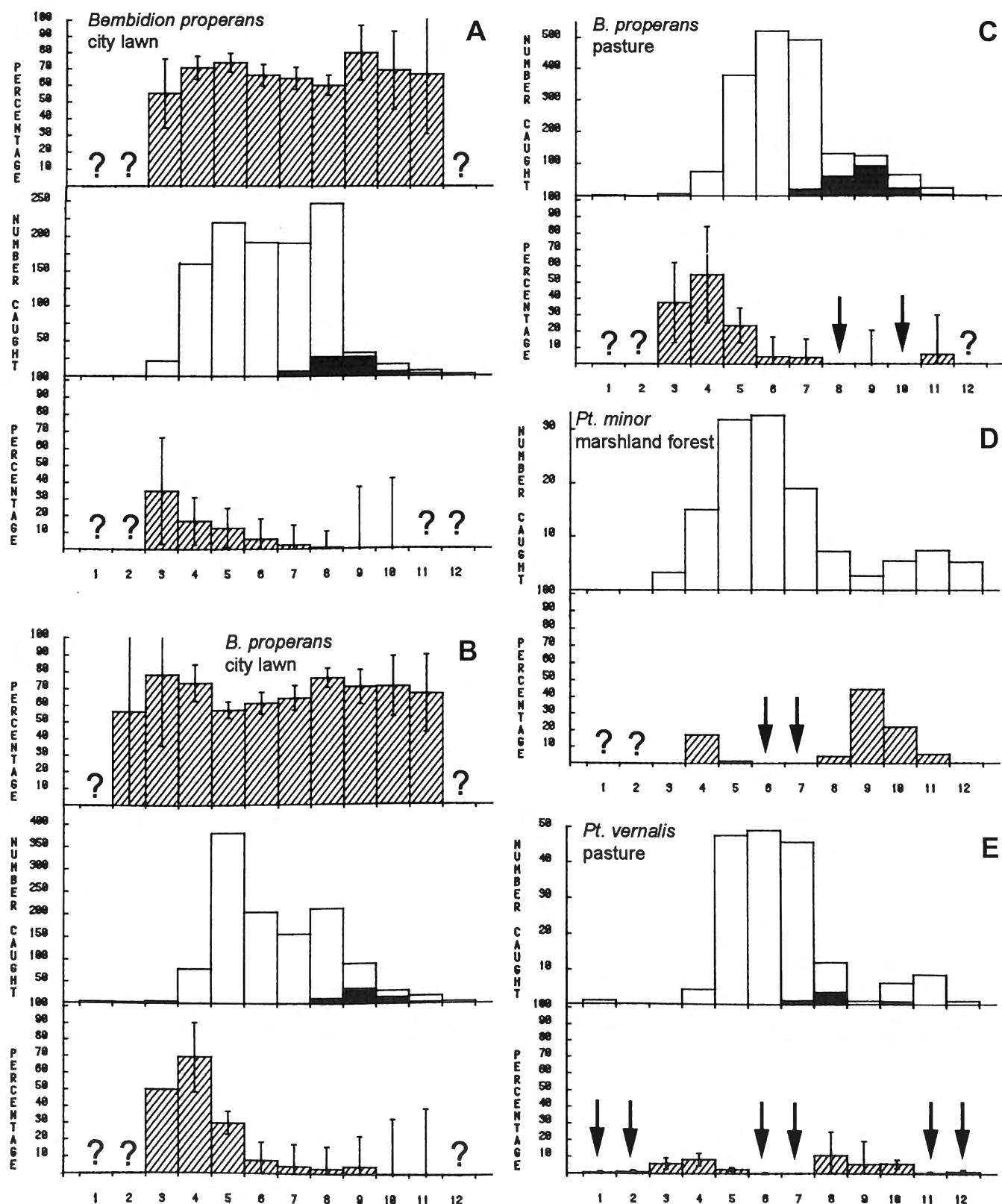


Fig. 5 (A-H) — Wing dimorphic and polymorphic carabid species: calculated percentages with functional flight muscles based on the number of macropterous individuals only, except for D, E and G; see legend Fig. 3 for further explanation. A-C: *Bembidion properans* (A-B: two recent lawns in the city of Ghent; uppermost figure represents the seasonal variation in the percentage (with 95% c.i.) of winged beetles for this wing dimorphic species, middle figure shows phenology of the life cycle (black columns: teneral beetles), compared to the seasonal occurrence of monthly proportions of beetles with functional flight muscles (lower figure; with 95% c.i. for large samples,?: months without data, arrows indicate zero-values based on large sample sizes); C: pasture), D: *Pterostichus minor* (marshland forest), E: *Pterostichus vernalis* (pasture).

