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The relevance of life-history theory for carabid species of Western Europe*

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ABSTRACT: By assuming that natural selection controls life-history traits evolutionary biologists try to construct evolutionary processes. Models should show how life-history traits that promote the fitness of individuals must lead to the life histories observed at present as well as those to expect in future.

The authors of this paper compare the generally occurring life histories among West European carabid species, and conclude that the traits governing these life histories differ significantly from those usually advanced by evolutionary biologists. Next to 'time of reproduction' especially 'dispersal power' and 'turnover frequency' of population units appear to be significant. They try to explain these departures from the generally accepted schemes, and emphasize the need to do more comparative investigations of life histories among groups of related species. As an example of the result to expect they give a provisional scheme of the dominant life history patterns of the carabid species of Drenthe in the North of the Netherlands.

1 INTRODUCTION

Evolutionary biologists try to understand evolutionary processes by imagining how natural selection most probably would lead to life histories that will maximize fitness of the individuals of the populations concerned. Which life-history traits can be assumed to most contributing to individual fitness? It is quite logical to suppose that traits which under the given conditions would maximize reproduction will give the individual the best chance to propagate its genes, and thus to best contribute to the fitness of the population. Under highly unstable conditions a maximum reproduction can be reached by producing as many eggs (or young) as possible, in order to compensate for unpredictable losses in future; this means: maximizing productivity, i.e. r-selection. Under stable conditions it seems better to give the young the best possible start, even when this would mean the production of a few young only, in order to provide them with the highest fitness possible under competition; this means maximizing efficiency, i.e. K-selection. These ideas of MacArthur & Wilson (1967) were extended, diversified and adapted to special circumstances in what is called 'life-history theory' (Stearns 1992; Roff 1992).

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2 LIFE-HISTORY THEORY

In the course of time most evolutionary biologists agreed that the most important life-history traits promoting fitness must be (1) brood size, (2) relative size of the young, (3) age distribution of reproduction, i.e. a single reproductive period per female : semelparity or more reproductive periods per female: iteroparity, (4) the interaction of reproductive effort with other energy-asking processes and thus with adult mortality, i.e. trade-offs between fecundity and survival of adults, (5) age of first reproduction. Depending on the general circumstances under which certain animals are living one or more of these five life-history traits would be promoted by natural selection. Efficient combinations of life-history traits are sometimes called 'strategies'. As most animals do not actively choose the most efficient combinations of life-history traits, in my opinion, the term 'strategy' (derived from military operations) gives a wrong suggestion. Most animals are passively manipulated by natural selection into a certain way of living, in which learning by experience allows only restricted modifications of the genetically fixed pattern. Therefore, I prefer to call combinations of life-history traits life-history patterns, i.e. combinations of traits that by 'trial and error' are brought together by natural selection in the genomes of individuals.

However, the development of life-history theory was mainly theoretical and stimulated the construction of models for special situations. This trend was heavily criticized by Stearns (1976), but apparently he let persuade himself by his colleagues that his criticisms were wrong, for in his book of 1992 he associates himself with the general trend in literature. In 1976 Stearns' criticism mainly concerned the fact that theory developed without sufficiently testing hypotheses with adequate field data. As a field ecologist this criticism of Stearns (1976) appealed to me.

3 LIFE-HISTORY TRAITS AMONG CARABID BEETLES

For a long time carabidologists have been fascinated by differences in wing development in relation to life histories and habitat selection. Larsson (1939) was the first to discriminate between spring and autumn breeders. Darlington (1943) following Darwin (1859) evaluated wing development in relation to dispersal and habitat selection. Lindroth (1945, 1949) brought life histories, habitat selection and wing development together in an imaginative picture of the development of the carabid fauna of Fennoscandia after the last Ice Age. Den Boer (1977) tried to give a comparable picture for the cultivated countryside Drenthe in the Netherlands, and Thiele (1977) composed an excellent review of our knowledge of the adaptations of carabid beetles in relation to habitat selection. Stimulated by the paper of Stearns (1976) and because I had available life-history data of more than 150 carabid species, at a carabid conference in 1978 in Rees-Grietherbusch I gave a provisional impression of the most important life-history traits among the carabid species of Drenthe by comparing the way of living of forest species with that of species of unstable habitats (Den Boer 1979). These data were supplemented by den Boer et al. (1980) for wing development and by Den Boer & Den Boer-Daanje (1990) for reproduction periods. Recently all this was worked out more completely by Den Boer & Van Dijk (1996), and I want to tell you what are our most important conclusions.

