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Autor: Kaufmann, Rüdiger / Juen, Anita

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Habitat use and niche segregation of the genus *Nebria* (Coleoptera: Carabidae) in the Austrian Alps

RÜDIGER KAUFMANN & ANITA JUEN¹

Occurrence of carabid beetles of the genus *Nebria* was investigated in the Austrian Central Alps (Obergurgl, Tyrol) by pitfall trapping and by manual sampling. Focusing on a single glacier foreland at about 2300 m a.s.l. highly species specific and stable small-scale (1–2 km) distribution patterns were linked to local environmental conditions. Local species associations were compared with patterns on a regional scale (≈ 15 km) comprising a variety of alpine habitats within an altitudinal range from 1800 to 3000 m a.s.l.

All five species found regionally were also present in the glacier foreland: *N. picicornis*, *N. jockischii* and *N. rufescens* usually characterised as ripicolous species, *N. germari* and *N. castanea* as high alpine species. Similarities of spatial distributions, however, did not reflect this grouping, neither locally in the glacier foreland nor on the landscape scale. Members of the genus *Nebria* were the dominant epigeic species near glacier fronts.

In the almost level glacier foreland species composition was determined by the status of soil formation, vegetation development, and the local moisture and temperature regimes. Since altitude was the dominating factor on the landscape scale, species associations appeared different in the glacier foreland and regionally. It is concluded that the heterogeneous conditions of glacier forelands facilitate co-occurrence of species which are otherwise largely separated by their different altitudinal ranges. Only *N. rufescens* was found to be strictly hygrophilic; *N. castanea* exhibited the most eurytopic pattern.

The life-cycle of all species found at this altitude was biennial. However, differences were found in the timing of their reproduction period following snow-melt and the larval stages which overwinter. Surface activity of the larvae was much higher in *N. rufescens* than in the other species.

Niche separation within these alpine habitats appears to be governed by environmental conditions. Subtle differences of life-cycles may be important with only 3 months of growing season. There were no indications that interspecific interactions, competition in particular, were important in structuring communities.

Keywords: Carabidae, ground beetles, *Nebria*, niche segregation, spatial pattern, alpine zone, glacier foreland, primary succession, life-cycle.

INTRODUCTION

Carabid beetles of the genus *Nebria* commonly occur in riparian and alpine habitats of the northern hemisphere (KAVANAUGH 1979). They cover a wide altitudinal range and typically occupy sites with sparse vegetation, such as gravel bars, scree, and boulders (BRANDSTETTER et al. 1993; MARGGI 1992). In a previous analysis of succession patterns on Rotmoos glacier foreland in the Austrian Central Alps several representatives of the genus *Nebria* appeared as dominating species within the epigeic fauna in pioneer and early successional communities (KAUFMANN 2001). Indications of highly specific, small-scale occurrence patterns of the congeneric species on mostly barren moraine grounds of similar appearance motivated a more detailed analysis of this niche segregation.

¹ Institute of Zoology and Limnology, University Innsbruck, Technikerstr. 25, A-6020 Innsbruck

Similar species-specific patterns were previously reported by GEREKEN (1994, 1995) from another Central Alpine glacier foreland with a slightly different set of species. She attributed them to local habitat properties and proposed to distinguish two ecological types of alpine *Nebria* species: (1) ripicolous species which in the alpine zone favour habitats similar to riparian ones and maintain an affinity to running water, and (2) high-alpine species, usually brachypterous, occurring above the treeline on more stable substrates. Of the five species found in the area of the current investigation, *N. picicornis* (FABRICIUS, 1801), *N. jockischii* STURM, 1815, and *N. rufescens* (STROEM, 1768) belong to the ripicolous type, while *N. germari* HEER, 1837, and the eurytopic *N. castanea* BONELLI, 1809 are high-alpine species. The former are restricted to altitudes below 2200 to 2400 m a.s.l., while the latter extend into the nival zone above 3000 m a.s.l. (BRANDSTETTER et al. 1993; MARGGI 1992). Recently deglaciated areas in glacier forelands are habitats where both these groups meet and overlap. These habitats are in many ways similar to riparian habitats, but they also have characteristics of the high-alpine and sub-nival belt.

With the high-alpine situation in mind, the most promising hypotheses about mechanisms of niche segregation include (1) specific preferences or preadaptations to local abiotic conditions, (2) preferences for locally available food resources or other biotic conditions, and (3) interspecific competition for living space or food availability induced by limitations of these resources. Even though abiotic limitations are usually considered more important in harsh environments than biotic interactions, competition cannot be ruled out entirely as a factor structuring communities. A comprehensive assessment of the first and to some extent also the second hypothesis seemed feasible by a detailed analysis of trapping material and environmental data available from the previous local-scale (1–2 km) study of glacier foreland succession (KAUFMANN 2001) in comparison with additional observations and manual collections from other nearby glacier forelands and alpine areas (scale 15 km). Factor analyses should clarify the environmental determinants of species associations on both scales. Life-history traits should be compared among species since they are considered crucial adaptive features of high alpine carabids (SOTA 1996). Concerning the third hypothesis on interspecific interactions, which in principle cannot be proved by a descriptive approach, only hints were to be expected from an analysis of the information available. Nonetheless, species overlaps together with habitat preferences over the entire life-cycle, as well as phenological traits might yield tentative indications.

