

Ecology of alpine carabid beetles (Coleoptera, Carabidae) in a Norwegian glacier foreland, with a special focus on claw wearing to indicate relative age

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Nine species of carabid beetles (Coleoptera, Carabidae) were pitfall-trapped during two years in an alpine glacier foreland of southern Norway. A two-year (biennial) life cycle was documented for *Nebria nivalis* (Paykull, 1790), *N. rufescens* (Ström, 1768), and *Patrobus septentrionis* Dejean, 1828. This was based on the simultaneous hibernation of larvae and adults. In *P. septentrionis*, both larvae and adults showed a considerable activity beneath snow. A limited larval material of *Amara alpina* (Paykull, 1790) and *A. quenseli* (Schönherr, 1806) from the snow-free period indicated larval hibernation. *A. quenseli* was, however, not synchronized with respect to developmental stages, and its life cycle was difficult to interpret. Measurements of claw lengths in eight species showed a considerable wearing during adult life. The data indicated that some individuals might hibernate a second time and thus experience two egg-laying seasons. Wearing of mandible tooth was not suited as age indicator in *Nebria nivalis* and *N. rufescens*, since some individuals hatched with a small tooth. Supplied with literature data, a “niche profile” is presented for each species. The most important ecological factors that contributed to niche segregation were: preference for vegetation-free ground, occurrence along the successional and time gradient, humidity or temperature preference, nocturnal versus diurnal activity, flight ability, food habits, phenology, and the ability to be active under snow.

Key words: Carabidae, carabid beetles, ecology, alpine, glacier foreland, niche, claw wearing.

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Introduction

Glaciers are melting worldwide due to climate change (Oerlemans 2005, Jomelli *et al.* 2011, Malcomb & Wiles 2013), and large foreland areas are made available for plant and animal colonisation. Such glacier forelands act as valuable natural laboratories for the study of primary succession, where distance from the glacier can be

used as a substitute for time. Beetles of the family Carabidae are characteristic inhabitants of glacier forelands, and their succession pattern has been described both in the Alps (e.g. Kaufmann 2001, Kaufmann & Raffl 2002, Kaufmann *et al.* 2002, Kaufmann & Juen 2002, Gobbi *et al.* 2006a,b, Gobbi *et al.* 2007) and in Norway (Vater 2006, 2012, Bråten & Flø 2009, Alfredsen 2010, Bråten *et al.* 2012, Vater & Matthews 2013, 2015).

The relatively simple ecosystems near glaciers invite for closer ecological studies of each carabid species. In a glacier foreland of the Austrian Alps, Kaufmann & Juen (2002) studied habitat use and niche segregation of five cold-adapted carabid species of the genus *Nebria* Latreille 1802. The species were more or less separated by factors like moisture, age and structure of the ground, degree of vegetation cover, or affinity to riparian outwash areas. All species had a biennial life-cycle, but differences were found in the timing of reproduction and the larval stages which overwinter.

Some alpine insects, like the herbivore chrysomelid beetle *Chrysomela collaris* Linnaeus, 1758, is able to fulfil its life cycle during the short snow-free summer, due to high assimilation efficiency and rapid growth of larvae (Hågvar 1975a,b). The adult beetles overwinter. For species which need more than one season to fulfil their development, the ability to hibernate in the larval stage is crucial. For instance, certain alpine species of Tipulidae (Diptera) have a biennial life-cycle. Their soil-living larvae need two years to reach maturity, and two age groups of larvae hibernate together (Hofsvang 1972). Adult Tipulidae have a very short life, just long enough for mating and egg-laying. In carabid beetles, adults have a longer life, and adults of alpine species may need to hibernate once before the ovaries are fully developed. The result is that young adults overwinter together with half-grown larvae. Therefore, carabids with both larval and adult overwintering diapause are advantaged in colonizing alpine zones compared with species without larval overwintering, which have to complete development during a short snow-free season (Refseth 1984, Sota 1996). Certain carabid species with larval overwintering are able to change from a one-year life cycle in the lowlands to a two-year life cycle in alpine habitats, but this is not possible for species which are only able to overwinter as adults (Sota 1996).

In an alpine glacier foreland close to a melting glacier in southern Norway, extensive studies of invertebrate succession have been performed (summary by Hågvar *et al.* 2017). The material included nine carabid species (Bråten & Flø 2009,

Bråten *et al.* 2012, Hågvar 2012, Hågvar & Ohlson 2013, Hågvar *et al.* 2017). Among these were two cold-loving *Nebria* species, of which *N. rufescens* (Ström, 1768) is common to the Alps. The large material from this project allows for a closer look at the ecology of seven carabid species (Figure 1). The present data include habitat use, moisture preferences, seasonal variations in surface activity, the identification of egg-laying period and hatching time, overwintering and possibilities of activity under the snow cover, and to a certain degree longevity and larval development. These data, combined with literature information, allows for a discussion about niche differentiation between species. Earlier, Erikstad *et al.* (1989) and Ottesen (1996) studied niche segregation for carabids in the same mountain area, based on a more limited number of parameters. The present data make it possible to sharpen the niche profiles.

An interesting question is whether adults may live long enough to experience more than one egg-laying season. This possibility was suggested by Kaufmann & Juen (2002) in an Austrian foreland. In the present study, claw wearing of hind legs has been used as an indication of relative age of adults. The material contained a variety of claw lengths within each species, from sharp and long claws in newly hatched tenerals to short remnants in old animals. The wearing of the tooth on left mandible in the two large *Nebria* species was also studied, and a correlation between claw and mandible wear was tested. Furthermore, individuals of one species, *Bembidion hastii* C. R. Sahlberg 1827, were marked and recaptured next year.

Claw-wear has been used in two sub-Antarctic carabid beetles to indicate that many individuals survive to breed in their third or later year of adult life (Davies 1987, Davies *et al.* 2007). Houston (1981) studied mandible wear as an age indicator in the two species *Carabus glabratus* Paykull, 1790 and *C. problematicus* Herbst, 1786 in northern England. It was concluded that some females lived for at least two, and probably three years, and that individuals with extreme mandible wear may die of starvation.

This paper contributes to the general ecology of each species. The question of adult longevity is discussed based on extensive data on claw

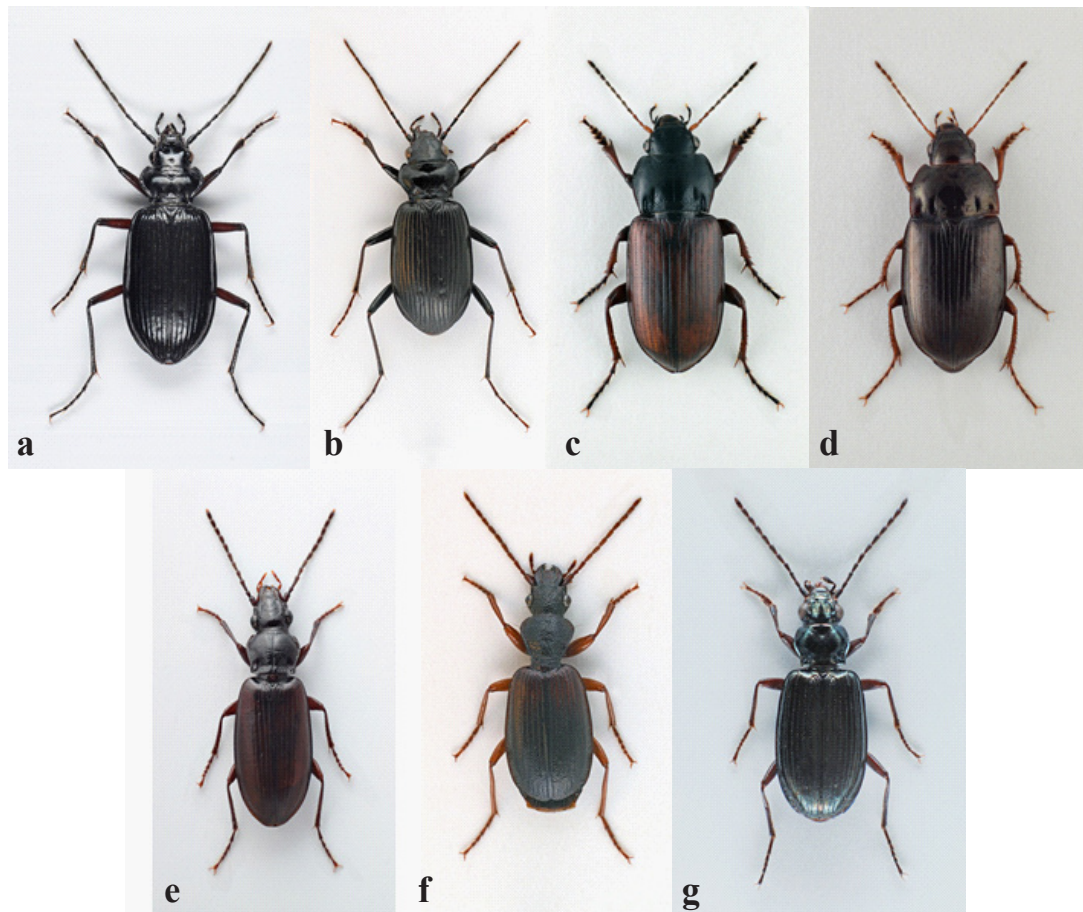


FIGURE 1. Seven carabid beetles from the glacier foreland. Upper row from left: **a.** *Nebria nivalis* (Paykull, 1790), **b.** *N. rufescens* (Ström, 1768), **c.** *Amara alpina* (Paykull, 1790), and **d.** *A. quenseli* (Schönherr, 1806). Lower row from left: **e.** *Patrobis septentrionis* Dejean, 1828, **f.** *Cymindis vaporariorum* (Linnaeus, 1758), and **g.** *Bembidion hastii* C. R. Sahlberg, 1827. Relative scales are not correct, as *Nebria* species are largest, and *B. hastii* is considerably smaller than the others. Photo: Oddvar Hanssen.

wearing. Niche differences are identified based on habitat use, phenology and life cycle.

Material and methods

The study area is the foreland of the Midtdalsbreen glacier snout, which is part of the 73 km² large Hardangerjøkulen glacier in southern Norway (Hordaland county, Ulvik municipality, 60°34'N; 7°28'E). The foreland is situated nearly 1400 m a.s.l., with an annual snow-free period of 3–4 months. The glacier has retreated about 1.2 km

since 1750, with increasing rate during the last decades. Between 2001 and 2011, the retreat was 154 m (Atle Nesje, pers. comm.).

The main material was collected during 2007 and 2008 by extensive pitfall trapping in six sites of the following age since deglaciation: 3, 39–40, 62–63, 78–79, 159–160, and 204–205 years (Figure 2). Every second week, twenty traps were emptied from each site (Bråten & Flø 2009, Bråten *et al.* 2012). Except for the youngest site of three years age, which was sampled only in 2008, the sampling program included two snow-free seasons with a total of twelve sampling