First of all we concluded that 'brood size' could not be a very important life-history trait among carabid species, because in poikilothermic animals reproduction is highly affected by temperature and amount of high quality food, also among carabids (Van Dijk 1983, 1986). Even under constant conditions individual egg production varies with a factor ten (Van Dijk 1979, 1994; Nelemans 1987). Hence, a high reproductive potency can hardly be expected ever to result in a correspondingly high production of young, the more so as larval mortality usually is very high and unpredictable. Second, most carabid species, at least in western Europe, are iteroparous, showing more reproductive periods in succeeding years; the few semelparous species, so far discovered, do not live under special conditions. Further, there were no 'trade-offs' between egg production and survival (Van Dijk 1979, 1994), nor between egg production and development of wings (Aukema 1991, 1994). On the contrary, the highest reproducing females survived best, and females that developed functional wings and wing-muscles produced more eggs than wingless females. The size of eggs differs between species, but there could not be found any relationship with dominating conditions: species producing a few big eggs both inhabit stable habitats like forest or old heath areas, and unstable habitats; the same applies to species producing many small eggs, and to the relationship between size of the beetles and size of reproduction.

The only life-history trait favoured by the evolutionary biologists of the life-history theory that appears to be important among carabid species is 'age of first reproduction'. Autumn breeders, which reproduce immediately after emergence, prefer stable habitats and usually produce many small eggs, i.e. potentially they have a high level of egg production. This is necessary to compensate for the usually very high mortality of young larvae under winter conditions (e.g. Van Dijk & Den Boer 1992). Spring breeders, which reproduce after having hibernated, usually produce less eggs and the eggs often are somewhat bigger, but under field conditions there is no actual difference in size of reproduction between spring breeders of stable and of unstable habitats.

An important life-history trait among carabid species appears to be 'dispersal power', a trait not appreciated by evolutionary biologists. Most species of stable habitats have low powers of dispersal, either being wingless or wing-dimorphic with a low fraction of fully winged individuals, or, if fully winged, not showing a high level of flight activities. Species of unstable habitats usually are constantly fully winged and show frequent flight activities. Dispersal power links 'turnover of local populations' with habitat preference. In unstable habitats carabid species show both high powers of dispersal and a high turnover of local populations, i.e. local populations only survive for a few years, but are frequently founded or refounded. In stable habitats carabid species show both low powers of dispersal and a lower turnover of local populations. In accordance with life-history theory in the most stable habitats, old forests and especially on mountains, we find a number of carabid species that produce low numbers of rather big eggs (*Carabus*, *Abax* and *Molops* species), and which often show some simple kind of parental care (Brandmayr & Zetto-Brandmayr 1979). But they form only part of the carabid fauna of old forest; there are also carabid species that lay many small eggs living in stable habitats, old forests included. Moreover, in other stable habitats carabid beetles with quite different reproductive potentials can be found. Hence, we can conclude that among

Table 1. Provisional scheme of a classification of life-history patterns of carabid species of Western Europe.