METHODS

Study area

The focus area of this study was the glacier foreland of Rotmoos glacier (2300–2450 m a.s.l.) in the Austrian Central Alps near Obergurgl, Ötztal, Tyrol (46°52' N, 11°02' E). This area represents a successional chronosequence covering about 150 years of glacial retreat. Additional high-alpine locations in the surroundings and other tributary valleys of Gurgl valley with or without recently deglaciated areas (Langtal, Rotmoostal, Gaisbergtal, Verwalltal, Königstal, Soom/Zirmkogel, Ramolkar) were surveyed for the occurrence of *Nebria* species (1800–3100 m a.s.l.). All sites (except one riparian gravel bar) were situated above the treeline. They included rocky terrain, scree, moraine till, riparian banks, and alpine grassland or heath; bedrock consists of quartzo-feldspatic amphibolite minerals (HOINKES &

THÖNI 1993). The snow free period in Rotmoos glacier foreland usually lasts from late June to September. Annual mean temperatures are around -1.5°C with summer means (June–August) around 6°C . Long term average precipitation in the region is 820 mm per year.

Sampling

The epigeal fauna in the Rotmoos glacier foreland was sampled using pitfall traps (diameter 7 cm). In 1995 27 traps were installed, in 1996–1998 70 traps (Figs. 1A–C) were in operation over the entire growing season from the end of June to late September or early October. Samples were taken at 14-day intervals (approximate). For each of the sampling sites in the Rotmoos glacier foreland local conditions were characterised in terms of vegetation cover, substrate texture and structure, soil parameters, temperature, moisture and sun exposure (quantitative or semiquantitative scales) (KAUFMANN 2001). Altogether 21 variables were used including indicator values for abiotic conditions derived from vegetation (LANDOLT 1977).

Pitfall trapping is considered to yield good estimates for relative abundances within species, provided that spatial resistances around the traps are similar, but does not necessarily reflect absolute densities of different species (see e.g. GREENSLADE 1964; THIELE 1977; BAARS 1979; LOREAU 1992). Similarly, in comparisons between adult and larval life stages pitfall catches show relative surface activities rather than abundances.

The regional survey conducted in July 1999 was done by manual sampling for 30 minutes per site. This data set was supplemented by data obtained by pitfall trapping (14 days) for Langtal (June 1996), Ramolkar (July 1998), and Soom-Zirmkogel (July 2000) (Fig. 2).

Species determination was done according to the key of FREUDE et al. (1983) supplemented by LOHSE & LUCHT (1989). Larval stages were determined with the help of CHARLES HUBER (Natural History Museum, Bern, Switzerland).

Calculations and statistics

Similarities of species distributions were calculated across all sites (pitfall traps or manual collection sites) using RENKONEN's percent similarity ($1-D_9$) for quantitative data and SØRENSEN coefficient (S_8) for presence/absence data (LEGENDRE & LEGENDRE 1998). Total catches of traps from 1996 to 1998 were used to compare species, stability of these similarities was assessed by yearly catches. Cluster analyses were based on unweighted pair group averages (UPGMA). Ordination of similarities was done by principal coordinates analysis (PCO) on two axes MVSP 3.1 (KOVACH 1998) being used for these analyses.

Correlations between species abundances and environmental factors were analysed by principal components analysis (PCA) using Canoco 4.0 (TER BRAAK & SMILAUER 1998). Because of the large number of environmental variables (in comparison to the number of sampling sites) a canonical analysis seemed inappropriate and a screening for possible influences was done by passive analysis. Species data were square-root transformed. The altitudinal gradient for the regional survey was analysed and tested by canonical correspondence analysis.

For comparisons of sex ratios and proportions of larval stages between species χ^2 -tests were employed. Where multiple comparisons were made in a post-hoc manner significances were down-scaled by BONFERRONI correction.