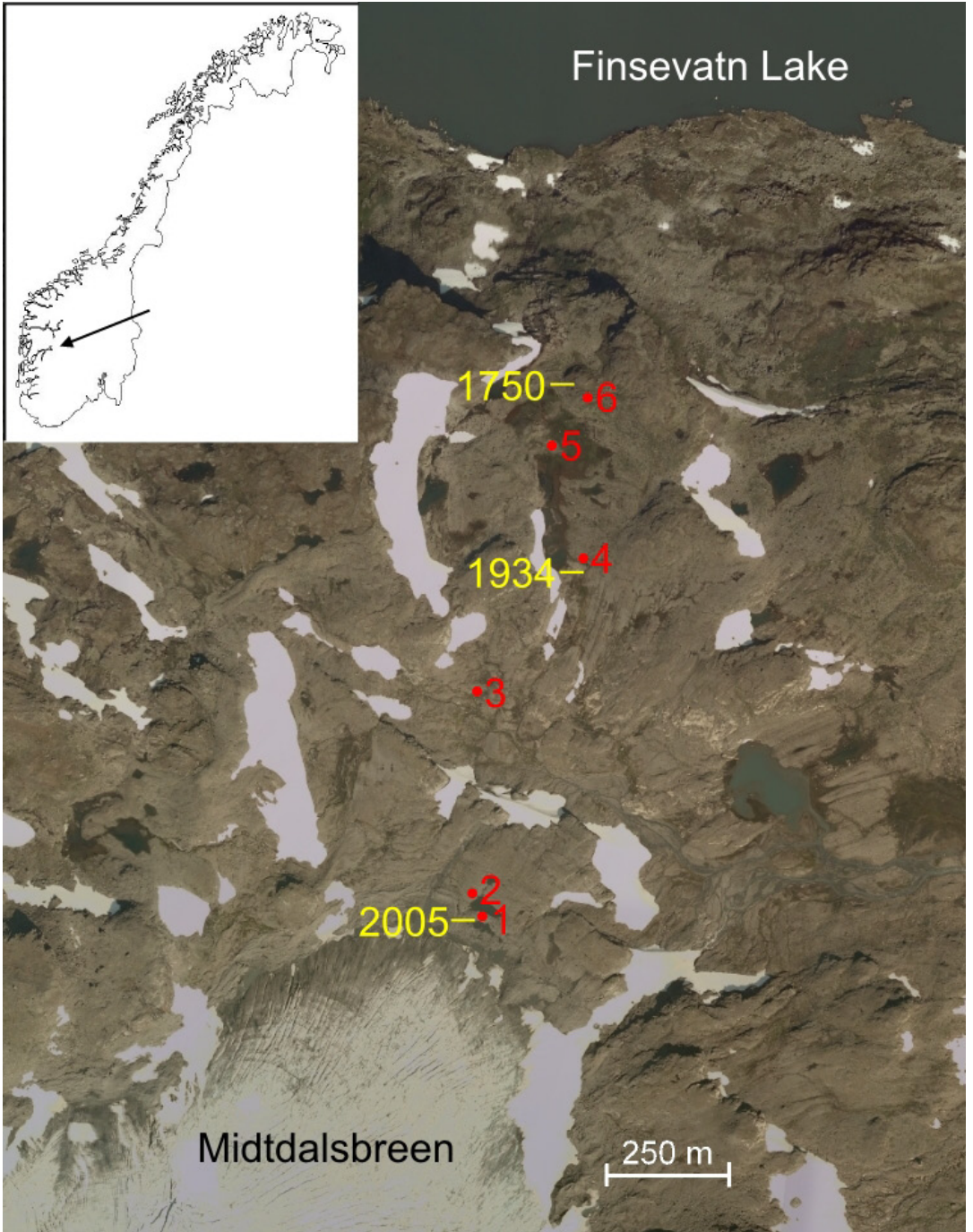


FIGURE 2. Air photo of the Midtdalsbreen glacier snout, with some moraines of known year shown in the foreland. With increasing distance from the ice, the sampling points 1–6 had the following age: 3, 40, 63, 79, 160, and 205 years. The position of the glacier in Southern Norway is indicated on the map. From Bråten *et al.* (2012).

periods, and a “winter” period between. The latter was the snow-covered period, including a few days (less than 14) before snow fall and after snow melt. Additional material was sampled from a six-year-old moraine by 50 pitfall traps in 2011. A total of about 3700 carabid specimens were collected. Seven species will be treated in detail: *Nebria nivalis* (Paykull, 1790), *Nebria rufescens* (Ström, 1768), *Amara alpina* (Paykull, 1790), *Amara quenseli* (Schönherr, 1806), *Patrobus septentrionis* Dejean, 1828, *Cymindis vaporariorum* (Linnaeus, 1758), and *Bembidion hastii* C. R. Sahlberg, 1827. Remarks will be given on two additional species: *Notiophilus aquaticus* (Linnaeus, 1758) and *Pelophila borealis* (Paykull, 1790).

Sex ratio (percentage males) was calculated for a standard two-week sampling period, if the number of individuals was at least 20. Females were dissected, and the number of full-sized eggs was counted from all sampling periods.

Larvae were identified according to Luff & Larsson (1993), and a combination of body length and width of head capsule were used to separate larval stages (Table 1). In five species, all three stages could be identified. The few *B. hastii* larvae were estimated to be in stage 2, while no larvae were trapped of *Cymindis vaporariorum*.

Within each species, it was observed that claws were worn over time. While newly hatched individuals (teneral) always had long and sharp claws, individuals with various degrees or claw wearing were seen (Figure 3). The study presents extensive data on claw length, in order to use claw wearing as an indicator of relative age. Measurements of claw length were done in a stereomicroscope with 50 x magnification, with a microscale in one ocular. Claw length of a given individual is the mean value of the four claws on hind legs. Also, the length of the “tooth” on the left mandible was measured in the two large *Nebria* species (Figure 4), to check a possible correlation between wearing of claws and jaws.

During 6.–9. August 2015, 280 specimens of *B. hastii* were trapped alive on a ten-year-old moraine, given a white spot of correction fluid on the elytra, and released again. The animals were kept close to 0°C during transport and treatment



FIGURE 3. Claws from different individuals of *Nebria nivalis* (Paykull, 1790). While newly hatched individuals have long and sharp claws, they are gradually worn down during life.

by use of snow. Resampling was made 4.–10. August 2016. Among 159 specimens, five marked animals were recorded (Figure 5).

The Welch two sample t-test (Welch 1947, 1951) was used to compare length of claws or width of pronotum between sites or sexes. If data were not normally distributed, Wilcoxon rank test was used (Bauer 1972, Hollander & Wolfe 1973). The dependence between claw and mandible tooth length, presented as scatter plots, was studied by correlation.

Results

Phenology and wearing of claws and jaws

Bembidion hastii C. R. Sahlberg, 1827

Phenological data from various years and ages

TABLE 1. Pitfall-trapped larvae of Carabidae sorted into assumed stages according to body length and width of head capsule.

Species	Larval stage	Length (mm)	Width of head capsule (mm)
<i>Amara quenseli</i>	I	3.5–4.0	0.64–0.74
	II	4.5–7.5	0.84–0.94
	III	8.0–10.0	1.06–1.36
<i>Amara alpina</i>	I	6.0	0.90
	II	6.0–11.0	1.16–1.26
	III	12.0–14.5	1.64–1.80
<i>Patrobus septentrionis</i>	I	4.5–5.0	0.58–0.70
	II	7.5–10.0	0.90–1.12
	III	11.0–16.0	1.16–1.80
<i>Nebria nivalis / rufescens</i>	I	5.0	0.84–0.86
	II	10.0	1.20
	III	10.0–15.0	1.45–1.62
<i>Pelophila borealis</i>	III	12.0–15.5	1.46–1.54
<i>Bembidion hastii</i>	II?	6.0–8.0	0.76–0.78

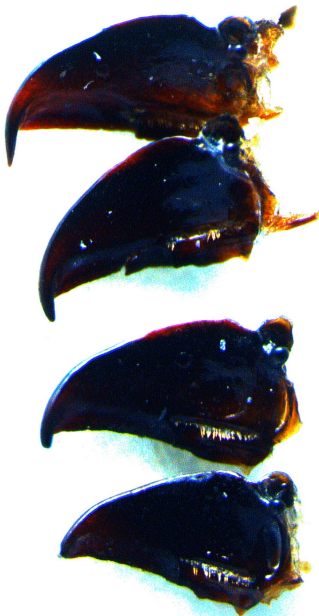


FIGURE 4. Left mandible of *Nebria nivalis* (Paykull, 1790), with varying degree of wearing of mandible tooth. The upper is of from newly hatched specimen.



FIGURE 5. A marked specimen of *Bembidion hastii* C. R. Sahlberg, 1827, recaptured after one year.

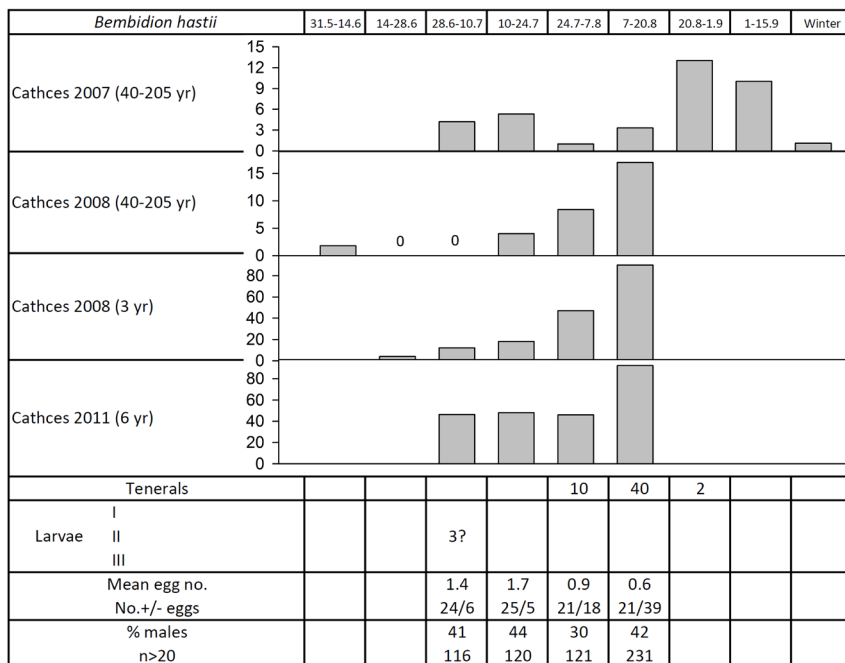


FIGURE 6. Phenological data for *Bembidion hastii* C. R. Sahlberg, 1827. For each sampling period, catches per 20 pitfall traps are shown. A zero means no catches although traps were operating, while no information means that traps were not operating. Sampling year and age of the ground are given to the left. Mean numbers of mature eggs per female included the empty females. The number of females with and without mature eggs are given. If the number of males was 20 or higher, the percentage of males was calculated.

of the ground are presented in Figure 6. Highest surface activity was rather late, in August, during and after hatching. Females with full-sized eggs (up to six per female) were found during four sampling periods (throughout July and August), with highest number of eggs per female in July. Percentage of males was always low, between 30 and 44.

A high number of this small pioneer species was trapped during 2011 on a six-year-old moraine. In Figure 7 the animals from each sampling period have been sorted according to claw length. Tenerals, which appeared in August, had sharp claws around 0.18 mm, while the shortest claw on old animals was only 0.04 mm. If newly hatched animals are regarded as one cohort with respect to variation in claw length, one cohort covers about 0.05 mm (shortest teneral claw was 0.16 mm, and the longest claw of 0.20 mm must have been from a newly hatched individual, although fully coloured). At hatching time, older adults were also

present, with a span in claw length from 0.04 to 0.15 mm, which may indicate two additional age groups (Figure 7). Both these potential age groups contained females with full-sized eggs (having claws from 0.06 to 0.14 mm). These data indicate that some adult beetles may experience three summer seasons: Hatching in the first summer without producing eggs, and then producing eggs during the two succeeding summers. Five resampled, marked individuals support this assumption (Figure 8). They belonged to the oldest animals in the population when resampled, with claws between 0.09 and 0.11 mm. Since tenerals were not observed at the time when they were marked, they were assumed to be at least one year old at that time. Three of the resampled specimens were egg-producing females.

Claw wearing seemed to be rather slow, since overwintered adults in July had claw lengths up to 0.16 mm, close to teneral length. Furthermore, egg-laying females which were supposed to be at

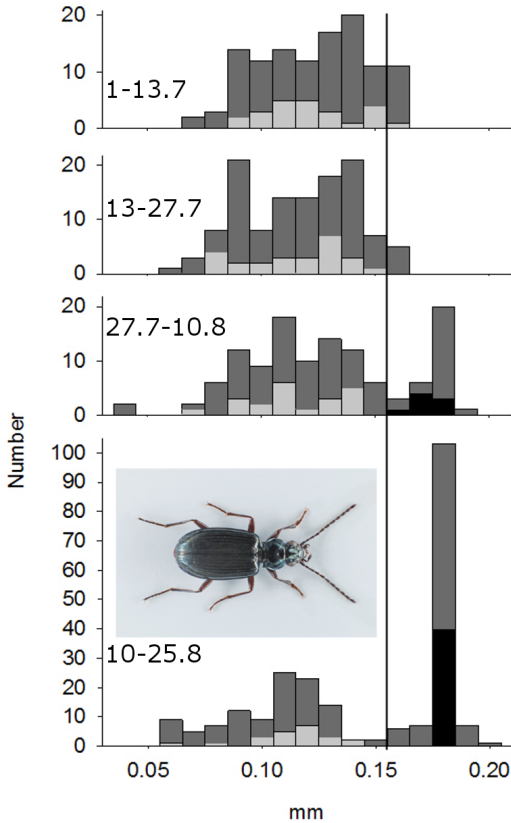


FIGURE 7. Seasonal variation in claw length for *Bembidion hastii* C. R. Sahlberg, 1827. Black = newly hatched teneral, light grey = females with at least one mature egg, dark grey = others (males and remaining females). In this species, not all females were dissected, so the light grey category are minimum values.

least one year old (tenerals did not develop eggs in their hatching year) had claws up to 0.14 mm in August, when the new generation appeared.

Two smaller data sets from 40-year-old ground in 2007 and 3-40-year-old ground in 2008 were in accordance with these conclusions. Claws of tenerals, which appeared is August, were 0.18-0.19 mm long, while claws in all sizes down to 0.04 mm were found.

***Nebria nivalis* (Paykull, 1790)**

The time of maximum catches varied between sites and years, from the last half of June to early August (Figure 9). Tenerals were mainly

trapped in July, which corresponds well with Lindroths (1945) observations from late July. The fourteen larvae recorded, of which eleven were trapped during winter, indicated that third instar hibernated, probably in an active state beneath snow. Females with full-sized eggs were recorded from medio June to medio August. Maximum number of mature eggs found in one female was seven. The percentage of males varied between 35 and 63.

