Life Cycles and Habitats of the Northern European Agabini (Coleoptera, Dytiscidae)

by A. N. Nilsson

Abstract: The northern European Agabini includes three genera: *Agabus* Leach, *Ilybius* Erichson and *Platambus* Thomson. In this group, the following five types of life cycles have been recognized: (1) univoltine spring breeders which have summer larvae and overwinter as adults, (2) univoltine species that breed from summer to autumn and overwinter as eggs, (3) semivoltine spring breeders that overwinter first in the egg stage and the second winter as adults, (4) semivoltine summer breeders that overwinter first as larvae and the second winter as adults, and (5) species with flexible reproductive periods overwintering as larvae and adults.

Data from rearings, field studies, and literature were used to assign 40 different species to these groups. All species of *Ilybius* belong to the fourth group, the single species of *Platambus* was placed in the fifth group, and species of *Agabus* were represented in all but the fourth group.

The different habitats of the Agabini are viewed in relation to seasonality and productivity. Seasonality represents the constancy of the habitat, a characteristic that expresses the need for timing of the different life-cycle stages. Productivity is connected with the various rates of growth and development in different habitats.

Preferred habitats are listed for the species belonging to each of the five life-cycle groups. Most species of the first group are residents of permanent summerwarm waters of varying productivity. Also included are some chiefly southern species that occur in more temporary habitats. The second group includes only *Agabus fuscipennis* (Payk.), a species found in seasonal habitats of high productivity. The species in the third group also are associated with habitats of a high seasonality, though of varying, often lower, productivity. The *Ilybius* species, in the fourth group, are found in a wide spectrum of habitats. In the fifth group, with the exception of *Agabus bipustulatus* (L.), most species occur in habitats of low seasonality and low productivity.

The bearings of the recognized diversity in life-cycle patterns on phylogeny, ecology and distributions are briefly discussed.

Key words: Coleoptera Dytiscidae – Agabini – life cycles phenology – habitat characteristics – boreal wetlands.

Introduction

During the last decade much research was devoted to the study of insect seasonal cycles (TAUBER & TAUBER, 1981, for a review). The adaptations that determine the seasonal cycle of a species form a fundamental part of the life history, and thus have a direct bearing on its survival. The evolution of life cycles is associated with certain characteristics of the habitat (SOUTHWOOD, 1977), summarized into heterogeneity in space

and time. Different strategies have evolved to meet periods of habitat unfavorability in the cyclic changes associated with seasonal progression. Insect life cycles show an enormous diversity, with a corresponding pronounced flexibility (DINGLE, 1978; BROWN & HODEK, 1983). Each taxon has a ground plan that sets the available evolutionary alternatives. The traits that form the ground plan are fundamental to the biology of the species and do not vary within populations. Such traits are best studied using the comparative method. The objective of this paper is to compare the different kinds of life cycles, emphasizing phenological aspects, found in the northern European Agabini in relation to their habitats.

From what is known about dytiscid life cycles it seems that the Agabini has a unique position in the relatively wide spectra of patterns represented here. The tribe Agabini (sensu DE MARZO & NILSSON, in press) includes in North Europe the genera *Agabus* Leach, *Ilybius* Erichson and *Platambus* Thomson. GALEWSKI (1971) placed *Ilybius* in its own tribe, Ilybini, and several other workers have placed it in the Colymbetini (e.g. BURMEISTER, 1976). Although there are good reasons for all these classifications I prefer, in this context, to include *Ilybius* in the Agabini since larval structure and habitats are strikingly similiar and there are also very interesting aspects of the life cycles uniting it with *Agabus*. Both genera are most diverse in boreal regions and possess adaptations to the pronounced seasonal variations of high latitudes.

In a seasonal environment, as in northern Europe, the study of life cycles first of all must be related to the major annual changes in climatic conditions and in habitat favorability. Thus, of crucial interest in the Agabini is the overwintering (DANKS, 1978, for a general review) and the eventual occurrence of periods when the habitat may dry out. Besides the timing of major seasonal events, life cycles are dependent on the rates at which development is possible in different habitats. Important parameters in this context are temperature and production of prey organisms.

It is essential to have a good knowledge of larval morphology in order to study life cycles. This is available for the Agabini mainly due to the works of GALEWSKI (1966, 1980) and NILSSON (1982a, 1982b). However, more detailed studies on the two first larval instars of *Agabus* are necessary.

The comparative study of life histories of the Dytiscidae is still in need of more research. A combination of field studies and experimental

work, as performed in carabids (THIELE, 1977), will provide a better understanding of dytiscid ecology and evolution. I will here try to summarize the current knowledge of life cycles of the Agabini of northern Europe with respect to habitats. Many species are widely distributed, and thus apt to show a clinal variation in important parameters such as voltinism (TAUBER & TAUBER, 1981). However, most data used are from northern Europe and the phenotypic expressions found here will be used to define the life cycles.

Habitat characteristics

The Agabini in northern Europe is found in a wide range of habitats (NILSSON, 1979), including estuarine, riverine, lacustrine and palustrine wetlands (COWARDIN et al., 1979). About 50 species are encountered in this region and species richness is rather uniform, without the pronounced south-north gradient found in most other insect taxa. In Sweden, the southernmost province Scania has 31 species, while the northernmost one, Torne Lappmark, has 33. From these figures it is evident that agabine species are frequent residents of temperate, boreal and arctic wetlands.

I will not here attempt to present a complete classification of dytiscid habitats. This has already been discussed at length by GALEWSKI (1971) and LARSON & COLBO (1983). Rather the focus will be on ecological factors of direct importance for the performance of different life cycles. SOUTHWOOD (1978) viewed habitat characteristics against the axis of time and space. It was found that the spatial components were most closely associated with migration and colonization. These aspects of the life cycle will not be discussed here. The time axis, or the heterogeneity in time, may be discussed in terms of durational stability, constancy, and predictability (SOUTHWOOD, 1978). The durational stability of most natural agabine habitats is high. This is also the case with the predictability, though certain exceptions occur, e.g. rock-pools. The major component of constancy is seasonality, i.e. the temporal variation in the carrying capacity strictly follows the season. Seasonality increases generally with higher latitudes and there are also striking differences between habitats with respect to the duration of the wet phase and to the temperature regime. Another factor that must be added is the productivity of the habitat, as it so directly influences the time required for growth and development. Two major components of productivity are nutritional conditions and input of energy.

Thus the habitats of the Agabini will be viewed against the axis of seasonality and productivity (Fig. 1). It is assumed here that differences observed in life cylces are adaptive to different kinds of habitats (SOUTHWOOD, 1977). A high seasonality of the habitat in this context means that the timing of the different phenophases must be very good. Growth is limited to a short wet phase and the periods of drought and freezing must be met with in a resistant stage or escaped from. However, timing is less important in a low seasonality habitat, in which growth and reproduction are possible at most seasons. Productivity acts mainly on the rate at which development is possible. In low productivity habitats longer life cycles should be favoured. Though not found in the studied region, higher temperatures of warmer regions could make it possible for several generations to come into being in a year, giving rise to at least bivoltine life cycles.