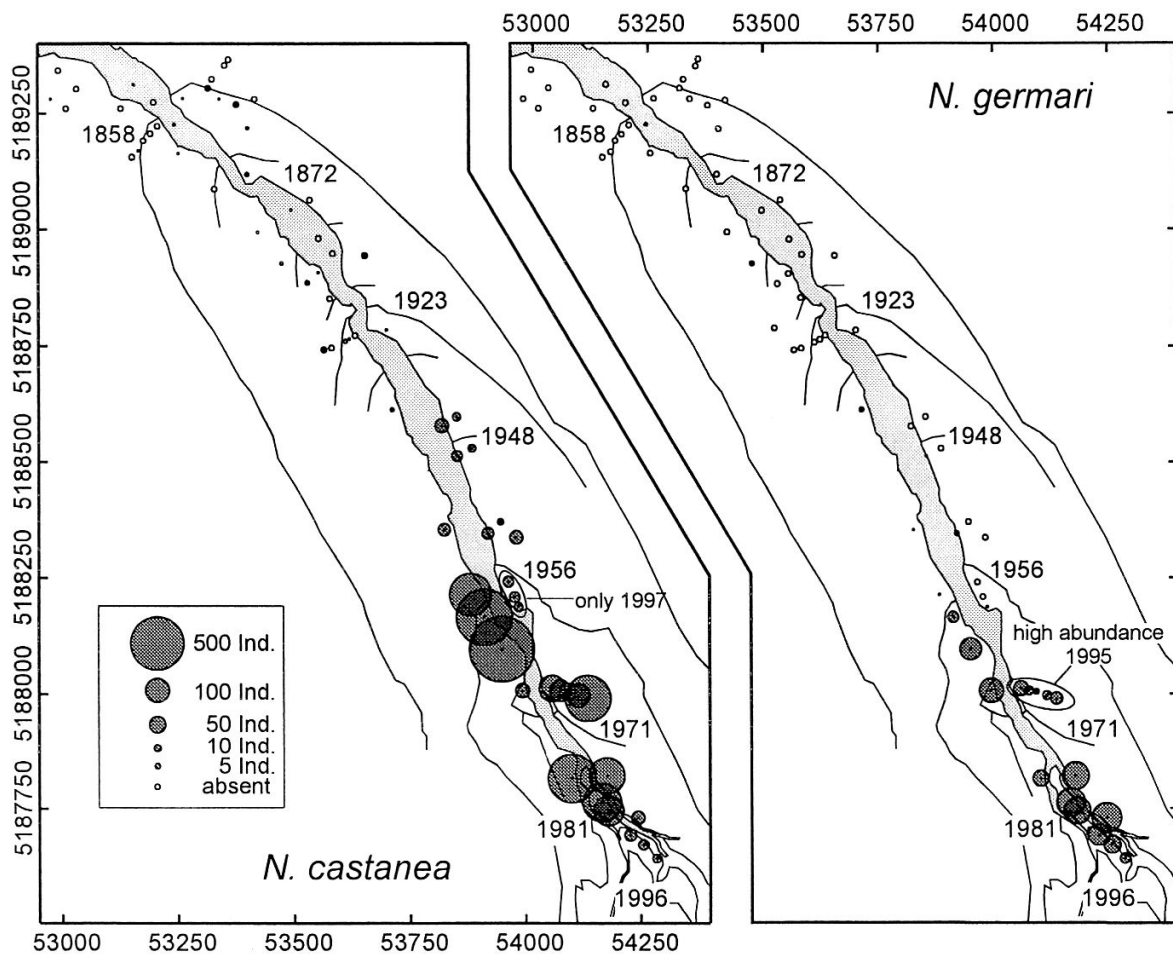


Fig. 1A. Distribution pattern of *Nebria castanea* and *N. germari* within the Rotmoos glacier foreland. Total catch of adults 1996–1998 (symbol size reflects number of individuals), small open symbols denote absences. Positions of glacial retreat are indicated (JÜEN 1998, PATZELT pers. comm.), the shaded area marks the alluvial outwash plain of the glacial stream. GAUSS-KRÜGER coordinates (Austrian datum) are in meters.

Partial redundancy analysis (RDA) in combination with significance tests by Monte Carlo resampling (Canoco 4.0) was employed to separate interaction effects of co-occurring species from environmental effects.

RESULTS

Spatial distribution patterns in Rotmoos glacier foreland

Species of *Nebria* dominated in recently deglaciated and successional young sites and were also present in outwash areas of the glacier brook and tributaries. They were less abundant, but still present, in sites with a fully developed cover of vegetation. Each species had a distinct distribution pattern (Figs. 1A–C).

Two species pairs had considerable overlap in their occurrence patterns (Fig. 3). The first pair were *N. castanea* and *N. rufescens* (Figs. 1A–B, Fig. 3). Both occurred mainly at 20–40 year old sites and were then present over the whole area (*N. castanea* was found at almost all, *N. rufescens* at most of the sites), but *N. castanea* extended much further into the young and pioneer sites where *N. rufescens* was rare. *N. rufescens*, on the other hand, was more frequent in the outwash sites (but not consistently so). The second pair with high similarity, *N. germari* and *N. jockischii*, co-occurred at the youngest sites (ice free < 15 years). Distinct differences were that