This large species inhabited the 2005-moraine together with *B. hastii*, but it also occurred in older sites. Because the material was limited within each year, data on claw length from 2007, 2008 and 2011 were merged (Figure 10). Claws of seven tenerals varied between 0.42 and 0.46 mm, but claws worn down to less than half of that (0.18 mm) were found. No females with claws above 0.40 mm contained eggs, indicating that egg-laying occurred after hibernation. Overwintered females with mature eggs in early July had claws up to 0.40 mm, so only moderate wearing seemed to occur since hatching the preceding summer. Even some old females, with claws down to 0.28 mm, contained fully sized eggs.

If a cohort covers a range of about 0.04 mm, as indicated by the tenerals, (or maybe slightly more due to few tenerals measured) there may be several cohorts of adults at hatching time: tenerals (0.42–0.46 mm), one-year-old adults laying eggs for the first time (about 0.34–0.40 mm), and two-year-old adults laying eggs again (about 0.26–0.32 mm). Perhaps there even could be some animals in a fourth cohort (0.18–0.24 mm). In that case, some adults live for three years.

While all tenerals had long claws, the “tooth” on the left mandible varied strongly in size among tenerals (Figure 11). Correlation between claw and tooth length was significant ($p=0.02$), but weak (0.23).

***Nebria rufescens* (Ström, 1768)**

The highest catches were recorded in July. Females with mature eggs were found from early June to early August. Highest number of mature eggs in one female was 22. The percentage of males varied between 33 and 47. Two larvae, in second and third instar, were trapped during

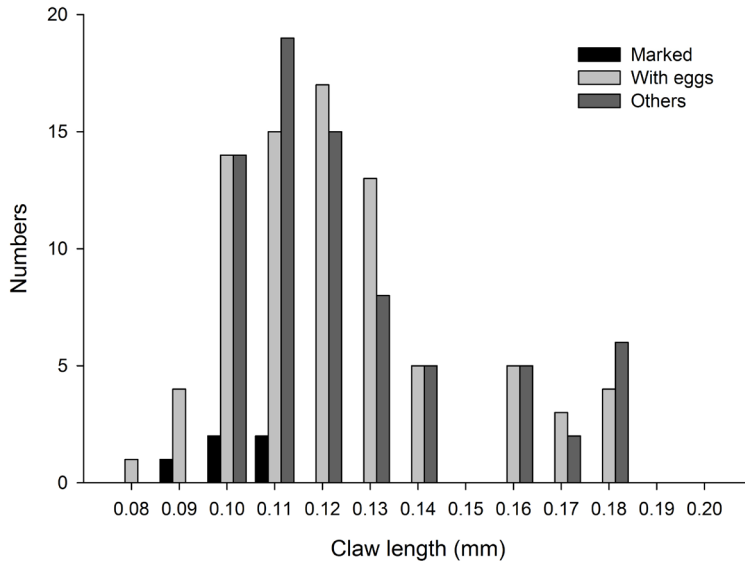


FIGURE 8. Claw length distribution in a population of *Bembidion hastii* C. R. Sahlberg, 1827, trapped in early August 2016. Black bars show five specimens which were recaptured after being marked with a white spot on the elytra one year earlier. Light grey = females with at least one mature egg, dark grey = others (males and remaining females). Further explanation in text.

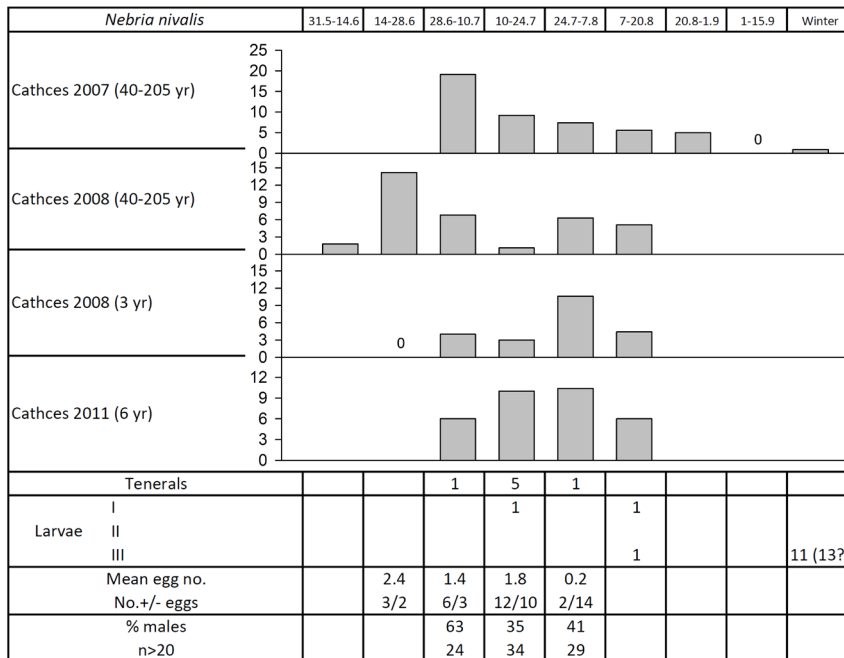


FIGURE 9. Phenological data for *Nebria nivalis* (Paykull, 1790). For further explanation, see legend to Figure 6.

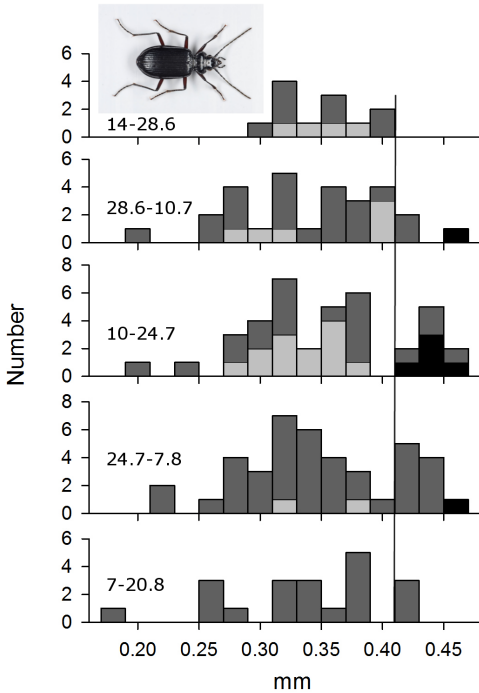


FIGURE 10. Seasonal variation in claw length for *Nebria nivalis* (Paykull, 1790). Black = teneral, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs).

winter, maybe under snow (Figure 12). The life cycle seems to be very similar to *N. nivalis*.

Claw data from 2007 and 2008 were merged (Figure 13). Teneral, with claws between 0.42 and 0.46 mm, hatched mainly in July, but long-clawed females did not develop eggs during their first summer. The large total span of claw lengths (0.24–0.46 mm) indicated at least two cohorts in addition to teneral. Overwintered females with developed eggs had up to 0.44 mm long claws in June, and up to 0.40 mm in July, which means that claw wearing is not very strong during the first year. This supports the assumption of three, and perhaps four, adult cohorts. Even old females, may be in their third summer, produced eggs. As in *N. nivalis*, there were also males among the oldest animals.

Like *N. nivalis*, all teneral had long claws, but the “tooth” on the left mandible varied strongly among newly hatched specimens (Figure 14). Correlation between claw and tooth length was significant ($p=0.001$), but weak (0.29).

***Cymindis vaporariorum* (Linnaeus, 1758)**

The catches of this species were relatively evenly distributed throughout June, July and

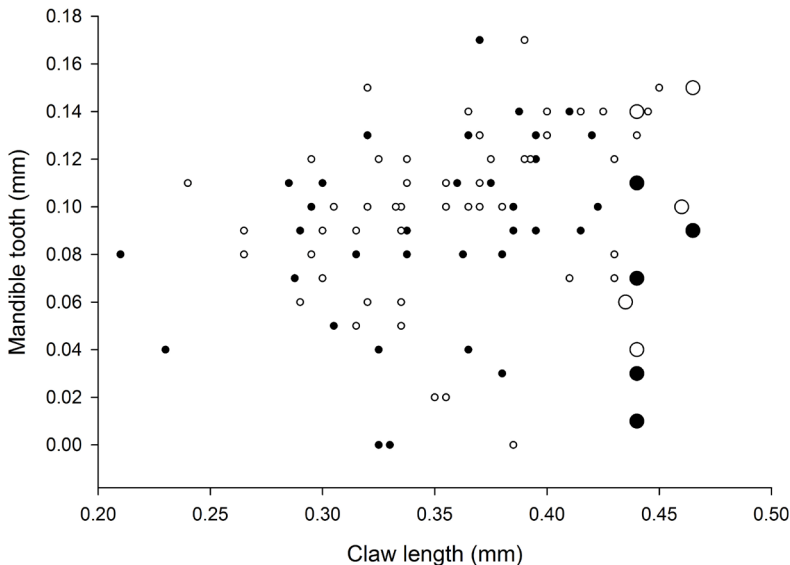


FIGURE 11. Scatter plot on the relation between claw length and size of mandible tooth in *Nebria nivalis* (Paykull, 1790). Closed dots are males, and open dots females. Large dots indicate newly hatched individuals (teneral). A male teneral on 0.44/0.14 is concealed behind a female symbol.

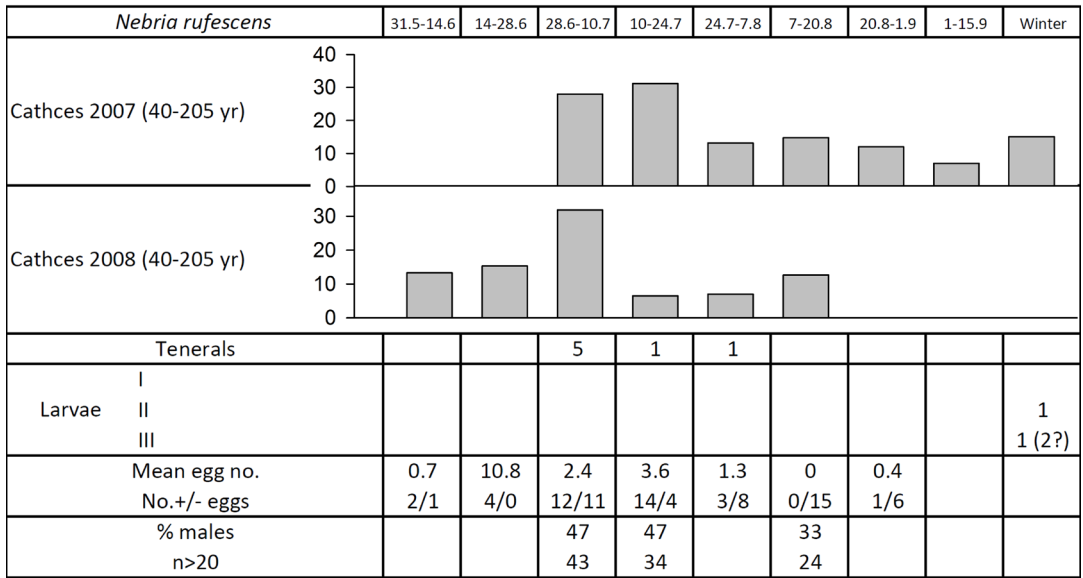


FIGURE 12. Phenological data for *Nebria rufescens* (Ström, 1768). For further explanation, see legend to Figure 6.

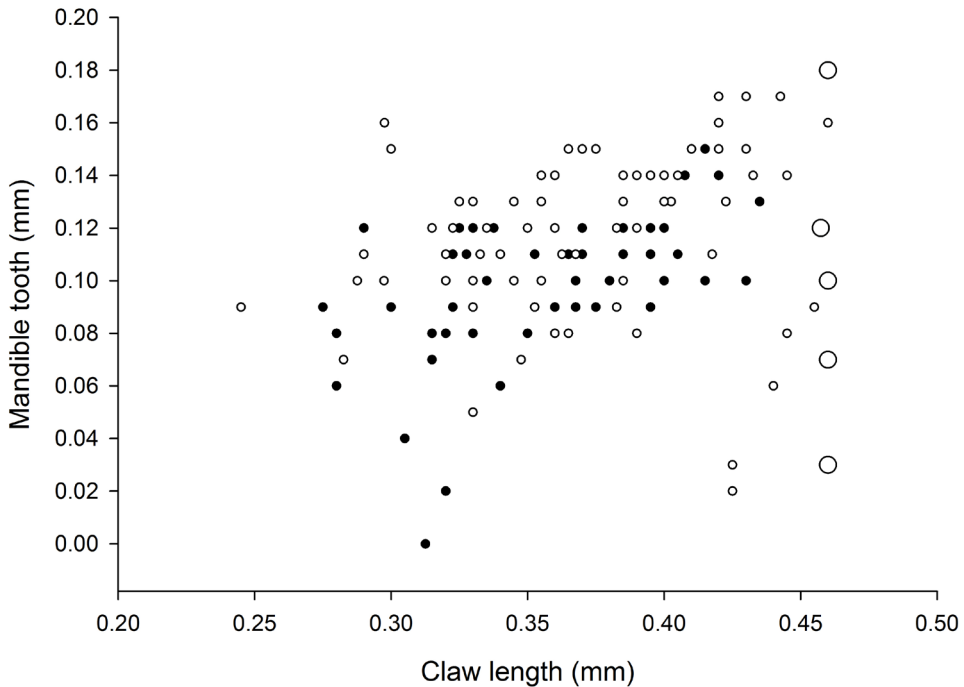


FIGURE 14. Scatter plot on the relation between claw length and size of mandible tooth in *Nebria rufescens* (Ström, 1768). Closed dots are males, and open dots females. Large dots indicate newly hatched individuals (tenerals).