Low seasonality habitats, like springs, have a relatively low, steady productivity of prey organisms (LINDEGAARD & THORUP, 1975). In the high seasonality habitats, like in autumnal pools, a high productivity will have the form of seasonal pulses. This is most pronounced in spring when culicid larvae are abundant (LUMIAHO & ITÄMIES, 1981).

Seasonality

Low seasonality habitats are all characterized by a steady inflow of groundwater, e.g. springs and springfed streams. Water is present here in all seasons and the temperature is rather uniform. The agabine habitats of highest seasonality are temporary pools. The variation in length of the wet phase is important, and ephemeral, temporary, seasonal, and semipermanent, are terms that have been used to classify these habitats (STEWART & KANTRUD, 1971; NILSSON, 1984). There is thus a fairly even transition to permanent waters, and classification is also complicated because of interannual variation. WIGGINS et al. (1980) recognized temporary pools as either vernal or autumnal, with the wet phase lasting for 3–4 and 9 months respectively. In northern Sweden most temporary pools are autumnal, i.e. besides the accumulation of melted snow water in spring there is also a wet period in autumn due to heavy rainfall. In this region, because most temporary pools are shallow they freeze to the bottom in winter and the duration of the wet phase of autumnal pools is only about 4–5 months. The high degree of seasonality of temporary pools here includes two periods with water present, separated by a summer-dry and a winter-frozen phase. In the boreal region this is probably the most common pattern determining de-

velopment of temporary pools, at least in the more northern parts. Towards the south the milder winter conditions result in a thinner ice-cover and winter rains, and water exists during the whole winter.

In permanent surface-waters the degree of seasonality is considered intermediate. Water is present during all seasons though temperature shows considerable variation. In streams and rivers there is a concentration of agabine populations to the shallower littoral zone, and if water-levels are showing marked seasonal variations these will result in an increased seasonality of the habitat. Temporarily flooded lake and river margins are thus in this respect more similar to temporary pools.
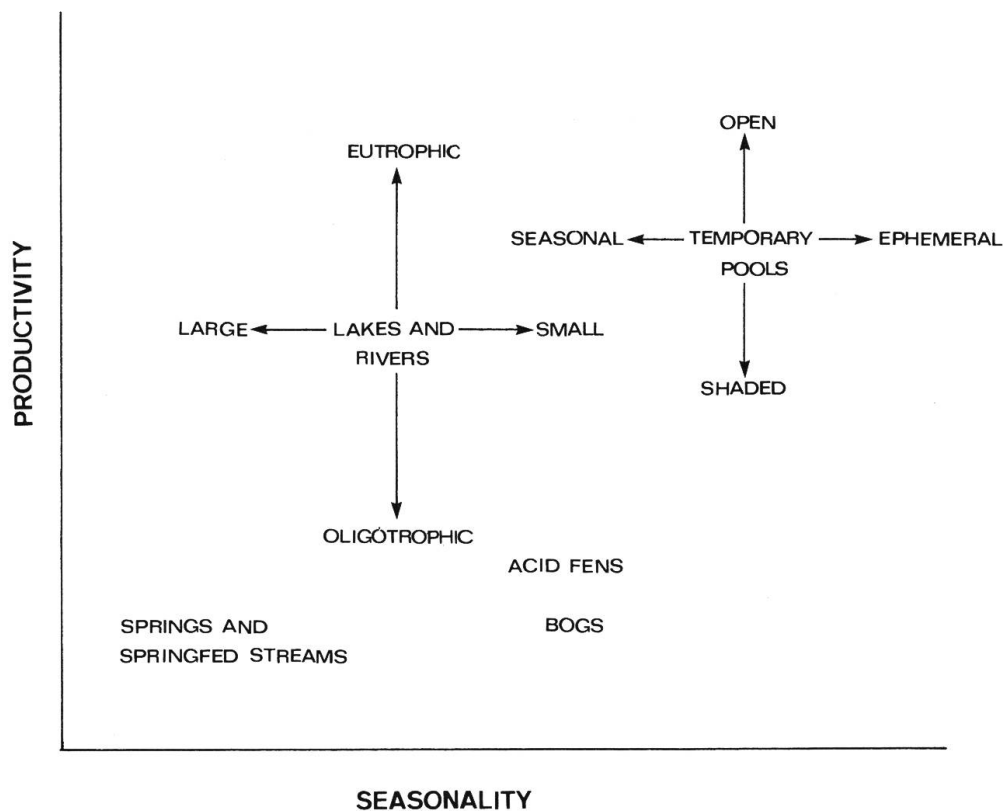

Fig. 1: Main habitats of the northern European Agabini arranged along the axes of relative seasonality and productivity.

Productivity

Productivity is influenced by so many factors that generalizations may be impossible to make. Factors that reduce productivity include low nutrient levels, low pH, highly coloured water and low temperatures.

The uniformly cool temperature found throughout the year in habitats with a high inflow of groundwater results in a low productivity. Other low temperature habitats are shaded forest pools, frequently found in spruce forests. Shading is also provided by the dense mats of vegetation found in bogs and fens.

Low levels of dissolved nutrients contribute to the low productivity of oligotrophic lakes and bog waters. This in the latter also is amplified by low pH and frequent occurrences of highly coloured water. These conditions are found in most habitats dominated by *Sphagnum*, of which acid fens and quag-mires are important agabine habitats. Temporary pools often maintain a high productivity due to an effective re-cycling of nutrients from the sediment and a faster decomposition of detritus during the dry phase (WIGGINS et al., 1980).

It is assumed here that a high general productivity is reflected in a high abundance of prey organisms preferred by the Agabini, especially the larvae. These are best characterized as polyphagous predators and prey selections is closely associated with size and vulnerability (PAJUNEN, 1983). Important prey items are larvae of Chironomidae and Culicidae, small oligochaet worms, larvae of Ephemeroptera, and, for some of the first-instar larvae, cladocerans.

In figure 1 some of the main habitats have been arranged graphically in the seasonality-productivity space.

Classification of life cycles

Classifications of dytiscid life cycles have been presented by various workers. WESENBERG-LUND (1912) recognized three different species groups: (1) both adult and larval stages overwinter, (2) adult stage overwinters with larval development in spring, (3) adults overwinter and larvae develop in summer. He correctly placed *Ilybius* in the first group and *Agabus* in the groups 1–2. Groups 2 and 3 of WESENBERG-LUND (l.c.) are hard to separate and *Agabus* should also be represented in his third group.