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- (1). Spring breeding (summer larvae)
well dispersing species with a high turnover of populations
 - a. macropterous species of unstable or temporary habitats
 - b. macropterous or wing-dimorphic species of unstable, stable or transitional and/or changing habitats
 - (2) Spring breeding (summer larvae)
rather badly dispersing species with a generally not very high turnover of populations and occupying stable habitats
 - a. macropterous species, possibly with low powers of dispersal
 - b. wing-dimorphic species with low powers of dispersal
 - c. brachypterous species with poor powers of dispersal
 - (3) Species with a complex reproduction cycle and variable developmental periods and occupying stable habitats
 - (4) Summer or autumn breeding (winter larvae)
well dispersing species with a high turnover of populations
 - a. macropterous species of unstable or temporary habitats
 - b. wing-dimorphic species of unstable and/or transitional or changing habitats
 - (5) Summer or autumn breeding (winter larvae)
rather badly dispersing species with a not very high or low turnover of populations
 - a. macropterous species of stable and/or transitional habitats
 - b. wing-dimorphic species of stable habitats
 - c. brachypterous species of stable habitats
 - (6) Late autumn breeding with summer diapause
low powers of dispersal and a low turnover of populations
 - (7) Winter or early spring breeding
inhabitants of open, sandy sites with a high turnover of populations
 - a. macropterous species with good powers of dispersal
 - b. wing-dimorphic species with rather good powers of dispersal
 - (8) Winter or early spring breeding
inhabitants of open, sandy sites with a not very high turnover of populations
 - a. wing-dimorphic or brachypterous species with low powers of dispersal

carabid species of Western Europe especially dispersal power, turnover frequency and habitat selection are closely associated, i.e. they form a life-history pattern that is weakly associated with 'age (time) of first reproduction'.

Therefore, for the carabid species of western Europe I consider 'time of first reproduction' as the primary life-history trait, among which we can distinguish again differences in dispersal power, turnover frequency and habitat selection. A more detailed treatment and a complete scheme of life-history patterns for 174 carabid species can be found in Den Boer & Van Dijk (1996) and is summarized in Fig. 1 and the tables 1 and 2 of this paper.

4 CAUSES OF DEVIATING LIFE-HISTORY PATTERNS AMONG CARABID BEETLES

We may wonder why our experiences with the dominant life-history traits of carabid beetles deviate to such a high degree from the predictions of life-history theory. In our opinion this is connected with a too simple idea of the effects of natural selection. Following Charles Darwin too strictly natural selection is often thought to be 'survival of the fittest'. But do only the 'fittest' survive and are the non-survivors always 'unfit'? Den Boer (in Den Boer & Reddingius 1996: Ch. 3) explains that natural selection is the 'non-survival of the non-fit', because only the individuals being 'non-fit' in some respect and those being 'unlucky' will die (being selected away) under a certain set of conditions. All other individuals will survive and reproduce, i.e. are positively selected. During its life time each individual passes through a number of such selective events, and during each event it may be 'fit' or 'unfit', or belong to the 'lucky' chance survivors or to the 'unlucky' chance victims. Among the reproducing individuals there may be some that under other sets of conditions would have been 'unfit' and others that were simply 'lucky' enough to escape so far from the current adverse conditions.

Therefore, under the complicated and variable conditions in the field we may not expect that females producing the highest numbers of eggs will always have the greatest progeny. Moreover, before these eggs have produced fertile females again many environmental processes and chance events may have changed this advantage to such an extent that it may have disappeared completely. And, as mentioned above, egg production among carabid beetles (and most other arthropods) is highly variable, by which females potentially able to produce a high number of eggs may not be able to realize this potential under field conditions. Therefore, it can be expected that quite different life-history traits will determine the fate of such species, as was demonstrated for carabid beetles of western Europe by Den Boer & Van Dijk (1996). Just as in the discussions around 'regulation of numbers' (Den Boer & Reddingius 1996) we cannot get an adequate picture of natural processes without taking the variability of the more important natural processes into account, i.e. models and ideas based upon deterministic thinking cannot be expected to give us a realistic insight into natural processes, in spite of the often appealing logic of such deterministic thoughts. Therefore, in my opinion life-history theory as it is presented by Stearns (1992) and Roff (1992) does not apply to animal populations (especially not to invertebrates) under natural conditions.

5 REQUEST TO ENTOMOLOGISTS

I told all this not only because our findings about the life-history patterns among carabid species remarkably deviate from the conclusions of life-history theory, but more to stimulate entomologists to think about the most important life-history patterns dominating other groups of arthropods. It would be highly interesting to compare the empirically found life-history patterns in many different groups of arthropods, and in this way to contribute to an improvement of life-history theory, making this theory less theoretical and more empirical. For, it is beyond dispute that

Table 2. Provisional classification of the carabid species of Drenthe (the Netherlands) according to the life-history patterns in the scheme of Table 1. The numbers behind the species are used in Fig. 1 and refer to Den Boer (1977: Table 2 and Appendix A, Part I).