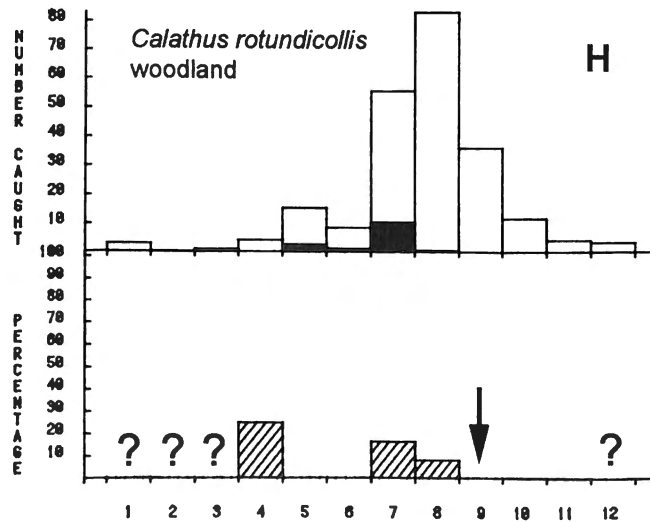
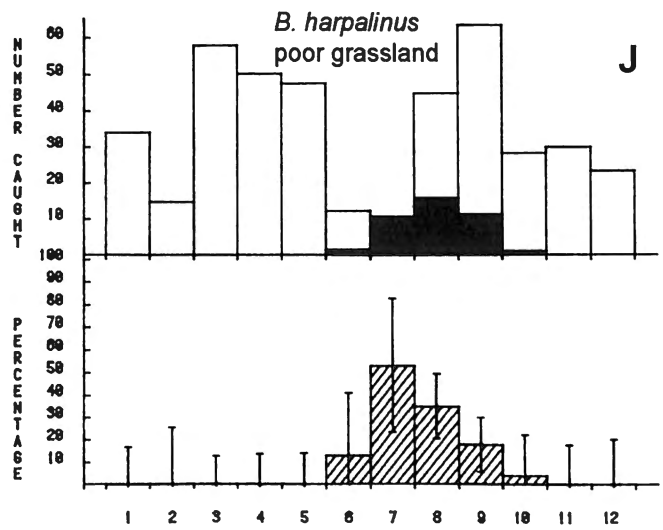
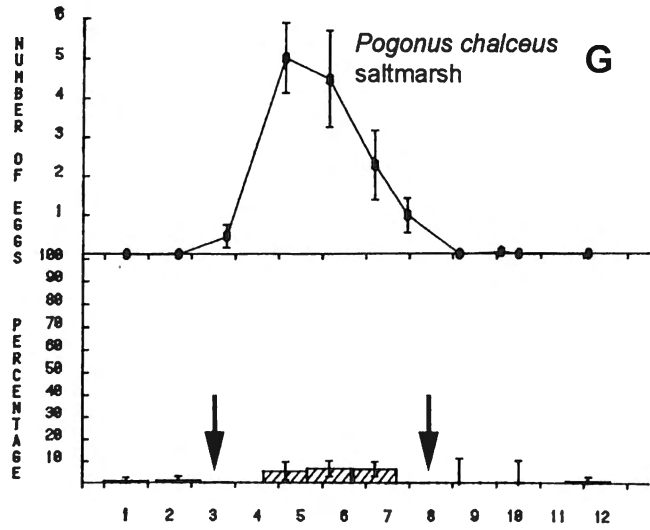
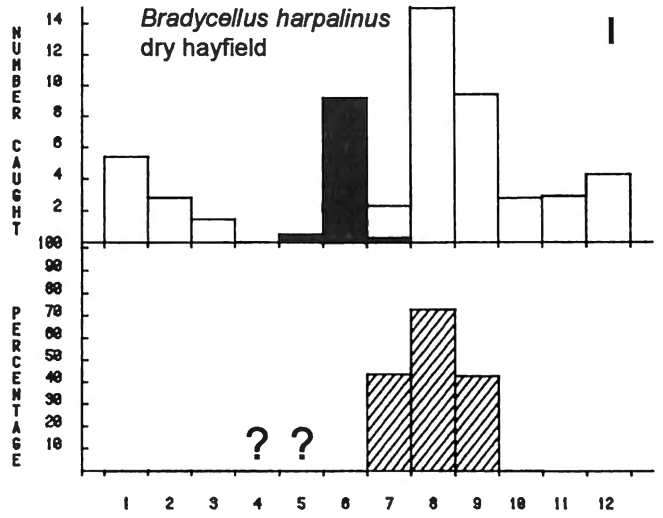
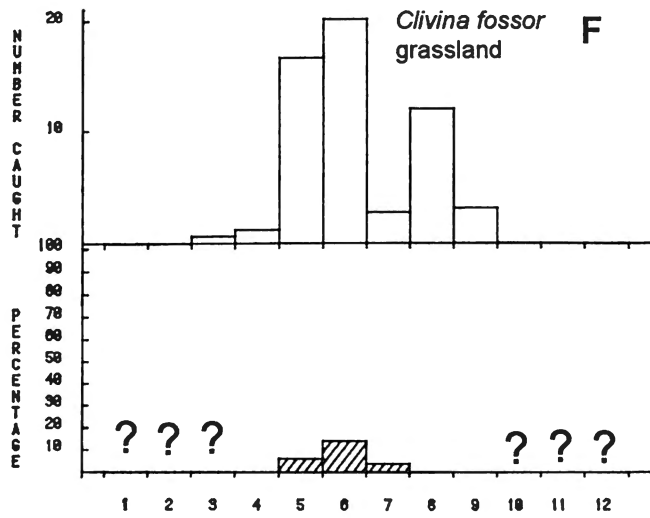