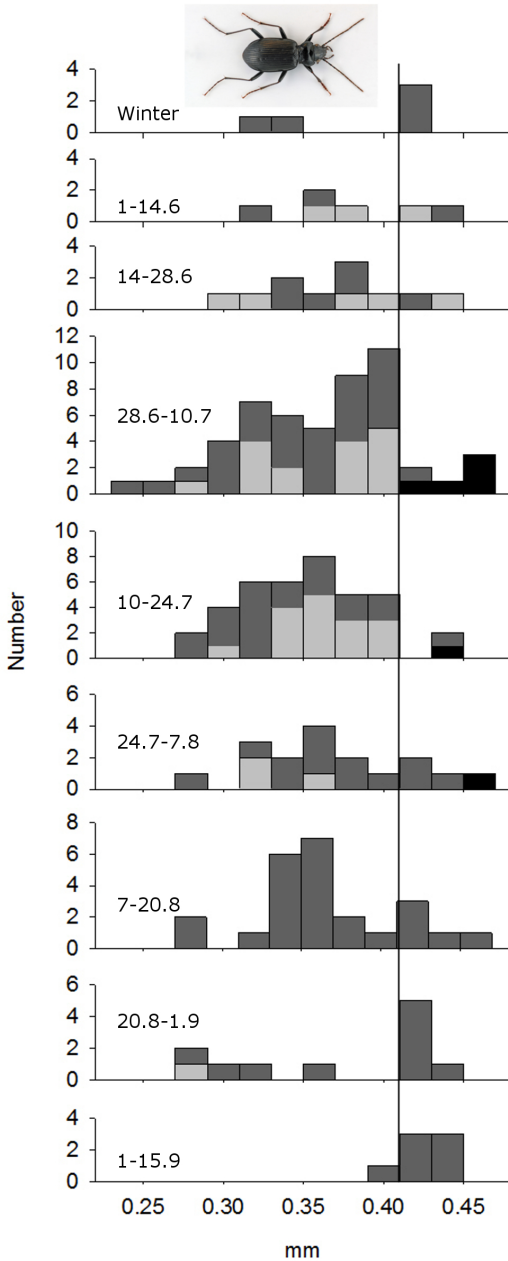


FIGURE 13. Seasonal variation in claw length for *Nebria rufescens* (Ström, 1768). Black = teneral, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs).

August (Figure 15). Egg production lasted from medio June to early August. The highest number of mature eggs per female was 10. Male percentage varied between 34 and 57. Larvae of this species were not trapped, and they are evidently not surface active.

Combined data from 2007 and 2008 showed a span in claw length from 0.16 to 0.30 mm (Figure 16). Claws of five teneral were between 0.27 and 0.29 mm, indicating two or more adult cohorts in the total material. Egg-laying females with claw length between 0.20 and 0.30 mm, indicate more than one cohort of egg-layers (which are supposed to have overwintered at least once). Four of the teneral were winter-trapped, and the fifth one in June 2008. Hatching just after snow melt seems improbable, since this implies entering winter as pupa. A better explanation is that all five teneral hatched in late 2007, but without having achieved their full colouration yet after snow melt. Autumn hatching is in accordance with the fact that July females with the longest claws often had eggs, and were supposed to have overwintered once. These females had in fact as long claws as teneral, indicating that claws are worn very slowly during the first year.

***Patrobis septentrionis* Dejean, 1828**

This species had the highest number of trapped individuals in the foreland (Figure 17). Maximum catches in both years were noted in early July. A special feature of *P. septentrionis* was the marked winter activity, with 42 adults and 83 larvae trapped, probably under snow (Figure 17). Nearly all winter active larvae were in the third and last stage, and the few larvae trapped during the summer indicated a gradual development towards third instar. Egg-carrying females were found from early June to early August, with up to 14 mature eggs per female. The percentage of males varied between 40 and 65.

A large material from both 2007 and 2008 showed a span in claw lengths from 0.15 to 0.34 mm (Figure 18). Seventeen teneral, mainly trapped in August, had claws between 0.27 and 0.34 mm, indicating a span of about 0.07 mm for a cohort. Shorter claws in the range 0.15–0.26 mm could represent two additional cohorts. Several

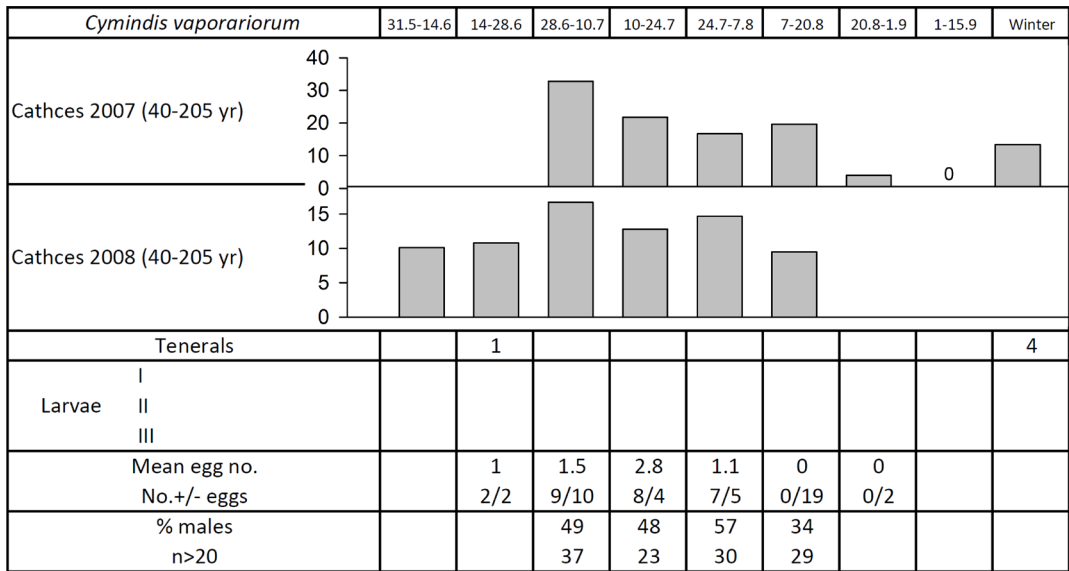


FIGURE 15. Phenological data for *Cymindis vaporariorum* (Linnaeus, 1758). For further explanation, see legend to Figure 6.

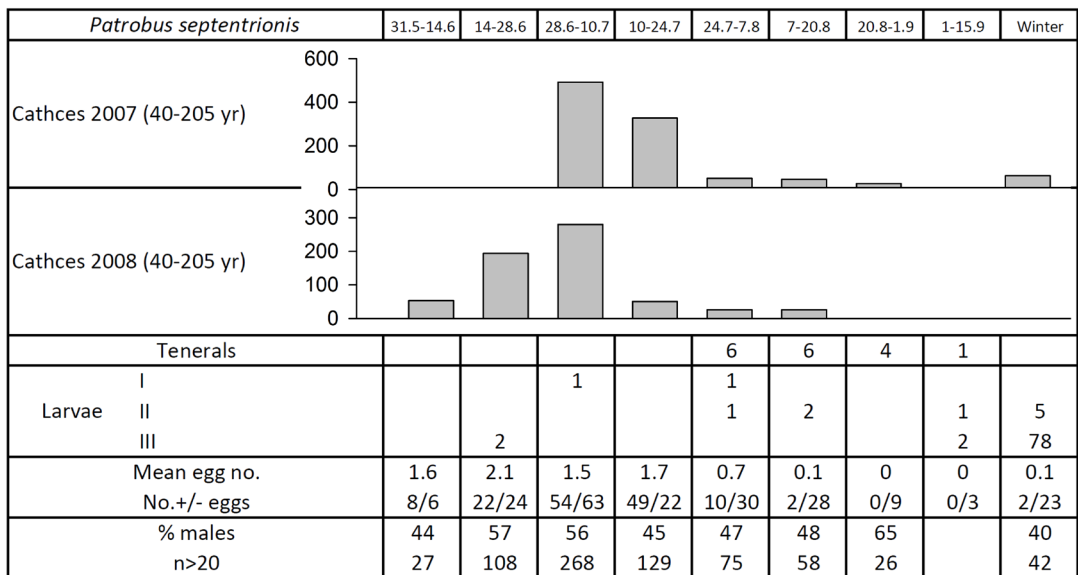


FIGURE 17. Phenological data for *Patrobus septentrionis* Dejean, 1828. For further explanation, see legend to Figure 6.

egg-bearing females, which were supposed to have overwintered at least once, had claws which overlapped with newly hatched specimens (more than 0.27 mm). This indicates a rather slow wearing.

P. septentrionis was trapped numerously both

on sand- and gravel-dominated ground with sparse vegetation (40 years old), and on older ground with closed vegetation. The younger, sandy ground was inhabited by animals with slightly shorter claws ($p=0.003$). During the period 10–24 July, mean claw length was 0.24 mm on sandy ground, and

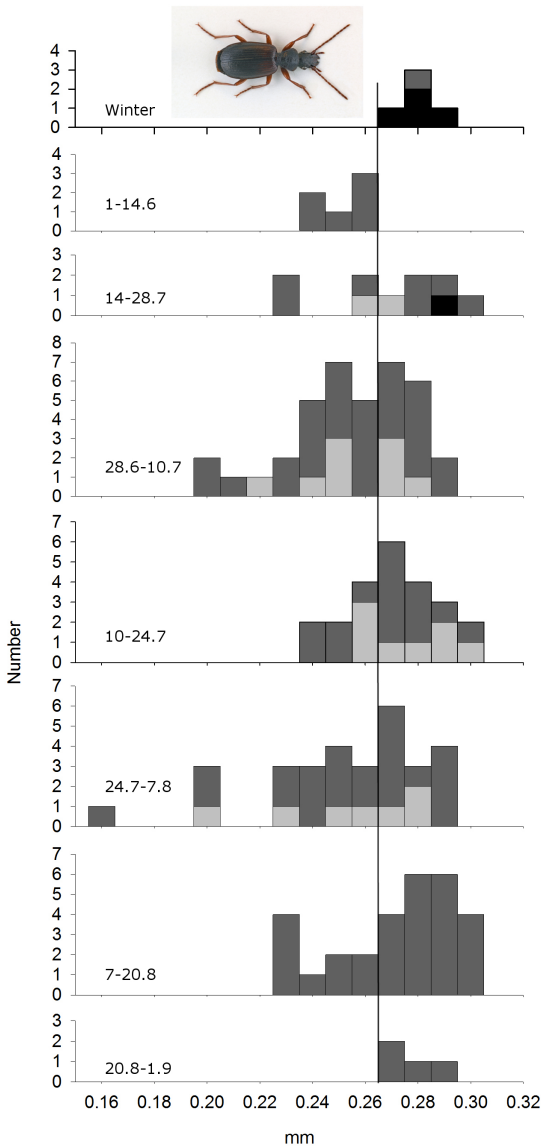


FIGURE 16. Seasonal variation in claw length for *Cymindis vaporariorum* (Linnaeus, 1758). Black = teneral, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs).