A. the most abundant species (mentioned in Fig. 1).

- (1). a. *Agonum sexpunctatum* (18: wet), *Amara aenea* (21: agr.), *A. communis* (26: agr.), *A. famelica* (30: wet), *A. familiaris* (31: agr.), *A. plebeja* (35: agr.), *Anisodactylus binotatus* (42: agr.), *Asaphidion flavipes* (44: agr.; Coll.), *Harpalus affinis* (99: agr.), *Loricera pilicornis* (112: wet; Coll.), *Pterostichus minor* (135: wet; 95% macr.), *P. nigrita/rhaeticus* (137: wet; see Koch & Thiele, 1980), *P. quadriveolatus (angustatus)* (130: burn), *P. vernalis* (140: wet).
- b. *Agonum fuliginosum* (9: wet, forest borders; 28% macr.), *Amara lunicollis* (34: wet, grass; macr.), *Bembidion lampros* (54: agr., wet; 17% macr.), *Clivina fossor* (86: agr., wet; 90% macr.), *Dyschirius globosus* (95: agr., wet; 0.1% macr.), *Notiophilus palustris* (122: forest borders; 7% macr.), *Pterostichus diligens* (133: wet, grass; 4% macr.), *P. strenuus* (139: meadows, forest; 23% macr.).
- (2). a. *Agonum assimile* (6: forest borders), *Notiophilus rufipes* (124: forest; Coll.), *Pterostichus oblongopunctatus* (138: forest), *P. versicolor (coerulescens)* (132: heath, poor meadows).
- b. *Syntomus (Metabletus) foveatus* (114: sandy heath; 1.2% macr.).
- c. *Agonum ericeti* (8: peat moor), *Carabus nemoralis* (78: forest), *C. arvensis* (75: heath), *Pterostichus lepidus* (134: sandy heath)*.
- (3). *Abax parallelepipedus (ater)* (1: forest; brach.), *Calathus rotundicollis (piceus)* (73: light forest; 93% macr.), *Notiophilus aquaticus* (119: heathy areas; 1.2% macr.; Coll.), *N. biguttatus* (120: light forest; 74% macr.; Coll.), *Carabus cancellatus* (76: heathy areas; brach.).
- (4). a. *Harpalus rufipalpis (rufitarsis)* (106: poor grassland), *H. rufipes (pubescens)* (104: agr.).
- b. *Calathus fuscipes* (69: trans.; 0.9% macr.), *Pterostichus melanarius (vulgaris)* (141: agr.; 2% macr.), *Trechus obtusus* (146: forest borders; 3% macr.).
- (5). a. *Amara brunnea* (25: light forest), *A. equestris* (29: heath), *Broscus cephalotes* (66: sand), *Harpalus latus* (103: forest, heath), *H. quadripunctatus* (105: forest borders), *H. solitarius (fuliginosus)* (102: heath), *Nebria salina* (118: trans.), *Pterostichus niger* (136: all habitats).
- b. *Agonum obscurum* (17: wet grass; 0.1% macr.), *Calathus erratus* (68: sand; 0.2% macr.), *C. melanocephalus* (70: sandy heath; 0.2% macr.), *Cymindis vaporariorum* (89: heath; 6% macr.), *Notiophilus germinyi* (121: sandy heath; 3% macr.), *Olisthopus rotundatus* (125: heath; 21% macr.).
- c. *Carabus problematicus* (80: dry forest), *Cymindis macularis* (88: sand), *Pterostichus lepidus* (134: sandy heath)*, *Trechus secalis* (148: forest).
- (6). *Leistus rufomarginatus* (110: forest; macr.), *L. terminatus (rufescens)* (109: grass, trans.; macr.), *Nebria brevicollis* (117: light forest, trans.).
- (7). a. *Bradycellus ruficollis (similis)* (65: heath), *Trichocellus cognatus* (149: heath), *T. placidus* (150: light forest).
- b. *Bradycellus caucasicus (collaris)* (62: heath), *Bradycellus harpalinus* (64: grassy heath).
- (8). a. *Amara infima* (33: sand; 1.3% macr.), *Bembidion nigricorne* (56: sand; brach.).