BLUNCK (1913) recognized three different kinds of life cycles in *Agabus:* (1) early spring breeders with adult overwintering, (2) summer breeders with larval overwintering, and (3) autumn breeders with larval overwintering. His group 1 thus is identical with group 2 of WESENBERG-LUND (1912), and his other groups are a further division of group 1 of WESENBERG-LUND (l.c.).

GALEWSKI's (1971) comprehensive treatize on the biology of European Dytiscidae provides much information on life cycles, and their association with different habitats. This work gives no direct classification of life cycles, though different species are termed early spring, late spring and summer, and autumn breeders respectively.

In spite of their aquatic habitats, dytiscid life cycles have more in common with the terrestrial Adephaga, than with other groups of aquatic non-coleopteran insects. Besides phylogenetic relationship, an important factor is probably that in the Dytiscidae and the Carabidae the adults share the same habitat as the larvae, while in most other limnic insects the adults leave the water (HUTCHINSON, 1981). The current knowledge of the types of life cycles and annual rhythms of the Carabidae was treated by THIELE (1977). He recognized five main types of life cycles found in carabids, and this classification is here developed to fit the Agabini. The basic life-cycle pattern of temperate Dytiscidae belongs to THIELE's first group, i.e. spring breeders which have summer larvae and hibernate as adults. In the Agabini this pattern has evolved in different directions, and the following types of life cycles have been recognized (Fig. 2):

1. Univoltine spring breeders which have summer larvae and overwinter as adults.
2. Univoltine species that breed from summer to autumn and overwinter as eggs.
3. Semivoltine spring breeders that pass the first winter in the egg stage and the second winter as adults.
4. Semivoltine summer breeders that pass the first winter as larvae and the second winter as adults.
5. Species with flexible reproductive periods overwintering as larvae and adults.

1. Univoltine spring breeders which have summer larvae and overwinter as adults

To this group belong about 14 species of *Agabus*, with the subgenera *Gaurodytes* Th., *Arctodytes* Th., *Eriglenus* Th. and *Agabus* (s. str.) being represented. The majority of the species belong to *Gaurodytes*, including species from five of the species-groups recognized by ZIMMERMANN (1934).

In northern Sweden I collected adults of *A. affinis* (Payk.) and *A. biguttulus* (Th.) in late April and early May. These adults immediately
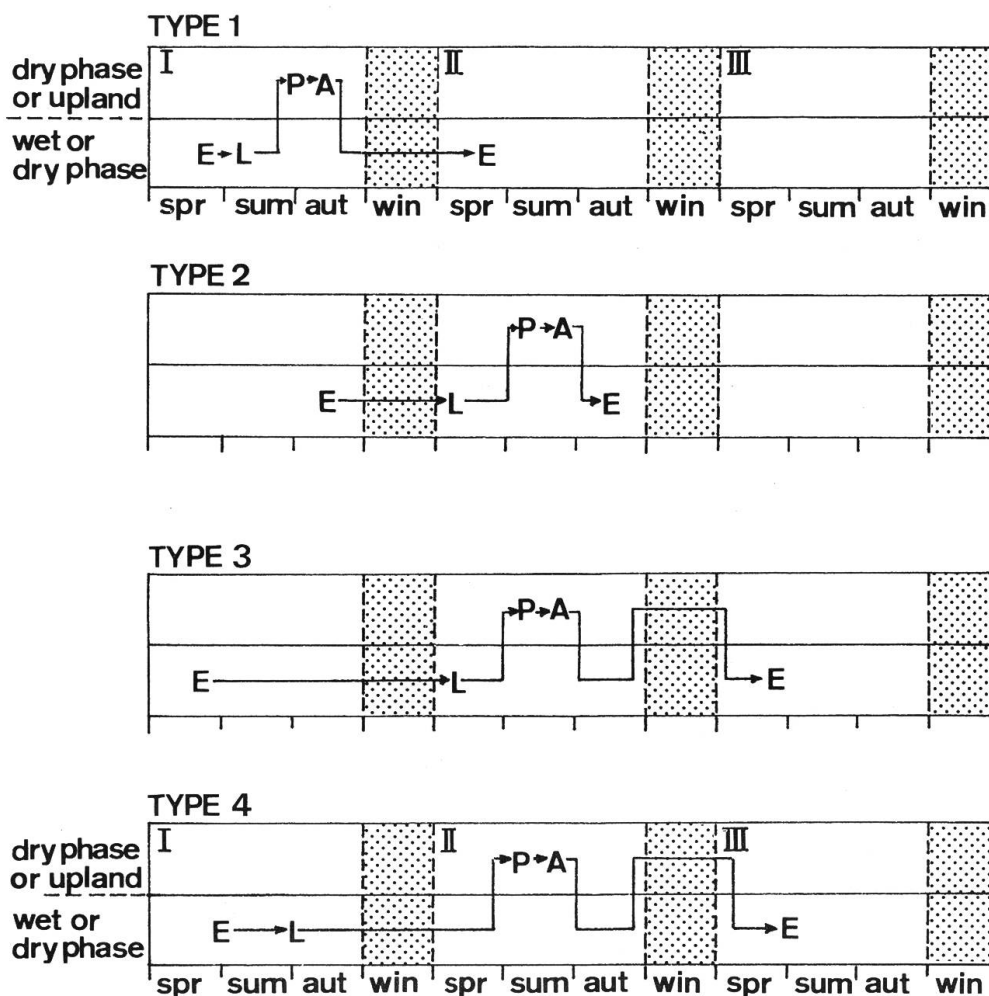
Fig 2: Life-cycle types recognized in the northern European Agabini. The fifth type has been omitted because of its flexible reproductive periods. The transformation of eggs (E) to larvae (L), pupae (P) and adults (A) is shown for each type (see text) in relation to season and year (I–III). Also indicated are the stages that temporarily leave the water.

produced eggs in captivity. The eggs hatched in mid May and the larvae reached their third instar in early June. I have only found larvae of the third instar in July, and teneral specimens from late July to August. In Poland, GALEWSKI (1974a) found fullgrown larvae of *A. affinis* in late August, and in France BERTRAND (1951) collected them in May. GALEWSKI (1980) collected in Poland third-instar larvae of *A. biguttulus* in early May and in mid July. Fullgrown larvae of *A. unguicularis* (Th.) in northern Sweden are found in late July, and teneral specimens are known to exist from late July to early August. In Poland, GALEWSKI (1972a) collected *A. unguicularis* females that laid eggs in the first half of April and in mid June. First-instar larvae appeared in late April, but in the field they

first were found in early May and late August. The second instar appeared throughout May and in mid August (GALEWSKI, 1972a), and the third one throughout May, in mid July, in late August, and in early September (GALEWSKI, 1963). GALEWSKI (1974a) noted a bimodality in egg-laying and appearance of larvae in *A. unguicularis,* and assumed that there are two generations of larvae, one in spring and one later in summer. However, in northern Sweden no signs of this have been observed, and this phenomenon probably results from a prolonged laying-period together with a longer reproductive season in Central Europe.