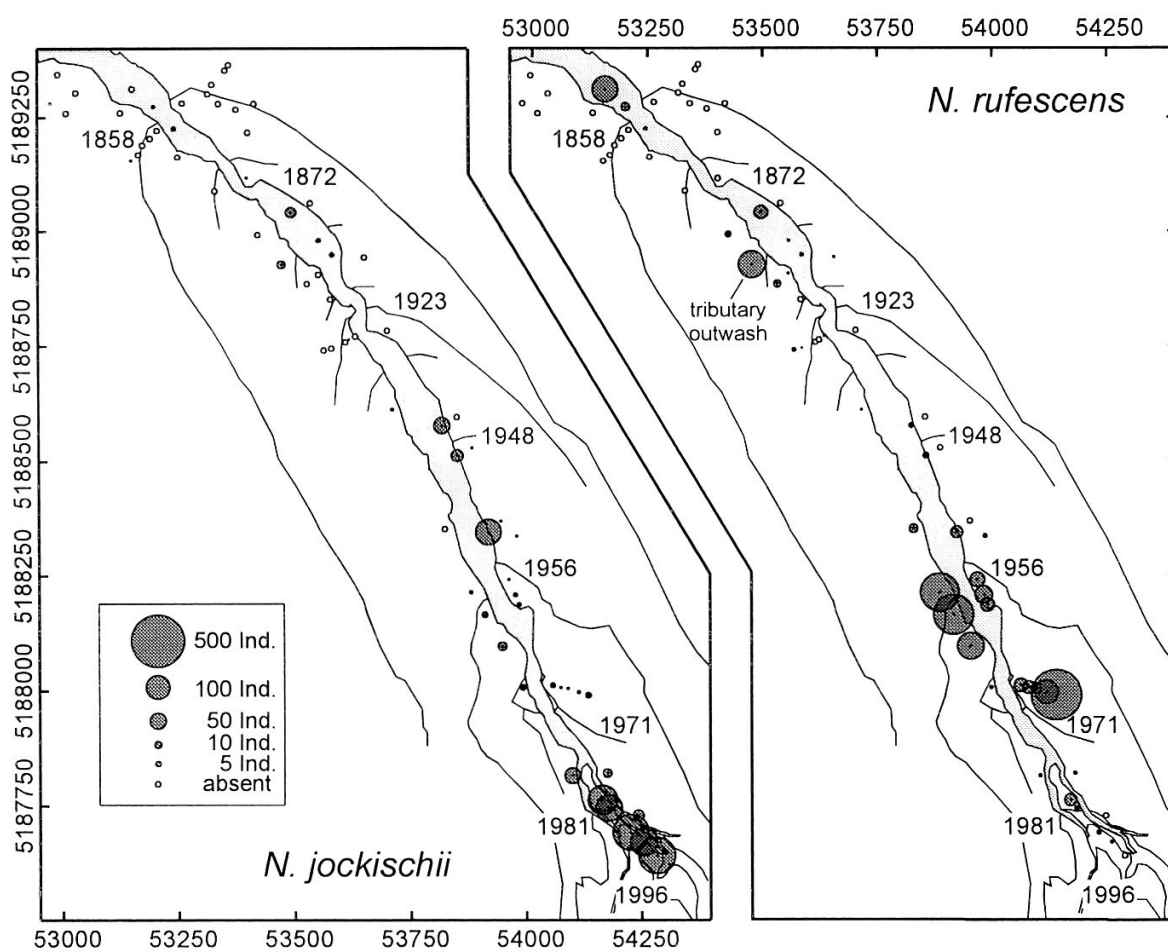


Fig. 1B. Distribution pattern of *Nebria jockischii* and *N. rufescens* within the Rotmoos glacier foreland. Symbols and notation as in Fig. 1A.

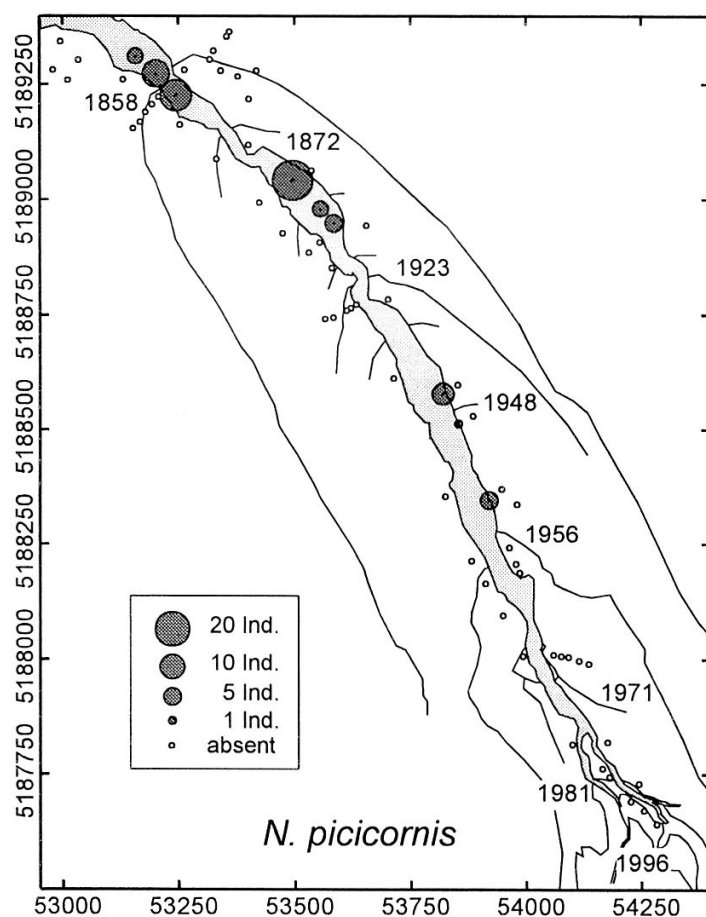


Fig. 1C. Distribution pattern of *Nebria picicornis* within the Rotmoos glacier foreland. Symbols and notation as in Fig. 1A.