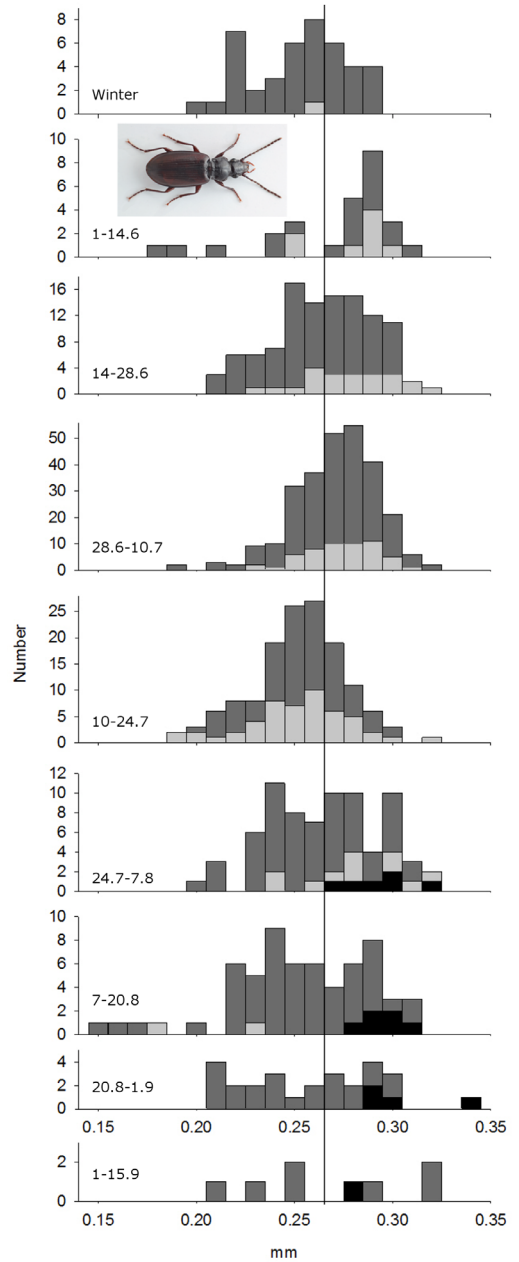


FIGURE 18. Seasonal variation in claw length for *Patrobis septentrionis* Dejean, 1828. Black = teneral, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs).

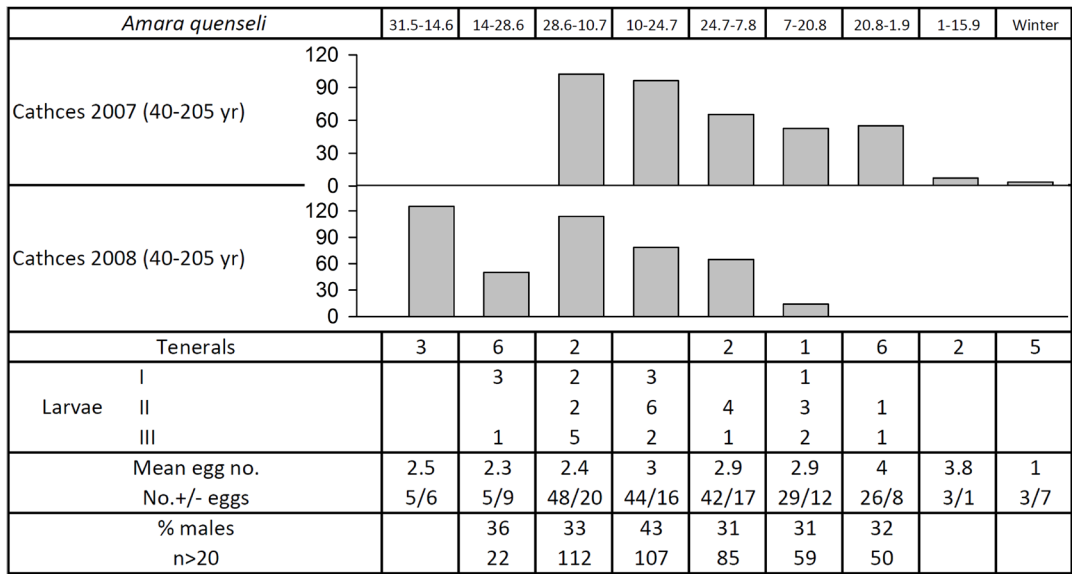


FIGURE 19. Phenological data for *Amara quenseli*. For further explanation, see legend to Figure 6.

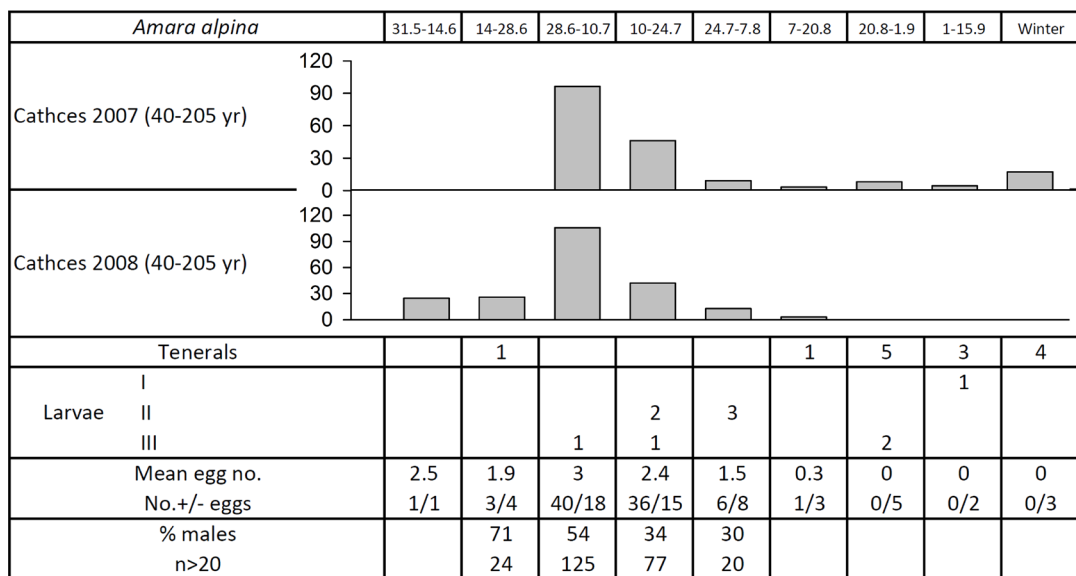


FIGURE 21. Phenological data for *Amara alpina* (Paykull, 1790). For further explanation, see legend to Figure 6.

0.26 mm on vegetated ground.

***Amara quenseli* (Schönherr, 1806)**

Catches were rather stable from early June to August (Figure 19). The percentage of trapped males was low, between 31 and 43. Females

carrying full-sized eggs were found throughout the snow-free period, and within the whole range of claw lengths. Maximum number of eggs per female was 18. Claw length varied from 0.16 to 0.29 mm (with one extreme of 0.08 mm), while 26 tenerals spanned 0.23 to 0.28 mm (Figure 20).

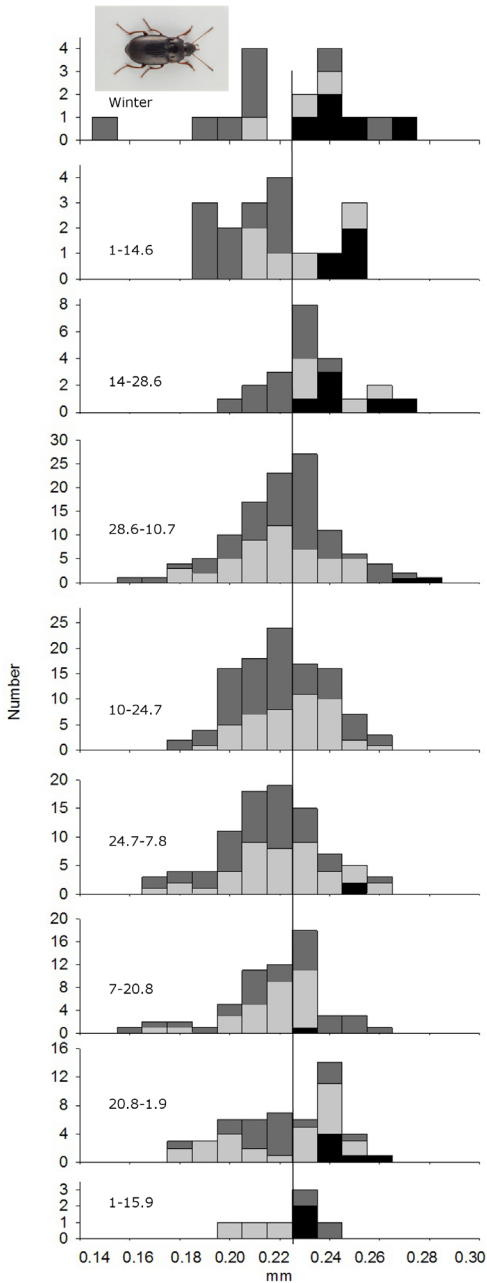


FIGURE 20. Seasonal variation in claw length for *Amara quenseli* (Schönherr, 1806). Black = teneralis, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs). Remark: Not all specimens of this abundant species were measured. For instance, catches were much higher in the period 1–14 June than indicated by the present figure (see phenology in Figure 19).

This may indicate two cohorts of adults. However, hatching was not clearly synchronized. In 2007, teneralis were trapped from medio August to medio September. In 2008, teneralis were found in all samplings, except in medio July. Four teneralis trapped during winter, and three more from early June, may have hatched the preceding autumn, not yet being fully coloured. However, six teneralis from the second half of June and two from early July have probably hatched after snow melt.

The larval material was difficult to interpret, since all stages were observed together from June to August. Also, teneralis were distributed throughout the snow-free period. The egg-laying season was very long, from June to September. The life cycle of this species seems to be badly synchronized.

Amara alpina (Paykull, 1790)

Figure 21 shows highest activity in July. Also, the egg production was most intense in this period. Up to ten mature eggs were found in one female. The larval material was limited and difficult to interpret. However, if we disregard the first instar larva in September, the larval material could indicate overwintering in the last instar. No larvae were trapped during winter. Percentage of males fell gradually from 71 in June to 30 in early August.

As in *P. septentrionis*, the younger, sandy ground was inhabited by animals with significantly shorter claws ($p < 0.001$). During the two sampling periods between 28 June and 24 July, mean claw length was 0.24–0.25 mm on sandy ground, and 0.31–0.32 mm on vegetated ground. Figure 22 shows that claws on sandy ground were mainly below 0.30 mm, but mainly from 0.30 mm and higher on vegetated ground. Sand-living animals were also slightly smaller, with a mean pronotum width of 2.29 mm versus 2.38 mm ($p < 0.01$). On sandy ground, pronotum width was not significantly different between sexes ($p = 0.16$), while females were slightly broader than males on vegetated ground ($p = 0.02$).

In the total material, fourteen teneralis had claws between 0.32 and 0.38 mm, while the shortest claw was only 0.14 mm. If teneralis indicate that a cohort covers a range of about

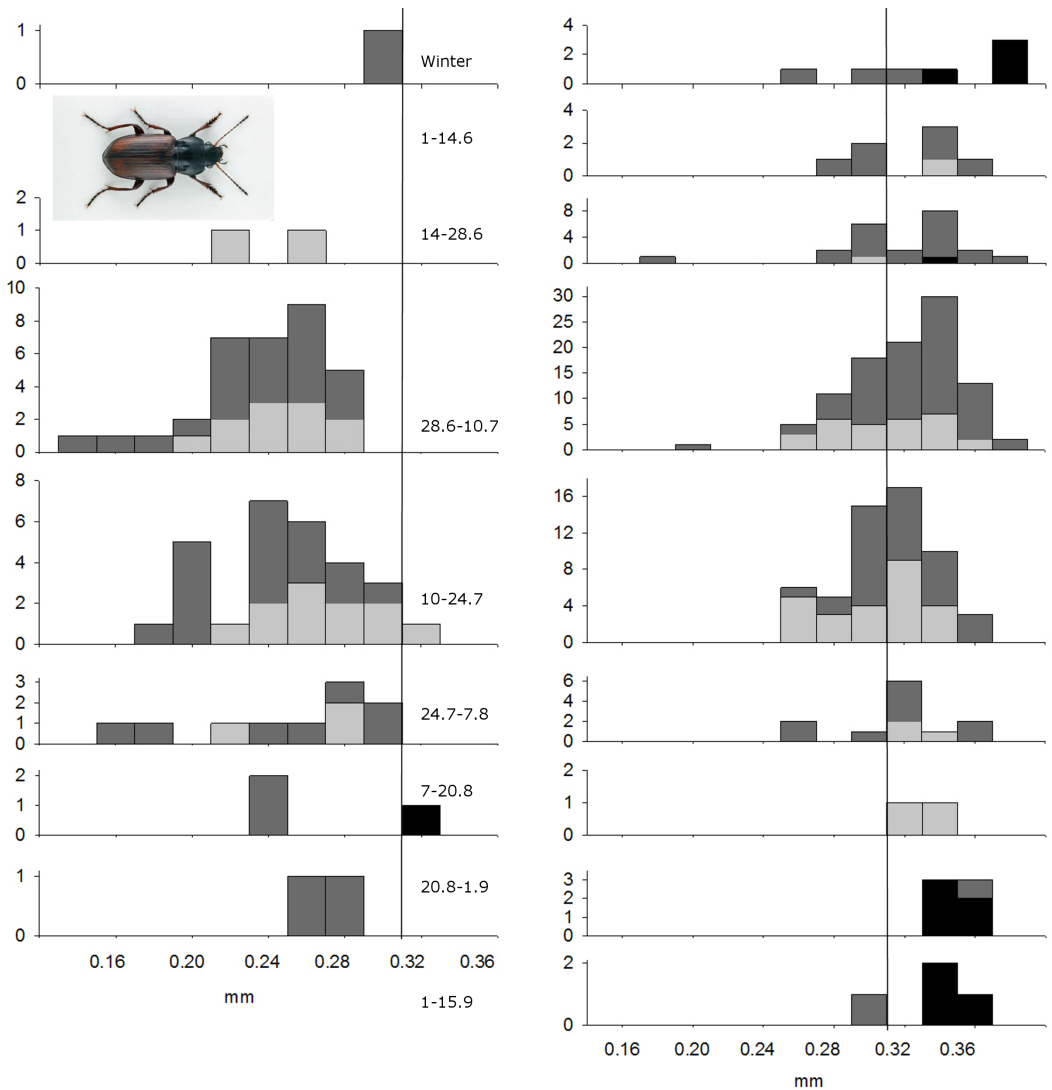


FIGURE 22. Seasonal variation in claw length for *Amara alpina* (Paykull, 1790). Black = teneral, light grey = females with at least one mature egg, dark grey = others (males and females without mature eggs). Left: animals from sandy pioneer ground. Right: animals from vegetated ground.