A. striolatus (Gyll.) is assigned to this group because larvae are found in spring and early summer and adults are active during the winter months (NILSSON & CUPPEN, 1983).

Two species of the *A. sturmii*-group (ZIMMERMANN, 1934) also belong to this group. In northern Sweden, adults of *A. arcticus* (Payk.) collected in mid May soon produced eggs that hatched after a few weeks (NILSSON, 1980). Larvae of all instars were found at many localities from mid June throughout July and August. PALM (1964) noted the occurrence of pupae and larvae ready to pupate in the first half of August. At more northernly sites (about 69°N), ERIKSSON (1972) collected third-instar larvae from late July to early September. He also noted a bimodal pattern in the occurrence of teneral adult specimens, and suggested that the emergence of adults took place in two different periods: one in late June/early July and the other in September. This probably means that the larvae that are not able to complete their growth in one season overwinter and pupate next spring.

In Scotland, JACKSON (1958) noted that oviposition in *A. sturmii* (Gyll.) was restricted to the spring and early summer. I have in Sweden found the third-instar larvae from early June to mid August, and in Poland GALEWSKI (1980) observed larvae from May to September. In Denmark SCHLICK (1894) found fullgrown larvae in late June which pupated in July. BALFOUR-BROWNE (1950) noted that he had taken teneral imagines in July, August and September.

Another species with this type of life cycle is *A. uliginosus* (L.). In Poland, GALEWSKI (1968) found second-instar larvae from early May to late July, and the third instar from late April to mid September. Larvae were most common in May and pupation and teneral adults were also observed in this month. The larvae found in late summer were probably connected with a prolonged period of oviposition in permanent ponds (GALEWSKI, 1968). In Hungary, GALEWSKI (1980) found larvae of *A. paludosus* (Fabr.) in May, and JACKSON (1958) concluded that oviposition

in this species chiefly occurred in spring and early summer. BALFOUR-BROWNE (1950) noted the presence of teneral adults in August and September.

Included in this group are also *Agabus nebulosus* (Forst.) and *A. conspersus* (Marsh.). These two southern species that ZIMMERMANN (1934) placed in his *nebulosus*-group both reach southern Scandinavia to the north. JACKSON (1958) observed egg-laying in *A. nebulosus* from late winter till spring. In Denmark, MEINERT (1901) noted the presence of larvae and pupae of this species in mid June and early July. BALFOUR-BROWNE (1950) collected teneral adults of both species during the whole summer (of *A. conspersus* also in October). It thus seems that over-wintering is only in the adult stage and that egg-laying might start very early, probably resulting in partly bivoltine life cycles.

The life cycle of *A. (Arctodytes) elongatus* (Gyll.) in northern Sweden has been described by NILSSON (1982c). Adults collected in late May produced eggs from which reared larvae were fullgrown in early July. Larvae were found from mid May to late June, and a single teneral specimen was found in early September.

In the subgenus *Eriglenus,* both *A. labiatus* (Brahm) and *A. undulatus* (Schrank) have this type of life cycle. In Scotland, JACKSON (1958) concluded that the oviposition period of *A. labiatus* is from November till April. In northern Sweden it is considerably later, mainly in May, and the two first larval instars have been found from late May to mid June. The third instar is common throughout June and July, though one larva was also found in late September. BALFOUR-BROWNE (1950) found a fullgrown larva in May, and GALEWSKI (1980) found them in Poland from April throughout May and June. Similar observations were made for *A. undulatus.* In North Germany, the oviposition was found to be in late March and April, with the larvae occurring from April to June (BLUNCK 1913). In Denmark SCHLICK (1894) found larvae in May and June, and one pupated in early July.

Specimens of *A. (Agabus) serricornis* (Payk.) held in captivity by Falkenström, deposited eggs from February to May (GALEWSKI, 1979). In northern Sweden the main oviposition period is in May, and the two first larval instars have been found from late May to early July. The third instar has been found from mid June to early August, and teneral adults from late July to late August. In Finnish Lapland newly hatched imagines have been observed from mid July to late September (ERIKSSON, 1972).

2. Univoltine species that breed from summer to autumn and overwinter as eggs

This type of life cycle is known for *A. (Gaurodytes) fuscipennis* (Payk). Adults of this species have been found in summer and autumn, and they die as winter approaches (HUGGERT & NILSSON, 1978). The two first larval instars in northern Sweden were found from early May to early June, and the third one from late May to mid June. Teneral adults were collected in July. In Poland, these larvae were found slightly earlier in the year, and some pupated in May (GALEWSKI, 1972b). This species in North America is represented by the subspecies *A. f. ontarionis* Fall (LARSON & NILSSON, 1985), and WATTS (1970) collected one fullgrown larva which pupated in early June. It seems that *A. fuscipennis,* together with *A. ajax* Fall, *A. coxalis* Sharp and *A. infuscatus* Aubé, form a natural group of species characterized by this kind of life cycle. There are reports of an absence of adults of *A. ajax* (LARSON, 1975) and *A. infuscatus* (LARSON & COLBO, 1983) in spring and early summer.

3. Semivoltine spring breeders that pass the first winter in the egg stage and the second winter as adults

To this group belong about 13 species of *Agabus (Gaurodytes),* representing four of the species-groups recognized by ZIMMERMANN (1934).

Most of the species of the *A. adpressus-* and the *A. chalconatus-*groups are placed here. Nothing is known about the immature stages of *A. adpressus* Aubé, and *Ilybius vittiger* (Gyll.) was transformed to another genus (NILSSON, 1983b).

This type of life cycle was first described by JAMES (1970) in *A. erichsoni* Gemm. & Harold. It was known that the closely related *A. chalconatus* (Panz.) and *A. melanocornis* Zimm. were able to produce dormant eggs (BALFOUR-BROWNE, 1950, JACKSON, 1958). The eggs of *A. erichsoni* in southern Ontario were deposited in May and June (JAMES, 1970) and hatched in the following March or early April. The two first larval instars were collected in April, and the third one in late April and May. Pupation was in mid June, with the appearance of teneral adults slightly later. In northern Sweden the eggs hatch a bit later in spring, when snow melts, and first-instar larvae have been collected from late April to late May. The third instar appears from late May to mid July. Data from Poland (GALEWSKI, 1973) show good coincidence with southern Ontario, though third-instar larvae were already found in late March. In a habitat where larvae of this species are very abundant in spring, I was able to collect single first-instar larvae also in late Septem-

ber and early October. It thus seems that hatching can start already in autumn, and that the larvae then can develop during winter in a warmer climate. A similar observation was made by GALEWSKI (1973) regarding *A. subtilis* Er., when he found single larvae also in the autumn. The chief period of larval development in this species is identical to that of *A. erichsoni*. In southern Sweden young larvae of *A. subtilis* have been found already in November and December (leg. B. W. Svensson).