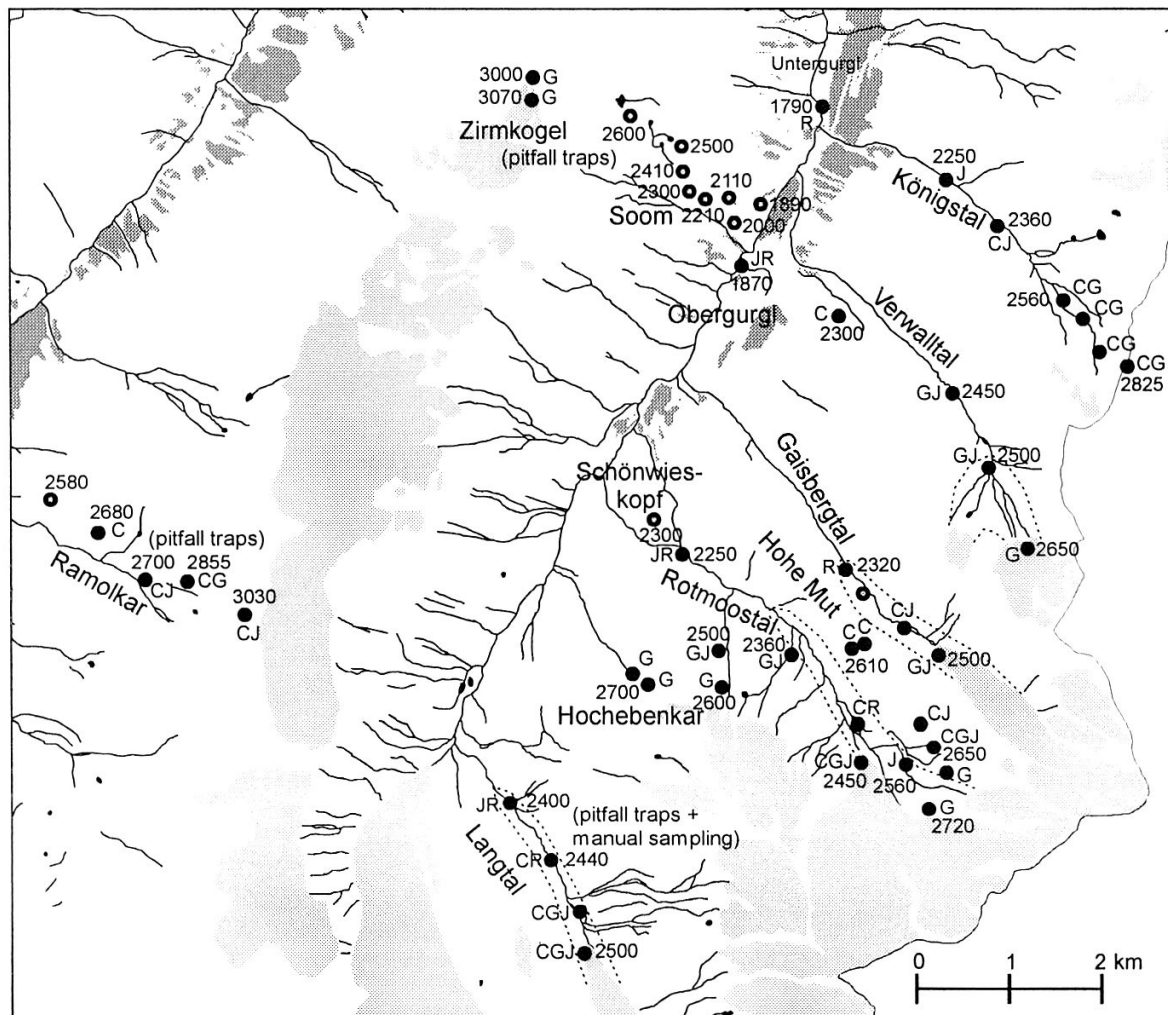


Fig. 2. Survey of the distribution pattern of *Nebria* species in the surroundings of Obergurgl, Ötztal, Tyrol. Codes for presence C: *Nebria castanea*, G: *N. germari*, J: *N. jockischii*, R: *N. rufescens* (open circles: no *Nebria* found). Results from manual collections in 1999 (30 minutes per site) together with pitfall catches (14-day) obtained between 1996 and 2000. Numbers give altitude (m a.s.l.). Light shading: glaciers. Dotted lines: glacier forelands. Dark shading: forests.

N. germari had much higher abundances in the age range 20–40 years, but was absent at older sites where *N. jockischii* was still caught sporadically, and that *N. jockischii* was more conspicuously present in the outwash sites. *N. picicornis* showed a distinct pattern with its exclusive occurrence in the outwash plain of the glacial stream (Fig. 1C); it was caught much less often than the other species.

The three species commonly characterised as ripicolous (*N. jockischii*, *N. rufescens*, and *N. picicornis*) exhibited quite different distribution patterns. They overlapped in the central outwash plain, but usually when one of the species was very abundant the other two occurred in low numbers only. Within the two high alpine species, *N. germari* occupied a subsection of the distribution range of *N. castanea*; while the first was restricted to barren moraines, the latter preferred initial vegetation and extended into mature sites.

The species specific spatial patterns remained quite stable over the years with only minor fluctuations as shown by ordination of year to year similarities (PCO on percent similarities, Fig. 4). *N. castanea* was only present at 3 sites about 40 years old in 1997, and *N. germari* was unusually abundant in a 25 year old area in 1995 (marked in Fig. 1A). Changes between the years 1995/1996 could be estimated only

Tab. 1. Niche overlaps of *Nebria* with other epigeic species in the glacier foreland. Numbers are percent niche overlaps (RENKONEN's percent similarity). Ranked are species with highest overlaps out of all species determined from pitfall samples.