0.06 mm, females with full-sized eggs could easily cover two age groups (0.20 to 0.36 mm). Furthermore, the long claws of several egg-bearing females on vegetated ground, overlapping with the range of teneral, indicate a rather slow wearing. Figure 22 document hatching in autumn (late August and early September). Also, four teneral trapped during winter were probably from the autumn hatching, and perhaps even one from

June, if full coloration takes time.

***Pelophila borealis* (Paykull, 1790)**

A small material of about 40 animals was mainly trapped in late June and early July (Bråten & Flø 2009, Bråten et al. 2012). Females carrying mature eggs (up to 11), was found in this period and later in July. Among 30 specimens, 10 were males. Nearly all specimens were taken in a very

moist depression close to the edge of a pond, on 79-year-old ground. Claw length varied between 0.23 and 0.38 mm. Three larvae in their last instar were trapped in August.

Notiophilus aquaticus (Linnaeus, 1758)

Of this small, diurnal species, about 80 specimens were trapped on 63-year-old ground and older, mainly in June and July (Bråten & Flø 2009, Bråten *et al.* 2012). No larvae were taken. Data on egg-bearing females, or claw lengths, are lacking.

Habitat factors and spatial overlap between species

Throughout the foreland, soil moisture varied according to topography. The response to moisture can be well illustrated at two of the sampling plots, on 63 and 79-years-old ground. Here, half of the traps were placed on dry ridges dominated by drought-tolerant lichens on sand-dominated soil, and the other half in moist depressions with *Salix herbacea* and mosses typical for snow beds, or near water. Table 2 illustrates that catches of several species were influenced by soil moisture in these two plots. *Cymindis vaporariorum*, *Notiophilus aquaticus*, and *Amara quenseli* were xerophilic species, *Amara alpina* was

rather indifferent, while the two *Nebria* species, *Patrobis septentrionis*, and *Pelophila borealis*, were hygrophilic.

Table 2 also shows that animals could occur outside their humidity preference, so their field distribution was determined both by preference and tolerance to humidity variations. This can be illustrated by looking at species combinations in each of the 120 permanent traps, i.e. spatial overlap between species pairs. Table 3 shows the percentage of traps containing various species pairs, represented by at least one individual of each species. Xerophilic species like *C. vaporariorum* and *A. quenseli* were, for instance, often trapped together with the hygrophilic species *P. septentrionis*. In practise, all species in the foreland had a certain contact with all the other carabid species – with one exception: The super-pioneer and open-ground specialist *B. hastii* had no contact with the three latest colonisers: *C. vaporariorum*, *N. aquaticus*, and *P. borealis*.

Large and bold numbers in Table 3 show the percentage of traps in which each species was taken in at least one specimen. *P. septentrionis*, the most numerous species in the total carabid material (Figure 17), was taken in the highest number of traps (76 %). Although the species showed a preference for moist soil (Table 2), it evidently

TABLE 2. Pitfall catches of various Carabidae species in some clearly dry versus clearly wet habitats. The number of traps was the same each year in dry and wet habitats. Site age was 63 years in area I and 79 years in area II.

Area	Year	<i>Cymindis vaporariorum</i>		<i>Notiophilus aquaticus</i>		<i>Amara quenseli</i>		<i>Amara alpina</i>		<i>Nebria rufescens</i>		<i>Nebria nivalis</i>		<i>Patrobis septentrionis</i>		<i>Pelophila borealis</i>	
		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
I	2007	14	7	8	3	99	28	4	1	0	6	1	5	15	144	0	0
I	2008	20	5	13	1	118	59	28	8	3	6	0	4	12	135	0	0
II	2007	9	1	4	2	157	48	9	8	25	67	1	20	18	341	0	25
II	2008	8	1	8	7	86	42	12	21	12	42	1	12	12	239	1	9
Total catches		51	14	33	13	460	177	53	38	40	121	3	41	57	859	1	34
% in dry habitats		78 %		72 %		72 %		58 %		25 %		7 %		6 %		3 %	

TABLE 3. Bold, large numbers show the percentage of traps in which a given species was found. Other numbers show the percentage of traps in which a certain species pair was trapped together (minimum one individual of each species). For instance, *Bembidion hastii* occurred in 29 percent of the traps, and together with *Nebria nivalis* in 18 percent of the traps. In the other half of the Table, some ecological characters which were common for species pairs are indicated. Species names have been abbreviated in the upper row.

	<i>Bem. has.</i>	<i>Neb. niv.</i>	<i>Neb. ruf.</i>	<i>Ama. alp.</i>	<i>Ama. que.</i>	<i>Pat. sep.</i>	<i>Cym. vap.</i>	<i>Not. aqu.</i>	<i>Pel. bor.</i>
<i>Bembidion hastii</i>	29	18	3	16	4	11	0	0	0
<i>Nebria nivalis</i>	Pioneers	38	18	28	17	27	8	9	7
<i>Nebria rufescens</i>		Coldadapted	35	28	28	31	18	18	10
<i>Amara alpina</i>	Pioneers	Pioneers		69	35	59	36	22	11
<i>Amara quenseli</i>					46	38	28	24	10
<i>Patrobus septentrionis</i>		Hygrophilic	Hygrophilic	Generalists		76	43	25	14
<i>Cymindis vaporariorum</i>					Xerophilic		46	24	6
<i>Notiophilus aquaticus</i>				Generalists?	Xerophilic		Xerophilic	29	5
<i>Pelophila borealis</i>		Hygrophilic	Hygrophilic			Hygrophilic			14

had a wide moisture tolerance. *A. alpina*, which showed no clear moisture preference according to Table 2, was the next most numerous species in the total material, and dropped into 69 % of the traps. *P. septentrionis* and *A. alpina* behaved like habitat generalists in the foreland. Next in trapping frequency were two xerophilic species: *A. quenseli* and *C. vaporariorum*, both occurring in 46 % of the traps. Then followed *N. nivalis* and *N. rufescens*, with 38 and 35 %, respectively. The xerophilic *N. aquaticus* occurred in 29 % of the traps. Two obvious specialists were among the lowest percentages: The open-ground species *B. hastii* (29 %) and the strongly hygrophilic species *P. borealis* (14 %). *B. hastii* was usually accompanied by *N. nivalis* and *A. alpina*, forming a characteristic pioneer community. *P. borealis* was always accompanied by *P. septentrionis*, and often by the two *Nebria* species, forming a typical “hygrophilic community”. The percentage numbers in Table 3 depend of course on how the traps were placed. For instance, nearly all *Pelophila* specimens were trapped at the edge of a pond. Catches also depend on the abundance and surface activity of each species.

The lower left of Table 3 shows some ecological parameters that were in common

for certain species pairs: pioneers, hygrophilic, xerophilic, or cold-adapted species.

Discussion

Life cycle

A prolonged life cycle has been documented in many alpine carabid beetles, for instance at 2000-3000 m a.s.l. in Tyrol (DeZordo 1979a). In the Rotmoos glacier foreland in the Alps, all five *Nebria* species studied had a biennial life cycle (Kaufmann & Juen 2002). Also in alpine areas around Lake Kilpisjärvi in Finnish Lapland, Forsskähl (1972) found that prolonged life-cycles were common in alpine beetles. From Norway, Refseth (1984) reported two-year life cycles in the large species *Carabus glabratus* Paykull, 1790 and *C. violaceus* Linnaeus, 1758 from the sub-alpine zone.

The ultimate proof for a two-year life cycle is the simultaneous hibernation of larvae and adults. In the present study, this was documented for three species due to their winter active larvae: *Nebria nivalis*, *Nebria rufescens*, and *Patrobus septentrionis*. Regarding *Amara alpina* and

Amara quenseli, some considerations can be made based on the larval material trapped during the snow-free season. For *A. alpina*, hibernation in the third stage seems probable. However, there is a confusing record of a first instar larva from September. *A. quenseli* may have a flexible and non-synchronized life cycle, with the ability to overwinter in different larval stages, and without a standard time for hatching. This is what DeZordo (1979b) found at 2650 m a.s.l. in Austria. There, *A. quenseli* overwintered in all larval instars, as well as in the adult stage, and completed the life cycle in two or three years. This flexibility may explain its ability to live on Svalbard, where the snow-free season is very short and weather conditions unpredictable. In the present material, long-clawed, presumably young, females with eggs captured in July and early August (Figure 20) raises the question whether adults that hatch early in the snow-free season might develop mature eggs already the same summer. That would be in contrast to the other species, where adults must overwinter once before ovaries produce eggs.

The larvae of *B. hastii* and *C. vaporariorum*

are evidently not surface active and may have a subterranean life. The phenological data from these species are not in conflict with a possible two-year life cycle, but proof remains. Both species are late hatchers.

According to Sømme (1989), *P. borealis* has a one-year life cycle at Finse. The three larvae trapped in their last instar in August, and no winter catches of larvae, conform with this pattern. An adult trapped just after snow melt, with long claws (0.38 mm) and not yet fully coloured, may have hatched the preceding autumn. However, winter larvae should be searched for in this species, to check a possible biennial life cycle

Longevity

The following observations indicate that some adults may live for two years, which means that they experience three snow-free seasons: Hatching during the first, and two egg-laying seasons: 1) The recovery of marked specimens of *B. hastii*, mentioned above. (It was observed that the white marks were rather loosely attached after one year,

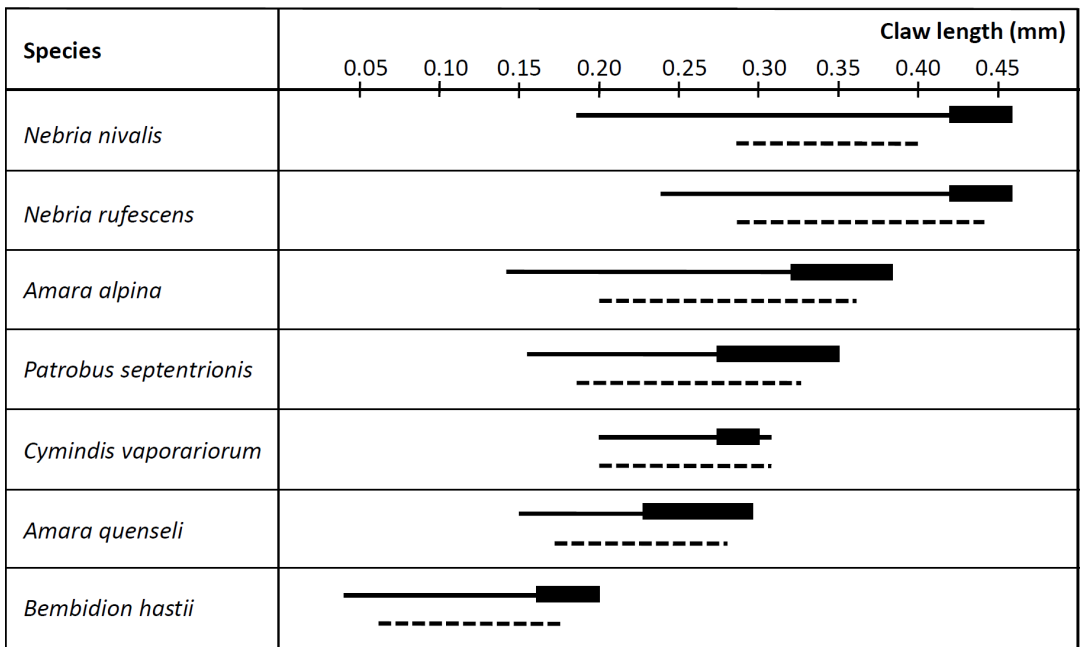


FIGURE 23. Total span in claw length for each species. The thick line shows the variation in newly hatched tenerals, while the stippled line represents females carrying at least one mature egg.

so the survival was probably better than indicated by the five recaptured animals). 2) A total span in claw length which exceeds twice the span of the teneral cohort would indicate three adult cohorts. In Figure 23, this is the case especially for the two *Nebria* species, *A. alpina*, and *B. hastii*. 3) Claw wearing appeared to be relatively slow. Some egg-producing females, which were supposed to have overwintered at least once, had relatively long claws in all species (Figure 23). 4) Also, several old females with short claws were reproducing.