This type of life cycle also was described in *A. opacus* Aubé and *A. wasastjernae* (Sahlb.) (NILSSON, 1985b). In northern Sweden, the first-instar larvae of these species appear mainly in late April and early May and reach maturity in June. As discussed above, occasional larvae might already hatch in the autumn. The occurrence of single teneral adults in early spring, could be caused by aestivating larvae that fullfilled their growth in autumn. It seems likely that also *A. neglectus* Er. has this type of life cycle. GALEWSKI (1974b) collected fullgrown larvae of this species in late March and early May.

Information on the life cycles of *A. chalconatus* and *A. melanocornis* is contradictory. Even though some authors have not separated these species they probably have similar life cycles and are in this context best dealt with together. Egg-laying starts very early, and adults collected in November were found by WESENBERG-LUND (1912) to lay eggs when placed in an aquarium. Similar observations were made by BALFOUR-BROWNE (1950) who found eggs deposited in an aquarium in the autumn, but the larvae did not appear until the spring. However, JACKSON (1958) collected females in October, that laid their eggs from January to April. Dissected specimens had mature ovaries already in August and October, and she concluded that they laid principally from autumn till spring. She also noted that most of the eggs deposited in January had not hatched by the middle of August. In Italy, DE MARZO (1973) observed the oviposition of a female collected in February. Larvae have been observed from late summer till winter. GALEWSKI (1980) described the third instar taken in October in England and Germany. However, in Scotland larvae of all instars have been observed in late August by JACKSON (1958); although her note on the denticulate mandibles makes this record dubious. In Italy, DE MARZO (1973) collected larvae in January and February. Single first and second-instar larvae were observed in southern Sweden (leg. B. W. Svensson) in November and December.

Summarizing, there seems to be considerable variation in the life cycles in at least some species in this group. Oviposition might start al-

ready in the autumn and the eggs show a great variation in length of the dormant period. This variation should be studied quantitatively.

Much of the variation is due to climatic differences. In the boreal region the overwhelming majority of the eggs hatch immediately after the thawing of the surrounding ice.

In this group I have placed also some species belonging to the A. confinis- and A. congener-groups. Most probably also A. zetterstedti belongs here. The first instar larvae of these species have been collected very early in the spring, at the same time as those of the other species with overwintering eggs. Adults are present from early spring to autumn, and spend the winter on land. Females of A. congener (Thunb.) collected in early May were found to start their egg-laying immediately in captivity, and these eggs did not hatch during the whole summer when kept at about +5°C. Egg-laying in this species was observed also in August and September by Balfour-Browne (1950) in England and by Galewski (1968) in Poland. Observations indicate that most of the overwintered females have died off in mid July, and the new generation appears in late summer and early autumn and soon leaves the water. Under natural conditions the egg-laying occurs in spring, at least in the boreal region. The two first larval instars have in northern Sweden been collected from late April to early June, and the third one from mid May to late July, most frequently in June. In Finnish Lapland, Eriksson (1972) collected the second instars of A. lapponicus (Thoms.) and A. thomsoni (J. Sahlb.) from late June to mid July, and the third ones from late June to early August. Teneral imagines were collected from late July to late September.

The larval development of A. levanderi Hellén (=approximatus, Nilsson 1983a, nec Fall 1922) strictly followed in time that of A. congener at a studied locality in northern Sweden (Nilsson, 1983a).

The two first larval instars of A. confinis (Gyll.) in northern Sweden were collected throughout May, and the third instar from late May to mid July (Nilsson, 1980). Teneral imagines were found in August, as also noted by Eriksson (1972) in Finnish Lapland. Larson (1975) collected them in Canada from early July to early August.

Not very much is known about the life cycle of A. zetterstedti. In northern Sweden I collected larvae of all instars in mid June, the third one also in mid July (Nilsson, 1985a). Probably this species belongs to this group.

4. Semivoltine summer breeders that pass the first winter as larvae and the second winter as adults

To this group belong exclusively the *Ilybius* species. A detailed account on life cycles is found in GALEWSKI's (1966) comprehensive study of the immature stages of this genus. *Ilybius angustior* (Gyll.) and *I. vittiger* (Gyll.) were later treated by NILSSON (1981, 1983b). The former species has recently been shown to include also *I. picipes* (Kirby) (PERSSON, 1985), and the larvae assigned to *I. angustior* (NILSSON, 1981) in fact represent both species.

Oviposition takes place during the summer, chiefly in July (JACKSON, 1960), and the first-instar larvae were collected by GALEWSKI (1966) from July to late October. In northern Sweden they mainly occur in August, as do the second instar that in Poland were collected from September to November (GALEWSKI, 1966). It thus seems that the larval development starts somewhat earlier up in the north. The third instar was found in Poland from early September to mid April (GALEWSKI, 1966). In northern Sweden the fullgrown larvae do not leave the water for pupation until late May. Teneral imagines in northern Sweden occur in July and August, though GALEWSKI (1966) in Poland observed them already in April. Both JACKSON (1960) and GALEWSKI (1966) assumed that oviposition did not take place until the following year. This must be the case in northern Sweden, although the early emergence of adults in more southern regions leaves the possibility of oviposition in the same year open.

5. Species with flexible reproductive periods overwintering as larvae and adults

This group include the species in which larvae and adults are found all year round. This is the case for *Platambus maculatus* (L.) and for some *Agabus* species of the subgenus *Gaurodytes* that belong to the *A. guttatus* and *A. bipustulatus*-groups (ZIMMERMANN, 1934).

The most detailed description of the life cycle of *Platambus maculatus* was presented by LAVANDIER & DUMAS (1971) from the Pyrenees. Their study indicates that oviposition takes place from August to October as the first-instar larvae were collected from late August to early January, and were most frequent in November. The third instar was collected chiefly from early October to mid March, with single representatives found also in May and June. They concluded that the life cycle was univoltine. From these results only, the life cycle of *P. maculatus* would belong to another type: univoltine autumn breeders

overwintering as larvae. In Poland, GALEWSKI (1971) noted that the larvae of *P. maculatus* were not to be found before October or November and that pupation took place next spring. This picture changes when entering more northern regions. In Finnish Lapland, ERIKSSON (1972) observed third-instar larvae in early June and early July, and teneral adults in mid September. Both larvae and adults were present in all monthly samples (June–September) taken in a subalpine lake in Norway (BRITTAIN, 1978). Adults were most numerous in the September samples, and the highest number of larvae were taken in June. In northern Sweden young larvae were collected in July and October, and fullgrown ones in August and September.