**Pterostichus lepidus* seems to be both a spring and an autumn breeder (Van Dijk, pers. comm., and Paarmann, 1990).

B. less abundant species

- (1) a. *Acupalpus brunnipes*, *A. consputus*, *A. dubius*, *A. exiguus*, *A. flavicollis*, *A. meridianus*, *A. parvulus* (*dorsalis*) *Agonum albipes* (*ruficorne*), *A. dorsalis*, *A. gracile*, *A. marginatum*, *A. muelleri*, *A. piceum*, *A. thoreyi*, *A. versutum*, *A. viduum*, *Amara anthobia*, *A. ingenua*, *A. ovata*, *A. similata*, *A. spreta*, *Bembidion assimile*, *B. bruxellense* (*rupestre*), *B. doris*, *B. femoratum*, *B. obliquum*, *B. properans*, *B. quadrimaculatum*, *B. varium*, *Blethisa multipunctata*, *Dyschirius aeneum*, *D. luedersi*, *D. politus*, *D. thoracicus* (*arenosus*), *Elaphrus cupreus*, *E. riparius*, *Omophron limbatus*, *Oodes helopioides*, *Stenolophus mixtus*, *S. teutonius*.
- b. *Amara convexior*, *Badister dilatatus*, *Bembidion guttula*, *B. tetracolum* (*ustulatum*), *Calosoma inquisitor*, *Chlaenius nigricornis*, *Cicindela campestris*, *C. hybrida*, *Demetrias atricapillus*, *Dromius agilis*, *D. angustus*, *D. melanocephalus*, *D. quadrimaculatus*, *D. spilotus* (*quadrinotatus*), *Harpalus anxius*, *Notiophilus substriatus*, *Panageus cruzmajor*.
- (2) a. *Agonum krynickii*, *A. livens*, *A. moestum*, *Anisodactylus nemorivagus*, *Badister bullatus* (*bipustulatus*), *B. sodalis*, *B. unipustulatus*, *Bembidion humerale*, *Lebia chlorocephala*, *Odocantha melanura*.
- b. *Carabus clathratus*, *C. granulatus*, *Syntomus* (*Metabletus*) *truncatellus*, *Pterostichus anthracinus*.
- c. *Bembidion mannerheimi* (*unicolor*), *Carabus nitens*, *Cicindela germanica*, *Cychrus caraboides rostratus*.
- (3). *Carabus coriaceus*.
- (4) a. *Amara apricaria*, *A. aulica*, *A. bifrons*, *A. consularis*, *A. convexiuscula*, *A. fulva*, *A. majuscula*, *Asaphidion pallipes*, *Calathus ochropterus* (*mollis*), *Harpalus distinguendus*, *H. rubripes*, *H. smaragdinus*, *H. tardus*, *Trechus quadristriatus*, *T. discus*.
- b. *Calathus cinctus* (*erythroderus*).
- (5) a. *Amara pseudocommunis*, *A. kulti*, *A. praetermissa*, *A. quenseli*, *Miscodera arctica*, *Nebria livida*.
- b. *Calathus ambiguus*, *Synuchus nivalis*.
- c. *Calathus micropterus*, *Masoreus wetterhalli*, *Patrobus atrorufus* (*excavatus*), *Stomis pumicatus*.
- (6). *Leistus spinibarbis*.
- (7) a. *Bradycellus verbasci*.
- b. *Bradycellus csikii*.
- (8) a. *Bradycellus sharpi*.

Between brackets behind the species an indication of the preferred habitat
macr. = macropterous; brach. = brachypterous; agr. = occupying agricultural fields and other ruderal or disturbed sites; wet = occupying banks of pools and rivers and other wet sites; burn = reproduces at sites where woods or remnants of wood has been burnt; grass = prefers dense grass vegetations; trans. = occupying transitional sites between forest and heath or grassy vegetations; sand = occupying blown sand areas with only little vegetation; Coll. = specialized in the hunting of Collembles.