An argument against an adult life span of two years is that distribution curves for claw lengths do not show a clear separation into two or three adult cohorts. This may be due to a considerable overlap between cohorts. Figure 24 illustrates how two overlapping curves theoretically may merge into a broader curve with one peak.

Sømme (1989) referred as an unpublished result that adult *P. borealis* had a prolonged longevity in the Finse area, and presented three adult hibernations in his Figure 5. The co-occurrence of a long-clawed (0.38 mm) and a short-clawed (0.27 mm) specimen at snow melt in the 2008-material probably indicates more than one age class.

If a female has two egg-laying seasons, she produces two cohorts of offspring. In her second egg-laying season, she will live together with two other age groups of adults: beetles in their first egg-laying season, and teneral which are the result of eggs laid the year before. If larvae are also present from females of two different age groups, five cohorts may be present at the same time. This is schematically illustrated in Figure 25.

Kaufmann & Juen (2002) pointed to the fact that long-lived carabid adults could be an important resource if reproduction more or less failed in certain years due to unfavourable weather in the mountains. Then, surviving adults might succeed next year. From the Austrian Alps, Schatz (1994) suggested that *Pterostichus jurinei* (Panzer, 1803) could live for two years as an adult. Long adult life was documented in two sub-Antarctic carabid beetles by Davies (1987) and Davis *et al.* (2007). Claw wearing was used to indicate relative age, and it was operated with five claw-wear classes.

These classes were not clearly distinguished, and did not claim to closely represent year-classes. However, it was assumed that many individuals survived to breed in their third or later year of adult life. A long adult life compensated for a low and unpredictable reproduction rate. In some years, populations consisted largely of very old beetles, but these were still producing eggs.

Claw wearing versus mandible wearing

Claw wearing turned out to be a much better indicator of relative age than wearing of the left mandible tooth. While newly hatched specimens of the two *Nebria* species always had long and sharp claws, the mandible tooth of teneral varied much, and was sometimes relatively short (Figures 11 and 14). Perhaps individuals born with short mandible tooth died early due to feeding problems when the mandible tooth was worn down.

Although the present study refuses the use of the mandible tooth as an age indicator, Houston (1981) claimed that the parameter worked for the two species *Carabus glabratus* and *C. problematicus* in northern England. The four wear-categories used were not absolute, but it was concluded that an adult life of two or three years was highly probable.

Dispersal

Long-lived specimens which can endure longer migrations, may be valuable in keeping pace with the retreating ice edge. On 40-year-old ground with much open sand and gravel, specimens of *A. alpina* had significantly shorter claws than on vegetated plots (Figure 22). There are two possible explanations, or a combination: The pioneer population on sand was dominated by old individuals, and/or claws were faster worn down on sand. One teneral of *A. alpina* was trapped on sandy ground, so some reproduction does occur there. The slightly narrower pronotum of adult *A. alpina* on sand could be due to poorer food availability for larvae here. It was not due to a dominance of "small" males, since more than half of the animals (13 of 24) were females. The hypothesis is that the population on pioneer

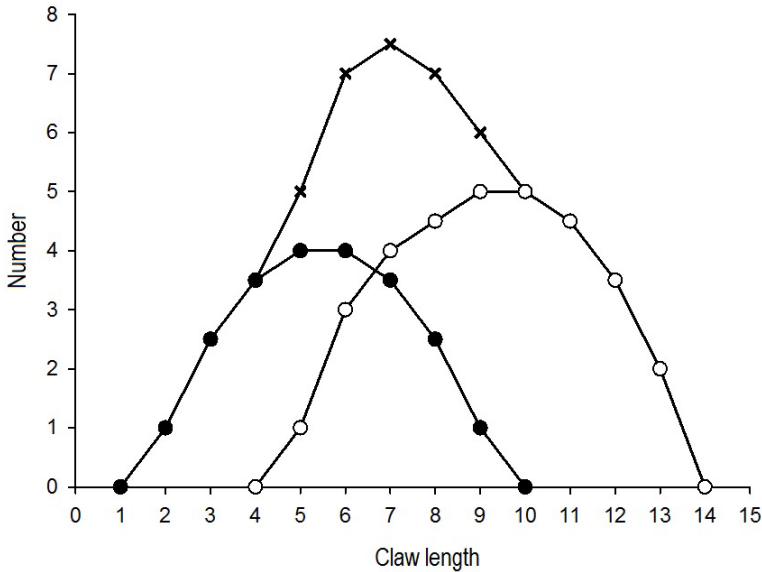


FIGURE 24. Schematic figure to show that two overlapping, bell-shaped curves may together produce one broader, bell-shaped curve.

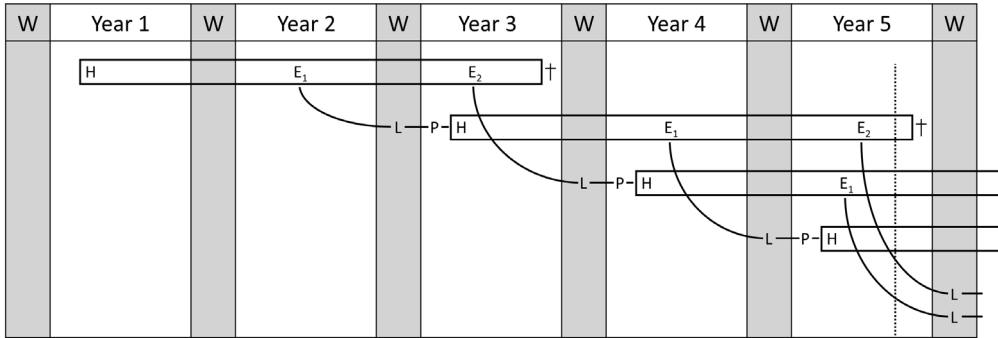


FIGURE 25. Phenological diagram for a species with long-lived adults that have two egg-laying seasons. The life of an adult beetle is within a frame, starting with hatching (H) in year 1. After overwintering (W), the first egg-laying (E1) occurs in year 2, and the second egg-laying (E2) in year 3 after another overwintering. L = overwintering larvae, and P = pupa. Since each generation of adults leaves two clutches of eggs, the number of simultaneous cohorts gradually increases. Late in year 5, as many as five cohorts may live together: Three age groups of adults and two groups of young larvae, from mothers of different age.

ground could be a combination of old, immigrated specimens with worn claws, and locally produced, small-sized specimens. Also *P. septentrionis* had slightly shorter claws on pioneer ground. None of the other species gave enough material on both sandy and vegetated ground to be tested for differences. Although the two mentioned

species have fully developed wings, flight may be absent, or rare. According to Lindroth (1945), *P. septentrionis* has been observed flying, but not *A. alpina*.

Lindroth (1945) stated that neither the two *Nebria* species had been observed flying, although their wings are fully developed. However, the

small *B. hastii*, which was numerous on open, pioneer ground, was referred to be an active flyer, which may explain its success as a pioneer species. The late colonisation by *C. vaporariorum* may be due to its lack of flight ability.

Compilation of ecological data for comparison between species

Table 4 gives an overview of ecological data for all nine species. Three species occurred along the whole successional gradient in the foreland, from 3 to 205 years: *N. nivalis*, *A. alpina*, and *A. quenseli*. *N. rufescens* and *P. septentrionis* colonised after 40 years, and *C. vaporariorum* after 63 years. A NMDS-plot showed high intercorrelation between the three significant environmental variables age, distance, and vegetation cover. The pioneers *B. hastii*, *N. nivalis*, and *A. alpina* were situated at the negative part of the first axis (Bråten et al. 2012). Up to about 40 years age, an organic soil layer was lacking, and vegetation was scarce. After 63 years, a thin layer of 1 mm was observed, and later, organic layers up to 19 mm were found, although local variation was large (Hågvar et al. 2009). *B. hastii* was only present as long as the vegetation was more or less open (until about 40 years). All other species accepted a closed vegetation, although colonising at different ages. In the Alps, Both Kaufmann & Juen (2002) and Gobbi et al. (2007) found that the age of the ground in a glacier foreland was an important factor for the distribution of carabid species.

All species were active throughout the snow-free period, but the time of peak activity differed somewhat. The two *Amara* species were most active in June or the first half of July. *C. vaporariorum*, *P. septentrionis* and *N. rufescens* had their highest activity around the first half of July. *N. nivalis* showed high activity on the moraine in July/August, but earlier on older ground (June/July). The small *B. hastii* was characteristic by a late maximum activity, at the hatching time in August. An interesting phenological aspect was the strong winter activity of the last instar larvae of *P. septentrionis*, and of adults as well (Figure 17). The assumption is that this was due to activity beneath snow, since catches were low just before

snow fall and just after snow melt. Also a few large larvae of the two *Nebria* species were trapped during winter, but none from other species. On snow-free ground, only few carabid larvae were trapped. Most belonged to *A. quenseli*, with a mix of stages throughout the season.

The two *Nebria* species seemed to hatch mainly in July. *B. hastii* and *P. septentrionis* were “late hatchers”, mainly in August. Our assumption of August/September-hatching in *A. alpina* is supported by Lindroth (1945). The few *C. vaporariorum* teneral also indicated late hatching. *A. quenseli* may have unsynchronized hatching, with teneral collected partly early, and partly late in the snow-free season.

Full-sized eggs were recorded in all seven species throughout large parts of the snow-free season, indicating a long egg-laying period and high overlap between species. Although the maximum number of mature eggs in one female could be as high as 6 in the small *B. hastii* and 22 in the large *N. nivalis*, the mean number of eggs per female (with empty females included) was low in all species and rarely exceeded three. *A. quenseli* deviated from the other species by having mature eggs in many females rather late in the season. July was evidently important for egg-laying in all species. In this month, the surface activity of females was rather high for all species, and the majority of females contained mature eggs. The long egg-laying period for all species may be due to a slow egg production, indicated by rather few mature eggs per female at any time. This might have been compensated by egg-laying also in the following year.

The percentage of males was most often below 50. A large material of *B. hastii* throughout four sampling periods showed rather stable values of 30–44 % males. Also *A. quenseli*, with several high catches, had similar values (31–43 %). Even *N. rufescens* had low male fractions, while the four remaining species had one or more sampling periods where males dominated.

In literature, the term “breeding season” is often used for the time of highest pitfall catches. However, the term “breeding” is unprecise. Is it the time of copulation, egg-laying, or hatching? A high surface activity might as well be due to

TABLE 4. Parameters that characterize each of the nine carabid species. Some data are from literature.

Parameter	<i>Bombidion hastii</i>	<i>Nebria nivalis</i>	<i>Nebria rufescens</i>	<i>Amara alpina</i>	<i>Amara quenseli</i>	<i>Pterobius septentrionalis</i>	<i>Cymindis vaporariorum</i>	<i>Pelophilus boettii</i>	<i>Notiophilus aquaticus</i>
MORPHOLOGICAL									
Mean body length (mm)	5	10	11	9.5	7.5	9	9	10.5	5
Fully winged?	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Dimorph (Lindroth 1945)
TEMPORAL									
Highest catches of adults	Aug. and Sep.	Medio Jun. - medio Aug.	Jul.	Jun.-Jul.	Jun.-Jul.	Jul.	Jun.-Aug.	Late Jun.-early Jul.	Jun.-Jul.
Egg-laying time (females with full-sized eggs)	Jul.-Aug.	Medio Jun. - medio Aug.	Jun. and Jul.	Jul.	Jun.-Sep.	Jun. and Jul.	Medio Jun.-medio Aug.	Jul.	No data
Hatching time (teneral)	Aug.	Jul.	Jul.	Aug.-Sep?	Jun.-Sep?	Aug.	Aug.-Sep?	No data	No data
Dial activity (Ottesen 1985; Lindroth 1945, 1986; Andersen 1970)	Nocturnal	Nocturnal	Nocturnal	Nocturnal	Nocturnal	Nocturnal	Nocturnal	Nocturnal	Diurnal
Winter-trapped adults	Few	Few	Some	Few	Few	Many	Few	Few	Few
Winter-trapped larvae	None	Few	Few	None	None	Many	None	None	None
Summer-trapped larvae	None	Few	None	Few	Some	Few	None	Few	None
From egg to egg (years)	?	2	2	2?	2-3?	2	?	1 (Somme 1989)	No data
SPATIAL									
Successional site age (years)	3-40	3-205	40-205	3-205	3-205	40-205	63-205	79-205	63-205
Vegetation cover (%)	0-10	0-100	10-100	0-100	0-100	10-100	90-100	90-100	90-100
Depth of organic soil (mm)	0	0-19	0-19	0-19	0-19	0-19	1-19	4-19	1-19
Site age at highest catch (years)	3	79	79	205	79	79	160	79	63
Moisture preference (Bråten et al. 2012, Lindroth 1945)	Hygrophilic	Hygrophilic	Hygrophilic	Tolerant	Xerophilic	Hygrophilic	Xerophilic	Extremely hygrophilic	Xerophilic
Cold tolerant? (Krogerus 1960)		Yes, prefers 5 °C	Yes, prefers 8 °C						
Alpine/lowland (various literature)	Mainly alpine, but also lowland	Alpine, mainly upper zone	Alpine and lowland	Alpine	Alpine and lowland	Alpine and lowland	Alpine and lowland	Alpine and lowland	Alpine and lowland
Highest altitude (m) (Ottesen 1985, 1996, present study)	?	1700	1550	1700	1550	1625	1500	1340	1550
OTHER PARAMETERS									
Food habits	Predator	Predator	Predator	Omnivor	Omnivor	Predator	Predator	Predator	Predator
Max. ripe eggs per female	6	7	22	10	18	14	10	11	No data

high feeding activity. For instance, females which hibernate before egg-laying would need to feed intensely during spring to build up fat reserves and develop their ovaries. The term “breeding season” has been avoided in the present study. Instead, the phenology of egg-laying by the presence of mature eggs, and hatching time by documenting teneral has been described. For most species, there was a good overlap between highest catches and the most intense egg-laying period. However, in *B.*

hastii, highest catches were at the hatching time, after the main egg-laying period. The population increase due to hatching, combined with an ability to run fast in this small species, may explain this.