Though the main part of the population may have a similar pattern as the *P. maculatus* found in the Pyrenees (LAVANDIER & DUMAS, 1971), some of the adults apparently do not oviposite until the following year; this would result in overlapping generations.

Little is known about the life cycle of *Agabus guttatus* (Payk.). In Denmark, WESENBERG-LUND (1912) observed that females collected in November immediately oviposited when placed in an aquarium. Also BALFOUR-BROWNE (1950) assumed that oviposition was mainly in the autumn as he had only found teneral imagines in May and June. In Poland, GALEWSKI (1980) collected the larvae from June to September, and noted that some of them overwintered. In northern Sweden I collected third-instar larvae in all seasons, and teneral imagines only were observed in August.

The larva of *A. melanarius* Aubé was together with teneral imagines collected in August by BEIER (1927). Also in Germany, DETTNER (1976) found third-instar larvae in all monthly samples from April to October, except in May, and the number of adults were highest in May and August. Both BALFOUR-BROWNE (1950) and BANGSHOLT (1981) noted the presence of teneral imagines in late summer. In northern Sweden I have taken first-instar larvae in June and August, second-instar in August and September and third-instar from June to October. A single teneral adult was found in May.

The period of oviposition in *A. bipustulatus* (L.) is very long. In Scotland, JACKSON (1958) concluded from studies of ovarian development that egg-laying was principally in autumn, winter and spring. Similar findings had earlier been reported by BLUNCK (1921) and by BERTRAND (1928). In northern Sweden, I have collected the first-instar larvae from May to September. In a one-year series of monthly samples in the Netherlands Cuppen (in litt.) recorded the first instar from September

to April. BALFOUR-BROWNE (1950) noted the presence of "larvae of all ages in many months throughout the year", and of teneral imagines from May to September. JACKSON (1958) also found that in captivity eggs laid in late autumn produced imagines in the spring, and she assumed that these beetles would be ready for oviposition by the following autumn.

The taxonomic rank of *A. solieri* Aubé is controversial (BALFOUR-BROWNE 1950), and herein it is regarded as a montane subspecies of *A. bipustulatus*. In Finnish Lapland, ERIKSSON (1972) found a single first-instar larva in early August. The second instar was collected from late June to early August, during which time also the third instar was frequently encountered. Both fullgrown larvae and adults were found onwintering under ice in the spring. Soft, recently emerged imagines were found from early June to late September. These observations indicate no principal differences with regard to life cycles between *A. b. bipustulatus* and *A. b. solieri*.

Type of life cycle and habitat

The species here assigned to the first type of life cycle constitute a rather heterogeneous group with regard to habitat. Most of them, however, have an affinity to permanent waters with seasonal changes in temperature. Larval development cannot start until late spring and in northern Sweden not before late May, and it is not possible to complete the life cycle in many of the more temporary waters. *Agabus affinis* and *A. unguicularis* are associated with quagmires and acid fens with dense growth of *Sphagnum*; *A. unguicularis* occurs in more nutrient-rich sites. Adults of *A. biguttulus* only were found at the flooded margins of streams and rivers, and probably this is the main reproductive habitat of this species. In northern Sweden, these habitats are under water markedly later than the temporary waters arising from melted snow water. Both *A. arcticus* and *A. sturmii* are inhabitants of permanent waters, such as lakes, rivers and ponds. While *A. paludosus* is found in gently flowing streams, *A. uliginosus* inhabits temporary, grassy pools (GALEWSKI, 1980). The habitat of *A. elongatus* is small, shaded forest pools that have cool water and in most cases retain their water throughout summer. Both *A. labiatus* and *A. undulatus* are inhabitants of small, stagnant waters, that often are of a temporary character (GALEWSKI, 1980). The former, in northern Sweden, has a pronounced preference for more nutrient-rich seasonal ponds. This is also the case with *A.*

serricornis, a species also frequently found in eutrophic lakes. This type of life cycle is thus most often observed in permanent summer-warm waters of varying productivity. The species inhabiting temporary waters have a preference for the ones with higher productivity. At least in *A. labiatus* the main food is chironomid larvae, that are most abundant in early summer. The overwintering is chiefly in water (e.g. *A. arcticus, A. labiatus, A. serricornis)*. In habitats that freeze to the bottom, overwintering in ice is observed in *A. labiatus.*

The second type of life cycle, the univoltine egg-overwintering species breeding from summer to autumn, has so far only been confirmed in *A. fuscipennis.* This species passes the larval development in temporary habitats of a relatively high productivity, such as open seasonal pools and flooded lake- and river-margins. Adults are especially abundant in the vegetation-rich zone of eutrophic lakes. Larval development is very early in spring, and is associated with accumulation of melted snow water that causes flooding of lake margins. In late summer, water is required for oviposition, and the species is in this way excluded from vernal ponds. In populations of lake- and river-margins, eggs apparently must be deposited in the lake or river and in the following spring the young larvae migrate to the flooded margins.

The main difference found in the third type of life cycle is that the adults overwinter and do not reproduce until the following spring. This would allow for an exploration also of less productive habitats as it gives a longer time for adult feeding and ovarian development. It is not known whether, in some cases, adults oviposite in the same year as they emerged. This should be analyzed with a quantitative approach. The species assigned to this group are mainly inhabitants of temporary waters of varying, often lower, productivity. This kind of life cycle permits the exploration also of vernal pools as no wet phase is required for oviposition in the autumn. Production of prey organisms, mainly culicid larvae, is in these habitats concentrated to the spring, in northern Sweden mainly in May and early June. *Agabus erichsoni* is a common inhabitant of most grassy fens, often found together with *A. subtilis,* though this species is more restricted to higher productivity sites. *Agabus opacus* and *A. wasastjernae* are both inhabitants of smaller temporary waters in forest and along mire-margins. These habitats have quite cold water even in early summer, and thus have a relatively lower degree of productivity. *Agabus confinis* and especially *A. levanderi* have a certain preference for the flooded margins of small streams, though the former also inhabits other temporary waters. Both *A. congener* and

A. zetterstedti are inhabitants of temporary pools, though the former is strikingly eurytopic and can be found in most small stagnant waters and even in springs. *Agabus lapponicus* and *A. thomsoni* are both inhabitants of temporary pools in arctic and subarctic regions (ERIKSSON 1972). It seems that the species in this group overwinter out of water (GALEWSKI, 1964; ERIKSSON, 1972).