<i>Nebria castanea</i>	<i>Nebria germari</i>
49.1 <i>Nebria rufescens</i> (Carabidae)	47.7 <i>Nebria jockischii</i> (Carabidae)
32.7 <i>Nebria germari</i> (Carabidae)	42.7 <i>Fleutiauxellus maritimus</i> (Elateridae)
32.7 <i>Fleutiauxellus maritimus</i> (Elateridae)	39.3 <i>Pardosa nigra</i> (Lycosidae)
27.0 <i>Amara quenseli</i> (Carabidae)	32.7 <i>Nebria castanea</i> (Carabidae)
21.9 <i>Nebria jockischii</i> (Carabidae)	25.3 <i>Mitopus glacialis</i> (Phalangidae)
19.2 <i>Mitopus morio</i> (Phalangidae)	25.1 <i>Erigone tirolensis</i> (Erigoninae)
18.2 <i>Bembidion bipunctatum</i> (Carabidae)	20.6 <i>Meioneta nigripes</i> (Linyphiinae)
16.4 <i>Pardosa nigra</i> (Lycosidae)	18.8 <i>Simplocaria semistriata</i> (Byrrhidae)
13.8 <i>Simplocaria semistriata</i> (Byrrhidae)	17.9 <i>Bembidion bipunctatum</i> (Carabidae)
12.7 <i>Mitopus glacialis</i> (Phalangidae)	17.4 <i>Nebria rufescens</i> (Carabidae)
<i>Nebria jockischii</i>	<i>Nebria rufescens</i>
47.7 <i>Nebria germari</i> (Carabidae)	49.1 <i>Nebria castanea</i> (Carabidae)
39.3 <i>Fleutiauxellus maritimus</i> (Elateridae)	36.9 <i>Bembidion bipunctatum</i> (Carabidae)
29.9 <i>Mitopus glacialis</i> (Phalangidae)	28.8 <i>Fleutiauxellus maritimus</i> (Elateridae)
25.2 <i>Pardosa nigra</i> (Lycosidae)	28.3 <i>Mitopus morio</i> (Phalangidae)
21.9 <i>Nebria castanea</i> (Carabidae)	22.7 <i>Amara quenseli</i> (Carabidae)
20.0 <i>Erigone tirolensis</i> (Erigoninae)	22.7 <i>Simplocaria semistriata</i> (Byrrhidae)
16.7 <i>Pardosa saturator</i> (Lycosidae)	17.8 <i>Pardosa nigra</i> (Lycosidae)
14.5 <i>Meioneta nigripes</i> (Linyphiinae)	17.5 <i>Pardosa saturator</i> (Lycosidae)
10.7 <i>Rhaebothorax paetulus</i> (Erigoninae)	17.4 <i>Nebria germari</i> (Carabidae)
10.4 <i>Nebria rufescens</i> (Carabidae)	15.5 <i>Rhaebothorax paetulus</i> (Erigoninae)
10.2 <i>Simplocaria semistriata</i> (Byrrhidae)	10.4 <i>Nebria jockischii</i> (Carabidae)
<i>Nebria picicornis</i>	
51.9 <i>Janetschekia monodon</i> (Erigoninae)	
37.1 <i>Pardosa saturator</i> (Lycosidae)	
25.2 <i>Bembidion incognitum</i> (Carabidae)	
17.8 <i>Mitopus glacialis</i> (Phalangidae)	

for the subset of pitfalls already installed in 1995.

Distribution overlaps (RENKONEN's index) of *Nebria* with other epigeic species are shown in Tab. 1. These similarities may be interpreted as niche overlaps. For all *Nebria* (except *N. picicornis*) a congeneric species showed the highest degree of overlap (approx. 50%) among the approximately 200 epigeic species determined. The other congeners also ranked among the 10 or 11 most similar species. This clearly shows that, despite differences of the inhabited areas, habitat requirements among the *Nebria* species present were very similar in comparison to other taxa.

Survey of the regional distribution

In order to compare habitat use on a landscape scale with the findings from the Rotmoos valley, a survey of the distribution pattern of *Nebria* species over a

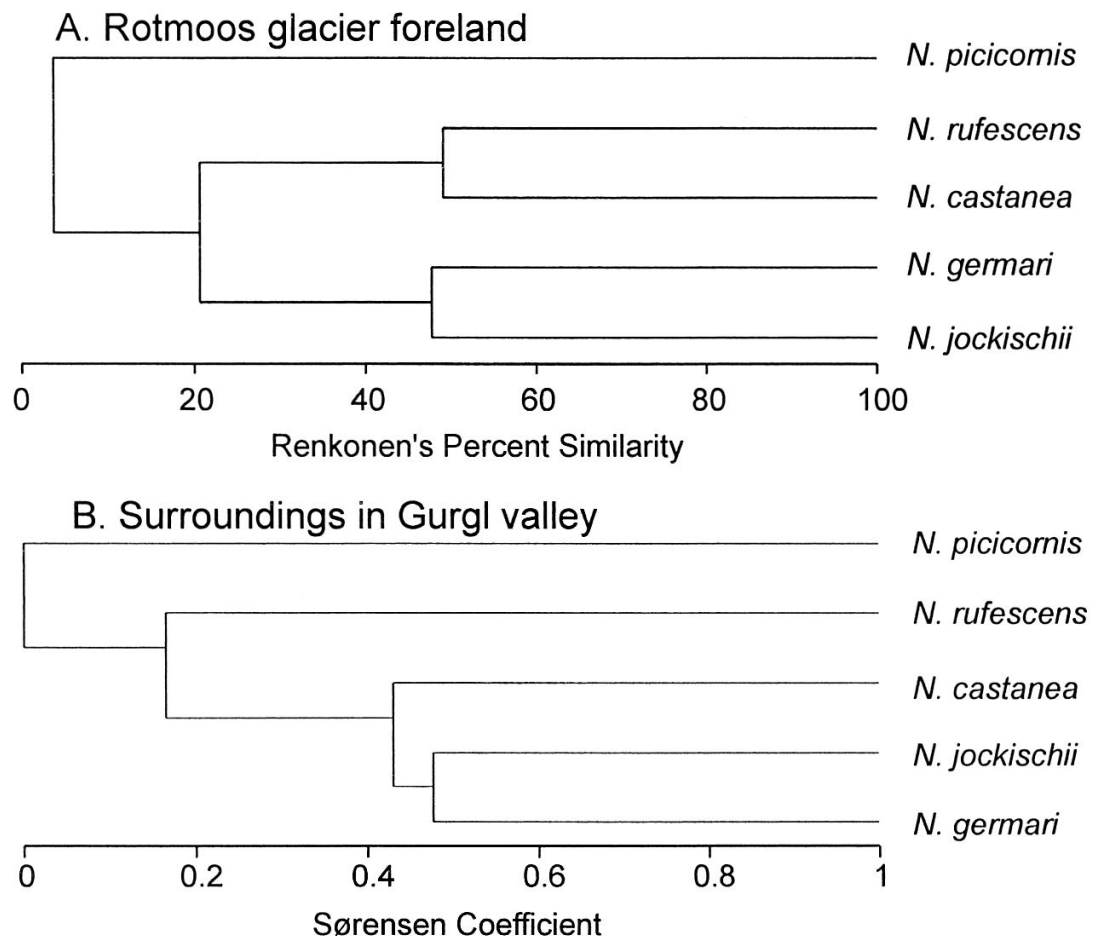


Fig. 3. Similarities of species distribution patterns (niche overlap) in Rotmoos glacier foreland (A) and in surrounding high alpine areas and neighbouring valleys and glacier forelands (B). Dendrograms by UPGMA-clustering of RENKONEN's percent similarities (A) (Rotmoos glacier foreland: pooled catches 1996–1998, sites of Fig. 1) and of SØRENSEN similarities (B) (other sites in Gurgl valley: presence/absence from manual sampling, sites of Fig. 2).