Fig. 5 (continued) — F: *Clivina fossor* (grassland), G: *Pogonius chalceus* (saltmarsh; number of ripe eggs per female plotted as indication of reproductive period), H: *Calathus rotundicollis* (woodland site), I-J: *Bradycellus harpalinus* (I: dry hayfield, J: dry poor grassland).

Table 2. — Compilation of literature observations of flight and main annual flight period in the ground beetle species, studied in this paper; **species** ordered in three groups as in results (spring breeders, autumn breeders and dimorphic/polymorphic species) and in alphabetic order within each group: **number of records**: * = low numbers, X = high numbers; number of symbols refers to the number of references with the species; data from: BASEDOW & DICKLER, 1981; BRIEL, 1962; BRIGGS, 1965; DEN BOER, 1971; DESENDER, 1986b and unpublished data; GREENSLADE & SOUTHWOOD, 1962; HAECK, 1971; HONEK & PULPAN, 1983; KADAR & SZENTKIRALYI, 1983; KERSTENS, 1961; LACMAN, in press; LINDROTH, 1945; MATALIN, 1994, 1997; MEIJER, 1974; VANHERCKE et al., 1980; VAN HUIZEN, 1979, 1980; ZHANG et al., 1997; ZULKA, 1994.

Species	number of records	flight period(s)
<i>Acupalpus flavicollis</i>	X*	?
<i>Agonum dorsale</i>	***	April-May, August
<i>Agonum muelleri</i>	***	April, September
<i>Amara aenea</i>	XXXX**	April-May, (September)
<i>Amara familiaris</i>	XXX***	April-July
<i>Amara tibialis</i>	*	April-May
<i>Anisodactylus binotatus</i>	XXX*	April-May, (September)
<i>Asaphidion curtum</i>	****	April-June
<i>Harpalus affinis</i>	X*	May-June
<i>Pterostichus versicolor</i>	**	May, end July
<i>Amara bifrons</i>	XX*****	July-August
<i>Harpalus attenuatus</i>	?	?
<i>Harpalus rubripes</i>	*	?
<i>Harpalus rufipes</i>	XXXXXX***	July
<i>Harpalus rufipalpis</i>	X	?
<i>Harpalus tardus</i>	?	?
<i>Leistus fulvibarbis</i>	?	?
<i>Leistus rufomarginatus</i>	?	?
<i>Nebria brevicollis</i>	*	May
<i>Trechus quadristriatus</i>	XXXXXX***	July-September
<i>Bembidion properans</i>	**	April-May
<i>Bradycellus harpalinus</i>	XXXXXX*****	July-August
<i>Calathus rotundicollis</i>	*	early August
<i>Clivina fossor</i>	***	May-June
<i>Pogonus chalceus</i>	?	?
<i>Pterostichus minor</i>	X*	?
<i>Pterostichus vernalis</i>	****	May, September

Many spring breeders, on the other hand, with a winter-diapause between emergence and reproduction, show a higher incidence of functional flight muscles before as well as after reproduction (in that case mainly post-teneral). Seasonal variability in flight muscle development in these species coincides with two known flight periods per year (references, cf. Table 2) related to habitat change to and from overwintering sites and sites for reproduction. After emergence and flight activity, adults of many summer-autumn breeders directly start reproduction. From then onwards the reproducing generation gradually dies off. The very short flight periods in these species can also be a partly consequence of other life history aspects. Many of these ground beetles indeed are known to be exclusively active during the night (DESENDER et al. 1984;