For estimates of dispersal power and turnover frequencies of the most abundant carabid species of Drenthe see Den Boer (1990a: Table 1; 1990b: Table 4).

species	no.	habitat	dp	Mar	Apr	May	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb										
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Anaphidion flavipes</i>	44	H+A	n	o	o	o	o	o	o	o															
<i>Pterostichus nigrintrhaeticus</i>	137	W	m	o	o	o	o	o	o																
<i>Pterostichus diligens</i>	133	W	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus minor</i>	135	W	d	o	o	o	o	o	o	o															
<i>Pterostichus strenuus</i>	139	F+W	d	o	o	o	o	o	o	o															
<i>Pterostichus oblongopunctatus</i>	138	F	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus quadriveolatus</i>	130	B	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Synotmus foveatus</i>	114	H+S	(d)	o	o	o	o	o	o																
<i>Agonum assimile</i>	6	F	(m)	o	o	o	o	o	o																
<i>Agonum ericeti</i>	8	H+P	b	o	o	o	o	o	o																
<i>Amara communis</i>	26	A+R	m	o	o	o	o	o	o	o															
<i>Amara familiaris</i>	31	A+R	m	o	o	o	o	o	o	o															
<i>Carabus nemoralis</i>	78	F	b	o	o	o	o	o	o																
<i>Loricera pilicornis</i>	112	W	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Amara famelica</i>	30	W	m	o	o	o	o	o	o	o															
<i>Carabus arvensis</i>	75	H	b	o	o	o	o	o	o																
<i>Amara aenea</i>	21	S+A	m	o	o	o	o	o	o	o															
<i>Dychirius globosus</i>	95	H+A	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus vernalis</i>	140	W	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus verticolor</i>	132	H	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Notiophilus aquaticus</i>	119	H	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Notiophilus palustris</i>	122	F	d	o	o	o	o	o	o																
<i>Notiophilus rufipes</i>	124	F	(m)	o	o	o	o	o	o																
<i>Agonum sexpunctatum</i>	18	W	m	o	o	o	o	o	o																
<i>Clivina fossor</i>	86	H+A	d	o	o	o	o	o	o																
<i>Harpalus affinis</i> X	99	A	m	o	o	o	o	o	o	o															
<i>Harpalus latus</i> *	103	H+F	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Notiophilus biguttatus</i> X	120	F	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Carabus cancellatus</i> X	76	H	b	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Calathus rotundicollis</i> *	73	F	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Cymindis macularis</i> *	88	S	b	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Bembidion lampros</i> X	54	W+A	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Harpalus quadripunctatus</i> *	105	F	m	o	o	o	o	o	o	o															
<i>Abax parallelepipedus</i> *	1	f	b	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Agonum fuliginosum</i> X	9	F	d	o	o	o	o	o	o	o															
<i>Anisodactylus binotatus</i> X	42	A	m	o	o	o	o	o	o	o															
<i>Harpalus solitarius</i> *	102	H	m	o	o	o	o	o	o	o															
<i>Agonum obscurum</i> *	17	H	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus lepidus</i> X	134	H+S	b	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Harpalus rufipes</i> *	104	A	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Amara plebeja</i> X	35	A	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Amara lunicollis</i> X	34	H+W	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Harpalus rufipalpis</i> *	106	R	m	o	o	o	o	o	o	o															
<i>Pterostichus melanarius</i> *	141	A	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Trechus secalis</i> *	148	F	b	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Cymindis vaporariorum</i> *	89	H	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Leisus terminatus</i> *	109	F+H	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Calathus erratus</i> *	68	H+S	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Broscus cephalotes</i> *	66	S	m	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Amara brunnea</i> *	25	F	n	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Calathus melanocephalus</i> *	70	H	(d)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Amara equestris</i> *	29	H	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Pterostichus niger</i> *	136	F+R	(m)	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Trechus obtusus</i> *	146	F+R	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Notiophilus germinyi</i> *	121	S	d	o	o	o	o	o	o	o	o	o	o	o	o										
<i>Olisthopus rotundatus</i> *	125	H	(d)	o	o	o	o	o	o	o	o	o	o	o	o										

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