larger area in the Gurgl valley and its tributary valleys was conducted in 1999 supplemented by data from pitfall traps for some sites (Fig. 2).

In this survey *N. castanea*, *N. germari* and *N. jockischii* were all commonly found in screes or cobbles at higher altitudes. *N. castanea* was the only species found also in alpine grasslands. In contrast to the high similarity in Rotmoos valley, *N. rufescens* and *N. castanea* were quite different, since the former was restricted to lower altitudes and was only found near brooks and streams. Thus, a ripicolous occurrence pattern is confirmed for *N. rufescens*; although it was not found in similar habitats in the two northern tributary valleys (Königstal and Verwalltal). However, an absence cannot be deduced from this cursory survey. *N. picicornis* was only found on riparian gravel bars about 10 km downstream (near Zwieselstein, outside the map area of Fig. 2). It was also absent from manual collections in the Rotmoos valley, where it was known to be present in limited numbers (see above). Canonical correspondence analysis with Monte Carlo tests yielded altitude as the dominating gradient separating species ($p < 0.001$) followed by the presence of vegetation ($p = 0.0025$) affecting mostly *N. castanea*.

Biotic and abiotic factors

Principal components analysis (PCA) was used to analyse correlations among species occurrences and to relate them to a variety of biotic and abiotic site characte-

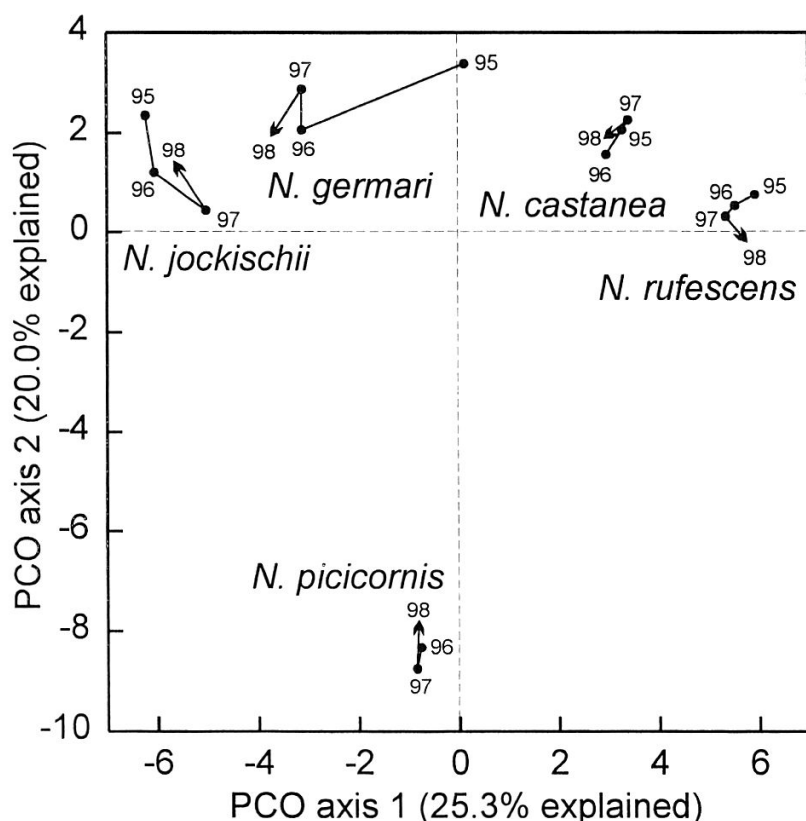


Fig. 4. Stability of spatial patterns in Rotmoos glacier foreland. Principal coordinates ordination (PCO) of percent similarities between yearly catches of adult (restricted subset of pitfall traps in 1995). Eigenvalues of axes are given as explained variability.

ristics (Fig. 5). This detailed analysis was done for the extensive data set available from Rotmoos glacier foreland. The preferred site conditions and influential factor complexes are summarised in Tab. 2 together with the typical habitat use derived from the survey of the surrounding areas.

The directions of species arrows in the ordination diagram again show the similarity between *N. germari* and *N. jockischii*, and between *N. castanea* and *N. rufescens*. In this analysis projections of the arrows upon one another approximate correlation coefficients, both for the species and for the environmental factors. Successional progress of soil formation, increasing vegetation cover, local moisture regime, and temperature appeared as major factor complexes. Nonetheless, correlations for most explanatory variables were moderate to low (< 0.5), indicating that local conditions can only partly explain the occurrence patterns. Indicator values for temperature and moisture obtained from the sparse vegetation (LANDOLT 1977) deviated from direct measurements of these parameters.