THIELE, 1977), as opposed to a lot of day-active spring species. Summer-autumn breeders like *Bradycellus harpalinus*, *Harpalus rufipes* and *Trechus quadristriatus* are caught especially flying at night (cf. HONEK & PULPAN, 1983; MATALIN, 1997; ZHANG et al., 1997). The high temperatures needed for flight further reduce the number of days with suitable conditions for flight in night-active species. Spring carabid beetles, on the contrary, are probably less constrained for flight because of their daytime activity and indeed regularly show two flight periods a year, related to habitat change. In some cases (e.g. *Bembidion properans*) the spring peak appears to be more important than the autumn peak (following from data on flight muscle functionality as well as from literature data on flight periods). This could reflect a synchronous de-

velopment of flight muscles after winter diapause in order to be able to recolonise the reproduction habitat as quickly as possible. During autumn the appearance of the new generation is much more spread, while shortening of daylength inhibits vitellogenesis and thus reproduction (THIELE, 1977). It is therefore possible that suitable hibernation quarters are then more easily reached by less energy-demanding activities such as walking instead of flying (more "time" available?).

A majority of the carabid beetles investigated seems to exhibit a significant "oogenesis-flight" syndrome: reproduction and reduced flight musculature are thus not independent events in their life cycle, i.o.w. there is a trade-off between reproduction and functional flight musculature. Reproduction as well as flight being both very energy-consuming activities, it seems plausible that resorption of flight muscles liberates energy (cf. ZERA & DENNO, 1997) and/or creates space to accommodate enlarging reproductive organs (cf. SOLBRECK, 1986; TADA et al., 1991). Flight activity during reproduction probably is hampered or even made impossible in some species because of an increased individual body weight (cf. MATALIN, 1997) and consequently higher wing loading. These hypotheses should be tested experimentally. Species where some individuals will and others will never be able to develop flight muscles (genetic flight muscle dimorphism) present interesting cases for such experiments.

In many ground beetle species, especially spring breeders, we observe a proportion of mature females *with* functional flight muscles, indicating a less deterministic version of the oogenesis-flight syndrome. This could have important side effects for the colonisation chances of such species. When migration is related mainly to seasonal changes between habitats for reproduction and for hibernation, straggling individuals leaving hibernation quarters will now and then end up in a site, never colonised before. Sporadic flight activity of ripe or at least inseminated females would strongly increase the chances for founding new populations. VAN HUIZEN (1990) came to a similar conclusion after dissecting 932 beetles belonging to 62 carabid species. Unfortunately, this author did not list the species or sample sizes, but gave pooled results, difficult to evaluate.

JOHNSON (1969) came to the conclusion that, in insects in general, processes of gonad maturation and degeneration/regeneration of flight muscles are coupled during morphogenesis. These processes would have been adaptively brought into phase in different ways according to the species. De- and regeneration of flight muscles are part of a labile system of morphogenesis, but are still insufficiently understood (RANKIN et al., 1986). Flight muscle development, because of its hidden aspect, has been studied insufficiently and the difference between ontogenetic (direct) and phylogenetic (evolved) flight muscle dimorphism is vague (JOHNSON, 1969). Variability in the synchronisation between egg production and a functional flight apparatus is more pronounced when both developmental pathways are reversible. JOHNSON (1969)

therefore concluded that the "oogenesis-flight syndrome" in many cases is labile and controlled mainly by the environment.

If dispersal (migration) contributes to individual fitness (survival and direct or indirect reproductive output), we expect that species, emerging during summer, will show flight activity immediately before their reproduction. At that moment, climatological conditions are most suitable and females are not yet carrying the extra weight of eggs (males not yet the extra weight of very much enlarged genital accessory glands). In spring-breeding species this is not the case. Climatological conditions during early spring and autumn are much more regularly below threshold values for flight. This might give an explanation for the higher incidence in such species of females with ripe eggs simultaneously with functional flight muscles (i.e. a less deterministic oogenesis-flight syndrome).

In some of the species investigated, flight muscles are resorbed after suitable hibernation quarters have been reached, and are regenerated next early spring. This indicates that the mere maintenance of a functional flight apparatus (even without flight activity) involves high energy investments. Consequently, migration and diapause do not run strictly in parallel in such cases.