The fourth type of life cycle, found in all species of *Ilybius*, differs mainly in that the eggs hatch earlier resulting in the overwintering of larvae. This is probably of pronounced importance for what kinds of habitats that can be successfully exploited. It is not known if agabine larvae can still survive after freezing in ice. Overwintering in *Ilybius* is only in the third-instar larvae, and as this one has the hardest cuticle it should be the best one fitted for survival in ice. I have at some occasions in late autumn and early winter found *Ilybius* larvae (*I. aenescens* and *I. crassus*), under an icecover in habitats that in winter freeze to the bottom. When at such a locality the ice was removed in mid winter, the larvae were found to be alive and moved slowly when disturbed. These larvae were all found in patches of moist moss upon the unfrozen sediment.

The *Ilybius* species are found in a wide spectrum of habitats. It should here be borne in mind that the adults are highly mobile and thus frequently found outside the reproductive habitat. The eurytopic species, like *I. aenescens* Th., inhabit all sorts of temporary ponds, acid fens and ponds. Other species, like *I. fenestratus* (Fabr.), *I. quadriguttatus* (Lac.) and *I. similis* Th., have mainly been found in lakes and in the surrounding quagmires. Some species, chiefly *I. crassus* Th. and *I. fuliginosus* (Fabr.), can also be found in springs and small streams. As a whole, the genus is better represented in habitats of lower seasonality, and in most cases the habitats do not freeze to the bottom in winter, or if so the bottom sediment remains partially unfrozen and is covered with at least patches of moss. The period of larval development is thus long: this has made it possible for them to exploit habitats of lower productivity and without the pronounced seasonal pulses. Adult overwintering is out of water (GALEWSKI, 1966).

The fifth type of life cycle: the species with flexible reproductive periods overwintering as larvae and adults, includes only species found in habitats of low seasonality. *Platambus maculatus* is an inhabitant of oligotrophic lakes and running waters. Both *A. guttatus* and *A. melanarius* are chiefly found in springs. The former is also often found in small, often springfed streams. *Agabus bipustulatus* has a very wide dis-

tribution in Europe, and is in Central Europe one of the most eurytopic species (BALFOUR-BROWNE, 1950; GALEWSKI, 1980). In more northernly regions it has a more restricted habitat-spectrum. In northern Sweden I have frequently collected it in springs, and also in some semi-permanent and seasonal ponds. The subspecies *A. b. solieri* is typically found in alpine lakes, ponds and rock-pools (ERIKSSON, 1972). The extended period of larval development found in these species makes them well adapted to the exploitation of habitats of low productivity and low seasonality. Overwintering of adults is in the water.

A review of life-cycle types and habitats in the northern European species of Agabini is given in table 1.

Discussion

The different types of life cycles found in the Agabini are phylogenetically very important, and will aid elucidation of the evolutionary history of this group. In this context it should be noted that similar phenotypic expressions do not imply the same underlying physiological mechanisms because convergence is widespread (TAUBER & TAUBER, 1981). Phylogenetic relationships within the Agabini are at present not satisfactorily understood. It is not even clear what genera should be included in this tribe. The basic dytiscid life-cycle pattern in the Agabini is found in four different subgenera of *Agabus*. All the other types are restricted to more homogeneous groups. Two of the life-cycle types are restricted to different species-groups of *Agabus (Gaurodytes)*. In this subgenus four of the five types of life cycles are represented, and this fact most probably constitutes an important part of the answer to the question – why are there so many species of *Agabus*?

Though a phylogenetic reconstruction of the Agabini is out of scope of this paper I will make some comments on the position of *Ilybius*. In this genus all species studied have the same characteristic type of life cycle. Morphologically *Ilybius* is most similar to the *chalconatus*-group of *Agabus (Gaurodytes)*. Indeed, one of the species in this group was recently transferred to *Ilybius* (LARSON & ROUGHLEY, 1983, NILSSON 1983b). Besides the morphological similarity the life cycles of these two taxa show some very derived patterns, and it seems possible that the *Ilybius* type of life cycle has evolved from the one present in this group of *Agabus cies. In this case Ilybius* is the sister-group of this *Agabus* group, a possibility that stresses the need of a revision of the genera in the Agabini.
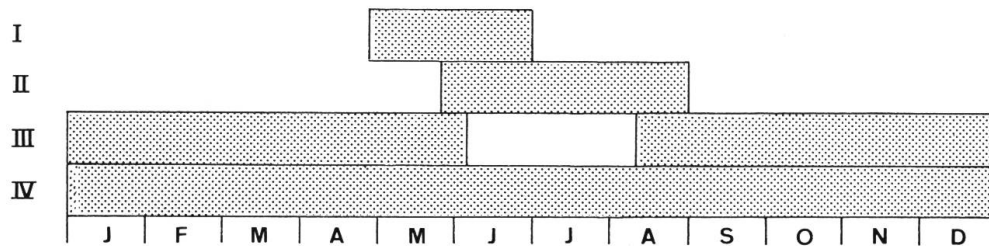
Fig 3: Annual period of larval development in the northern European Agabini: (I) life-cycle types 2–3, (II) life-cycle type 1, (III) life-cycle type 4, and (IV) life-cycle type 5.

The observed differences in life cycles are also important for the structure of agabine communities. Each type of life cycle is adapted to, and most successful in a certain kind of habitat. Within a given habitat differences in life cycles will reduce competition and make possible the co-existence of a higher number of species, if there is a shortage of resources. In this sense the most important difference is that found between egg, larval and adult overwinterers, as this mainly decides the time of larval development (Fig. 3). This period is probably the most important one with regard to utilization of the food resources (SPENCE, 1979). The flexible species (type 5) have the potential of a continuous larval development, limited only by the fact that pupation is restricted to the snow-free season. The *Ilybius* species (type 4) have their period of larval development separated to one in late summer/autumn (instar I–III and another in spring (instar III only). Most probably the larvae pass the winter in an inactive state, due to eventual freezing and low levels of oxygen. The species with adult overwintering only (type 1) pass their larval development during summer, and all species with the overwintering of eggs (type 2–3) have their larval feeding in spring and early summer.

In most cases agabine communities include species from more than one of these four main groups (Fig. 3), though in this situation one or two of the groups dominate. Most probably the four main groups correspond not only to a temporal partitioning of larval development but also to a utilization of different prey groups. The egg-overwintering species hunt mainly culicid larvae, and the species overwintering as adults have chironomid larvae as their most important prey. The overwintering larvae of *Ilybius* have the possibility of feeding on both these prey groups.

Most European species of Agabini have wide distributions, often extending from the temperate to the northern boreal or arctic zone. In some species the life cycles are altered with changing conditions, as noted above in e.g. *Platambus maculatus*. Other species, like *Agabus*

Tab. 1: A review of the life-cycle types, main habitats and gross distributions of the northern European species of Agabini. Also given are selected references for each species, mainly with regard to life cycles. The life-cycle types are numbered as in the text. Data in paranthesis are inadequately known.