Niche segregation

Background

The niche concept is a matter of definition. A broad

definition may include factors like geographical distribution and altitudinal zonation, but here we look for ecological differences between species within a given glacier foreland.

In the Rootmos glacier foreland of the Austrian Alps, Kaufmann & Juen (2002) studied habitat use and niche segregation among five carabid species of the genus *Nebria*. Several important niche factors were common to the present study: moisture, vegetation cover, temperature, and substrate. *N. jockischii* Sturm, 1815 and *N. germarii* Heer, 1837 preferred young and cool sites with highly structured and often unconsolidated substrate. *N. rufescens* was, as in the present study, hygrophilic, and had a high tolerance to vegetation. In the Alps, it was a typical inhabitant of snowbed vegetation. *N. castanea* Bonelli, 1810 had an intermediate position between these two habitats. Finally, *N. picicornis* (Fabricius, 1792) showed almost no correlation with the other species, but was bound to riparian outwash areas. In a glacier retreat zone in the Zillertal Alps, Gereben (1994) likewise stressed the different habitat affinities of six *Nebria* species, and that coexistence was possible due to environmental heterogeneity.

In the same mountain area as in the present study, Erikstad *et al.* (1989) studied resource partitioning between seven carabid species from six different habitats. All species could be segregated by at least one of three niche dimensions: habitat use, seasonal activity, and body size (used as an indicator of food choice). Four species were common to the present study: *N. aquaticus*, *P. septentrionis*, *C. vaporariorum*, and *A. alpina*. Two of them, *A. alpina* and *C. vaporariorum* occurred only in the driest habitat of the actual study, but the former species was larger. *N. aquaticus* was separated from the others by its small size and by being active at day time. As in the present study, *P. septentrionis* was hygrophilic.

Close to the present study site, covering 47 sampling sites and including more than 21 000 specimens, Ottesen (1996) searched for niche segregation in terrestrial beetles in relation to environmental gradients and phenology. Thirteen species of Carabidae were covered, and included all in the present study except *B. hastii*. Niche

segregation was studied based on guild, soil humidity preference, seasonal activity pattern, and altitudinal range. Most species were well separated along one or more of these niche dimensions. Ottesen (1996) concluded that soil moisture was the most important environmental factor for surface active beetles in the actual mountain area. Therefore, let us look closer at the moisture parameter in our study.

How precise is moisture as a niche factor?

Table 2 showed that xerophilic and hygrophilic species could be clearly identified from quantitative trapping data. A statistical analysis by Bråten *et al.* (2012) based on soil water data measured close to individual traps, came to corresponding results for *A. quenseli*, *C. vaporariorum*, and *P. septentrionis*. Also, older pitfall-studies from different habitats in this mountain area have confirmed moisture preferences in several carabid species (Erikstad *et al.* 1989, Ottesen 1996, and Table 5 compiled from Østbye & Hågvar (1996)).

Moisture preferences imply that topography influences the structure of the carabid community. In the actual glacier foreland, there is a “dry successional pathway” on dry ridges, and a “moist successional pathway” in moist depressions. These pathways have several species in common, but a different community structure (Hågvar *et al.* 2017). In the big picture, soil moisture matters.

However, as shown in Table 3, species with different moisture preferences often occurred in the same trap. There may be several reasons for this. Preferences are not absolute, and single individuals may sometimes pass through unfavourable habitats (the wingless *C. vaporariorum* must disperse by foot). Also, large parts of the foreland have a “medium” moisture which may be tolerable for both xerophilic and hygrophilic species. Furthermore, several of the species are active during night (Ottesen 1985), when hygrophilic species are favoured by the formation of dew and may use “dry” habitats for some hours. Finally, during snow melt and in rainy periods, soil moisture is high over large areas. The combined result is that soil humidity does not separate species in space as clearly as

TABLE 5. Number of individuals trapped during three snow-free seasons (1969–1971) near Finse in five different habitats. Compiled from Østbye and Hågvar (1996).

Species	Pioneer ground <200 yr (dry)	Oligotrophic heath (dry)	Eutrophic meadow (moist)	Snow bed (moist)	Tussock habitat (wet)
<i>Patrobus septentrionis</i>	21	22	273	140	149
<i>Notiophilus aquaticus</i>	65	2	23	7	3
<i>Amara alpina</i>	228		185		22
<i>Cymindis vaporariorum</i>	2				
<i>Nebria nivalis</i>			2		
<i>Nebria rufescens</i>				1	
<i>Pelophila borealis</i>					3

preference data might suggest.

Species with similar moisture preference may, of course, differ in microhabitat. For instance, the two xerophilic species *C. vaporariorum* and *A. quenseli* were both trapped in 46 % of the traps, but occurred together in only 28 %.

Unique combinations for each species

Table 4 allows us to extract parameters, or combinations, that are unique for each species:

Bembidion hastii is unique by being restricted to open pioneer ground, and gives up when the vegetation becomes more or less closed. It is the only species which is physically separated from certain other carabid species in the foreland (*C. vaporariorum*, *N. aquaticus* and *P. borealis*). It is also a small species, and has the latest seasonal peak in surface activity. Larvae may have a cryptic, subterranean life, as they are not taken in pitfall traps although adult population was high.

Nebria nivalis is the most cold-loving species, a high-altitude pioneer known to be a typical inhabitant close to glaciers, and even hunting on snow fields (Østbye 1963). It has a high tolerance for open ground.

Nebria rufescens has a similar ecology to *N. nivalis*, but is a somewhat later colonizer.

Amara alpina is a generalist, both regarding successional stage, vegetation cover, and moisture. It is an omnivore species (Hågvar & Pedersen 2015). Although occurring along the whole gradient, catches was highest at the oldest sampling site (205 years).

Amara quenseli has some characters in common with *A. alpina*: It is a generalist with respect to successional stage (although mainly in the medium range of the gradient, at 63 and 79 years), and it is omnivore (Hågvar & Pedersen 2015). However, *A. quenseli* is more xerophilic. Life cycle seems to be more opportunistic.

Patrobus septentrionis is unique by showing a considerable surface activity beneath the snow cover, both among adults and the third larval stage. This ability may reduce competition with other species, for instance by winter feeding.

Cymindis vaporariorum is separated from the other species by having lost the ability to fly. It is also the latest colonizer among carabids in the succession, and its activity is more evenly distributed throughout the snow-free season than in the other species. No larvae were trapped, indicating a cryptic life, perhaps within soil.

Pelophila borealis was trapped in the wettest sites and is an extremely hygrophilic species (Lindroth 1945, Ottesen 1996). This species is even able to hibernate enclosed by ice (Conradi-Larsen & Sømme 1973). It seems to be univoltine (Sømme 1989), which is special for such a large beetle at high altitudes.

Notiophilus aquaticus is a small, xerophilic, late colonizer. It is the only diurnal species among the nine (Ottesen 1985).

This means that within any species pair, there are certain ecological differences. Let us look at some of the most frequent species combinations. According to Table 3, *P. septentrionis* and *A. alpina* was the most common combination in

the foreland, as they occurred together in 59 % of the traps. Their diet separates the species, as the first is predator and the second omnivore. *P. septentrionis* is also characteristic by its winter activity in both larvae and adults, and by being more hygrophilic than *A. alpina*. Surprisingly, *P. septentrionis* was trapped together with the xerophilic *C. vaporariorum* in 43 % of the traps. The easiest explanation is that *P. septentrionis* is a very abundant and active species, also visiting dry patches outside its preferred moisture (at least by a few individuals). The xerophilic character of *C. vaporariorum* will limit their coexistence, and the latter is also more active late in the season. In this way we can check all species pairs with high spatial overlap in Table 3 and always find ecological differences between them in Table 4.

Important ecological factors that contribute to niche segregation seem to be: preference for open space, occurrence along the successional and time gradient, humidity preference, temperature preference, nocturnal activity versus diurnal, flying ability, predators versus omnivores, phenology, and the ability to be active under snow.

The present study adds several ecological parameters to earlier studies of carabid beetles in this mountain area (Erikstad 1989, Ottesen 1996): succession, winter activity, some information on larval stages and their activity, hatching time, egg-laying period, feeding habits, and longevity. Each species has achieved a more detailed “niche profile” (Table 4). Furthermore, the study has illustrated the large spatial overlap between species (at least by a few individuals), including “xerophilic” and “hygrophilic” species, and we have questioned the meaning of the term “breeding season”.

Some niche parameters from our study (Table 4) were not quite in accordance with earlier studies. *A. alpina* behaved as a xerophilic species in the habitats selected by Erikstad (1989), and as a rather hygrophilic species in the study of Ottesen (1996). Our data indicated “no moisture preference”, which may explain the discrepancy. Furthermore, highest catches generally occurred earlier in the study of Ottesen (1996), due to his sampling in warm, south-faced hills, contrary to our north-faced or flat sites. Another point is that

maxima may differ in time from year to year due to climatic differences (Østbye & Hågvar 1996, Erikstad *et al.* 1989). This shows that choice of habitats and years may affect the conclusions about preferences, phenology, and niches.

Further research

The larval ecology may be an important part of the niche profile of each species. Pitfall trapping indicated low surface activity of larvae, except for the high winter catches of *P. septentrionis* larvae. There is obviously a need to assess the subterranean habitat requirements of larvae (Kaufmann & Juen 2002). Furthermore, winter ecology is generally a neglected topic. It might be advantageous for both larvae and adults of *P. septentrionis* to be able to feed beneath snow, and to achieve a good start at snow melt. In coniferous forest, for example, several invertebrate groups, including beetles, have been found to be active in the subnivean air space, and even feeding. This is possible since ground temperature remains close to 0°C under a sufficiently thick snow cover (Hågvar & Hågvar 2011).

Food choice is a good parameter to separate species ecologically. However, are differences in body size a good indicator for different food choice, as used by Erikstad *et al.* (1989)? Of course, small carabids cannot handle large prey, but both can handle small prey, and also share it without competition if it is abundant. Based on gut content analyses, Hågvar & Pedersen (2015) found that on pioneer ground, the large *N. nivalis* and the small *B. hastii* had very similar gut contents, dominated by small chironomid midges (Diptera). Direct study of crop and gut contents should be given priority in the search of niche differences. Another approach is DNA-analysis of regurgitated crop content, which was demonstrated for alpine carabids in Austria (Raso *et al.* 2014). An interesting aspect was the documentation of intraguild predation.

Even though Table 4 lists several ecological parameters for each species, we do not know which factors are the most important, and whether quite other parameters matter more.

What really separates species ecologically in the

field, is perhaps only possible to decide through experiments and manipulation. An overlap in parameters like moisture preferences, phenology, food choice, etc. may not be problematic if space and food are sufficient. Limiting factors could for instance be access to suitable hiding places during day, various parameters which are connected to larval life, or other factors that are not measured by the present type of field study, like predation or climate.

The question of competition is hard to study. Neither the present study, nor Erikstad *et al.* (1989) or Ottesen (1996) documented that competition occurs. One possibility, suggested by Erikstad *et al.* (1989), could be to study the effect of removing one or several species by extensive and selective trapping.

Prolonged adult life is an interesting topic, and touches the question of k-strategies among carabids (Davies 1987, Schatz 1994). In the present material, even the oldest females with shortest claws often contained fully developed eggs. A good marking-recapturing method is needed to assess longevity with certainty. The large *Nebria* species could be good candidates for such a study. An adult longevity of three years could be expected from the wide range of claw lengths.

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