Functional flight muscles are expected to develop only when there is some selective advantage involved. This enables for example a rapid exchange between habitats for spring species while yielding much higher chances of survival in protected winter quarters. Extreme examples are species from habitats inundated during winter. An even stronger selection for the continuous presence of functional flight muscles is expected to occur in species from very unpredictable habitats (i.e. a habitat that cannot continuously be inhabited during the reproductive period). Such species need to be able to escape by flight at any time, for example from water floods after heavy rain, or from tides in saltmarshes. In such situations, a strong positive selection is expected for a permanent functional flight apparatus. At the end of this line of reasoning are examples of species that need flight for their normal daily activities (e.g. prey caught during flight or escape from predators in *Cicindela* or tiger beetles,...).

Maximal proportions of beetles with functional flight muscles in many species only reach low values, which can strongly differ between populations. This clearly indicates the complex regulation of flight muscle expression. Underlying mechanisms can be both autolysis/rebuilding processes and their regulation but also pure genetic flight muscle dimorphism. Experimental research is urgently needed for a better understanding of these processes. Regulation of autolysis and regeneration of flight muscles in the lifetime of individuals has hardly been studied in ground beetles. An important problem in this respect is that the observed phenotypic variation not necessarily reflects the genetic variability present in a population. Experimental studies on the regulation of flight muscle functionality of carabids were performed in *Nebria brevicollis* (NELEMANS, 1983, 1987) and in *Pterostichus oblongopunctatus* (VAN SCHAICK ZILLESEN

& BRUNSTING, 1984). Unfortunately, these two species rarely fly and therefore low fractions of individuals with flight muscles are observed in field situations. Favourable conditions during the larval ontogeny of *Nebria brevicollis* (such as sufficient food supply, short day-length) appear to enhance the expression of functional flight muscles in the resulting young adults. Results for *Pterostichus oblongopunctatus* lead more or less to an opposite conclusion, but the data seem less convincing. Some small experiments of BOMMARCO (1998) suggest that wing muscles of *Pterostichus cupreus* increase in size with increasing food availability. In a large scale biometric study on numerous ground beetle species (DESENDER, 1989b), we have regularly noted that individuals possessing flight muscles have a larger mean body size as compared to beetles with degenerated flight muscles. This seems to be in agreement with the results of NELEMANS (1983, 1987) on *Nebria brevicollis*. In her experiments, beetles raised under more favourable conditions (higher food supply, short day-length) not only developed flight muscles, but were also larger in size. The somewhat unexpected conclusion drawn from this observation is that under more favourable environmental conditions more beetles would be capable for flight. It contradicts the general idea that developing flight muscles and performing flight activity would largely be an adaptive escape reaction in a deteriorating habitat (cf. JOHNSON, 1969 for insects in general; VAN ZCHAICK ZILLESEN & BRUNSTING, 1984). Body size of beetles, on the other hand, is, at least partly, influenced by environmental conditions during ontogeny (cf. DESENDER, 1989a), which questions to some degree the term "adaptive".

Clearly, this study area offers a lot of new and original subjects for investigation. First, however, more empirical data are required, especially on other species and in other regions. Such field-collected data, along with those presented in this paper, are a first step towards straightforward experimental and physiological studies on flight muscle functionality and its underlying processes. Overall, our results suggest that flight muscle development, like other life history traits of ground beetles (such as habitat preference, life cycle timing, body size, abundance, hind wing development,...), is part of a suite of coadapted traits (DESENDER, 1986a).

In conclusion, a majority of the ground beetle species, investigated in this study, shows seasonal variation in the number of specimens with functional flight musculature. In many cases, this variability can be related to other life history traits. The complexity of the phenomenon is evident, and causes and effects in many cases are hard to distinguish, suggesting that flight muscle development is part of a suite of coadapted traits. The large interspecific variability in flight muscle functionality and the more or less pronounced occurrence of an oogenesis-flight syndrome is striking. This adds a further dimension to the already very large interspecific diversity in hind wing development of ground beetles (cf. DEN BOER et al., 1980; DESENDER, 1989b). Eventually, it increases the

value of ground beetles as model organisms in studies on dispersal and gene flow, population genetics, ecology and evolution.

Acknowledgements

This paper would not have been possible without the continuous help, during many years, from many students and colleagues: in particular Mark Alderweireldt, Léon Baert, Jean-Pierre Maelfait, Marc Pollet and Marc Van Kerckvoorde aided in the collection of large series of year cycle pitfall trap samples in different habitats of our country. Marc Van Kerckvoorde in addition helped by dissecting a number of series of ground beetles for their flight muscle development. P. Grootaert (RBINSc) and A. Huysseune (RUG) kindly revised previous drafts of this paper and H. Turin added useful review comments.

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