Species	life-cycle type	main habitat	distribution	selected references
Platambus maculatus (L.)	5	lakes and rivers	palaearctic	Lavandier & Dumas 1971 Brittain 1978
Agabus (Arctodytes) elongatus (Gyll.)	1	shaded forest pools	northern holarctic	Nilsson 1982c Larson & Nilsson 1985
Agabus (Gaurodytes) subtilis Er.	3	open temporary pools	eurosiberian	Galewski 1973
A. (G.) erichsoni Gemm. & Harold (*nigroaeneus* Er.)	3	temporary pools	holarctic	James 1970 Galewski 1973
A. (G.) chalconatus (Panz.)	3	temporary pools	european	Galewski 1980
A. (G.) melanocornis Zimm.	3	temporary pools	european	Jackson 1958 DeMarzo 1973
A. (G.) neglectus Er.	(3)	temporary (forest) pools	eurosiberian	Galewski 1974b
A. (G.) guttatus (Payk.)	5	springs and streams	eurosiberian	Balfour-Browne 1950 Galewski 1980
A. (G.) melanarius Aubé	5	springs	european	Beier 1927 Dettner 1976
A. (G.) b. bipustulatus (L.) & *b. solieri* Aubé	5	springs, temporary pools, alpine lakes	palaearctic	Blunck 1921 Jackson 1968 Eriksson 1972
A. (G.) striolatus (Gyll.)	(1)	temporary marshes	european	Nilsson & Cuppen 1983
A. (G.) sturmii (Gyll.)	1	lakes and ponds	eurosiberian	Jackson 1958
A. (G.) arcticus (Payk.)	1	lakes and rivers	northern holarctic	Eriksson 1972 Nilsson 1980
A. (G.) zetterstedti Thoms.	(3)	temporary pools	northern holarctic	Nilsson 1985b Larson & Nilsson 1985

Species	life-cycle type	main habitat	distribution	selected references
A. (G.) adpressus Aubé	?	lakes and running waters	northern holarctic	Larson & Nilsson 1985
A. (G.) wasastjernae (Sahlb.)	3	shaded forest pools	northern holarctic	Nilsson 1982c Nilsson 1985a
A. (G.) opacus Aubé	3	shaded forest pools	northern holarctic	Nilson 1985a
A. (G.) infuscatus Aubé	(2)	temporary tundra pools	northern holarctic	Larson & Nilsson 1985
A. (G.) confinis (Gyll.)	3	temporary open pools	northern holarctic	Nilsson 1980
A. (G.) fuscipennis (Payk.)	2	flooded lake and river margins	holarctic	Galewski 1972 b
A. (G.) uliginosus (L.)	1	temporary pools	european	Galewski 1968
A. (G.) paludosus (Fabr.)	1	streams	eurosiberian	Jackson 1958 Galewski 1980
A. (G.) nebulosus (Forst.)	1	temporary pools	southern european	Meinert 1901 Jackson 1958
A. (G.) conspersus (Marsh.)	(1)	temporary pools	southern palaearctic	Balfour-Browne 1950 Galewski 1980
A. (G.) affinis (Payk.)	1	acid fens	eurosiberian	Galewski 1974 a
A. (G.) biguttulus (Thoms.)	1	flooded lake and river margins	eurosiberian	Galewski 1974 a
A. (G.) unguicularis (Thoms.)	1	richer acid fens	eurosiberian	Galewski 1974 a
A. (G.) setulosus (J. Sahlb.)	?	streams	northern european	
A. (G.) congener (Thunb.)	3	temporary pools, acid fens	eurosiberian	Galewski 1968 Nilsson 1983a
A. (G.) lapponicus (Thoms.)	3	tundra pools	northern eurosiberian	Eriksson 1972
A. (G.) thomsoni (J. Sahlb.)	3	tundra pools	northern holarctic	Eriksson 1972 Larson & Nilsson 1985
A. (G.) moestus (Curtis)	?	tundra pools	northern holarctic	Larson & Nilsson 1985
A. (G.) pseudoclypealis Scholz (haraldi Håk. Lindb.)	?	streams	northern palaearctic	

Species	life-cycle type	main habitat	distribution	selected references
A. (G.) levanderi Hellén (approximatus auct, nec Fall)	3	streams	northern palearctic	Nilsson 1983a Larson & Nilsson 1985
A. (G.) clypealis (Thomson)	?	flooded stream margins	(eurosiberian)	Holmen 1980
A. (Agabus) serricornis (Payk.)	1	lakes and ponds	northern palaearctic	Eriksson 1972 Galewski 1979
A. (Eriglenus) undulatus (Schr.)	1	temporary shaded pools	european	Blunck 1913 Galewski 1980
A. (E.) labiatus (Brahm)	1	temporary pools	eurosiberian	Jackson 1958 Galewski 1980
Ilybius vittiger (Gyll.)	4	tundra and shaded forest pools	northern holarctic	Nilsson 1983b Larson & Roughley 1983
I. fenestratus (Fabr.)	4	lakes	eurosiberian	Galewski 1966
I. ater (DeGeer)	4	fens and ponds	eurosiberian	Jackson 1960 Galewski 1966
I. fuliginosus (Fabr.)	4	springs, lakes and ponds	palaearctic	Jackson 1960 Galewski 1966
I. similis Thoms.	4	small lakes	european	Galewski 1966
I. subaeneus Er.	4	grassy fens	holarctic	Galewski 1966 Larson 1975
I. quadriguttatus (Lac.)	4	fens and small lakes	european	Galewski 1966
I. crassus Thoms.	4	acid fens and springs	eurosiberian	Galewski 1966
I. angustior (Gyll.)	4	acid fens, temporary pools	holarctic	Eriksson 1972 Nilsson1981
I. picipes (Kirby)	4	acid fens, temporary pools	northern holarctic	Nilsson 1981 (as angustior) Persson 1985
I. guttiger (Gyll.)	4	fens and small lakes	european	Galewski 1966
I. aenescens Thoms.	4	acid fens etc.	eurosiberian	Galewski 1966

melanarius minimize environmental changes and choose only stable habitats like springs. Often the habitat preference varies in different regions; e.g. *Agabus bipustulatus* which is more stenotopic to the north.

Life-cycle patterns are also important in setting the distributional limits of some species. This is probably so in more southern species belonging to the first group with a preference for temporary habitats, including *Agabus striolatus, A. uliginosus* and *A. undulatus*. On the contrary, most markedly northern species of temporary habitats, like *A. confinis* and *A. opacus*, have semivoltine life cycles with egg-overwintering.

From what has been said above it is obvious that the here documented diversity of life-cycle patterns found in the Agabini will contribute to our understanding of the distribution, ecology and phylogeny of this inspiring group of aquatic Coleoptera.

Acknowledgements

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