Obviously, successional site age was related to soil formation and soil organic content (loss on ignition) and a decrease of bare substrate rich in viable interstitial cavities (boulders, cobbles, gravel). Superimposed was a gradient with increasing temperatures and incident sun irradiation. Both *N. jockischii* and *N. germari* were strongly related to this gradient, preferring the young and cool sites with highly structured and often unconsolidated substrate. Almost orthogonal and thus statistically unrelated to this first gradient, was a factor complex consisting of soil moisture, prolonged snow cover and snowbed vegetation with which *N. rufescens* was strongly correlated. *N. castanea* was intermediate between these two with a somewhat greater similarity to *N. rufescens*. The sequence of the species along ordina-

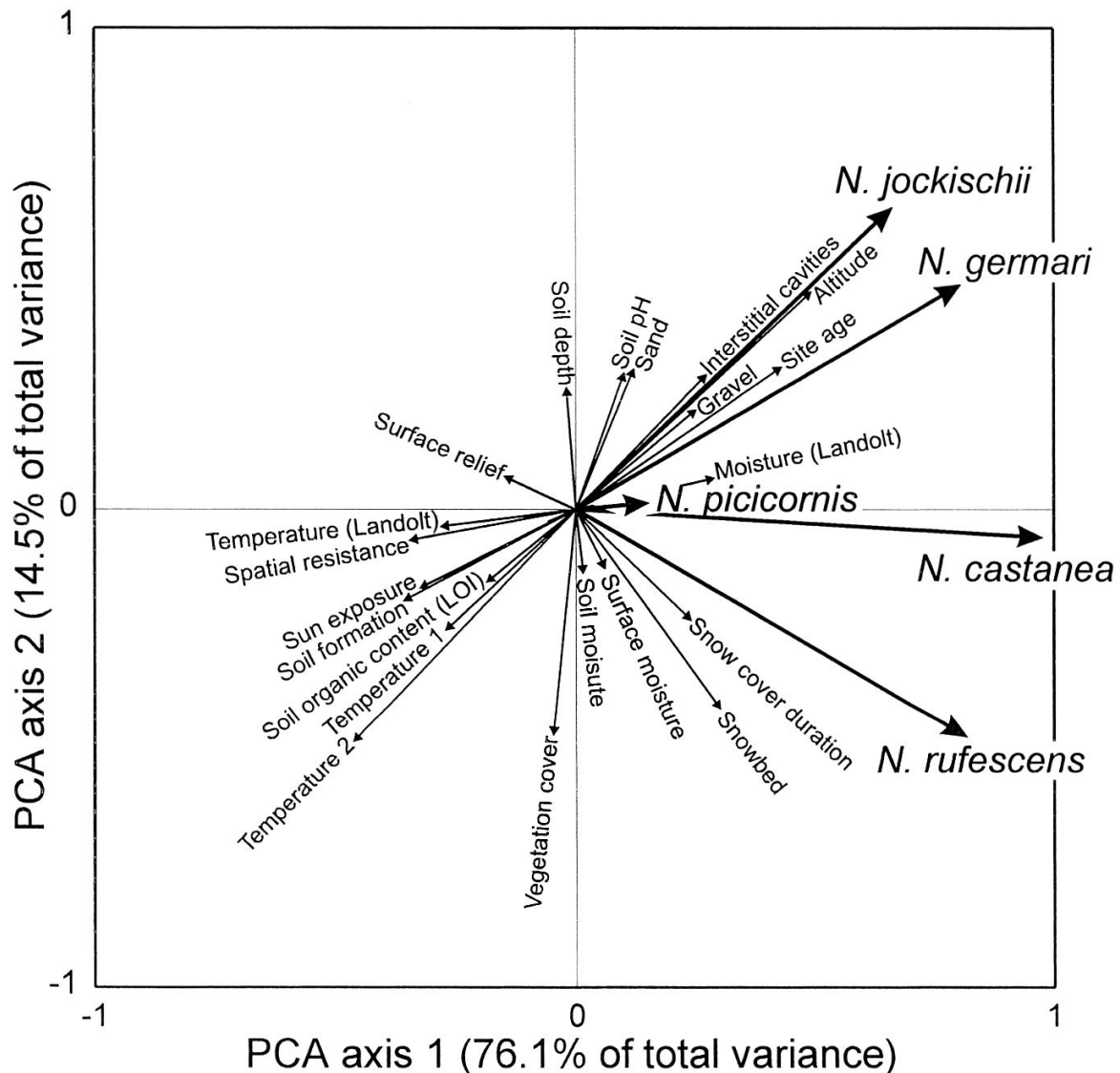


Fig. 5. Principal components analysis (PCA) of *Nebria* species from Rotmoos glacier foreland. Species correlations are shown together with passive analysis of environmental parameters (similarities of direction and arrow lengths approximate correlation coefficients). Eigenvalues of axes are given as percentage of total variance in species data.

tion axis 2 corresponding to vegetation cover discriminated the typical pioneer species of barren moraines, *N. jockischii* and *N. germari*, from *N. castanea* and *N. rufescens* with increasing tolerances to vegetation. *N. picicornis* showed almost no correlation with the other species, but appeared to be aligned with a third axis (not shown in Fig. 5) due to its exclusive occurrence in riparian outwash areas.

Looking for clues of competition, we tested for interactive effects among the *Nebria* species after accounting for all significant environmental factors. This was done separately for each species by partial canonical analysis (redundancy analysis) using all significant environmental variables (identified by forward selection) as covariates. We found no negative interactions as would have been expected with strong competitive effects.

Larval behaviour and developmental cycle in Rotmoos glacier foreland

Larvae of all species were present in pitfall catches. Their spatial patterns matched those of adults within the accuracy given by the limited number of larvae

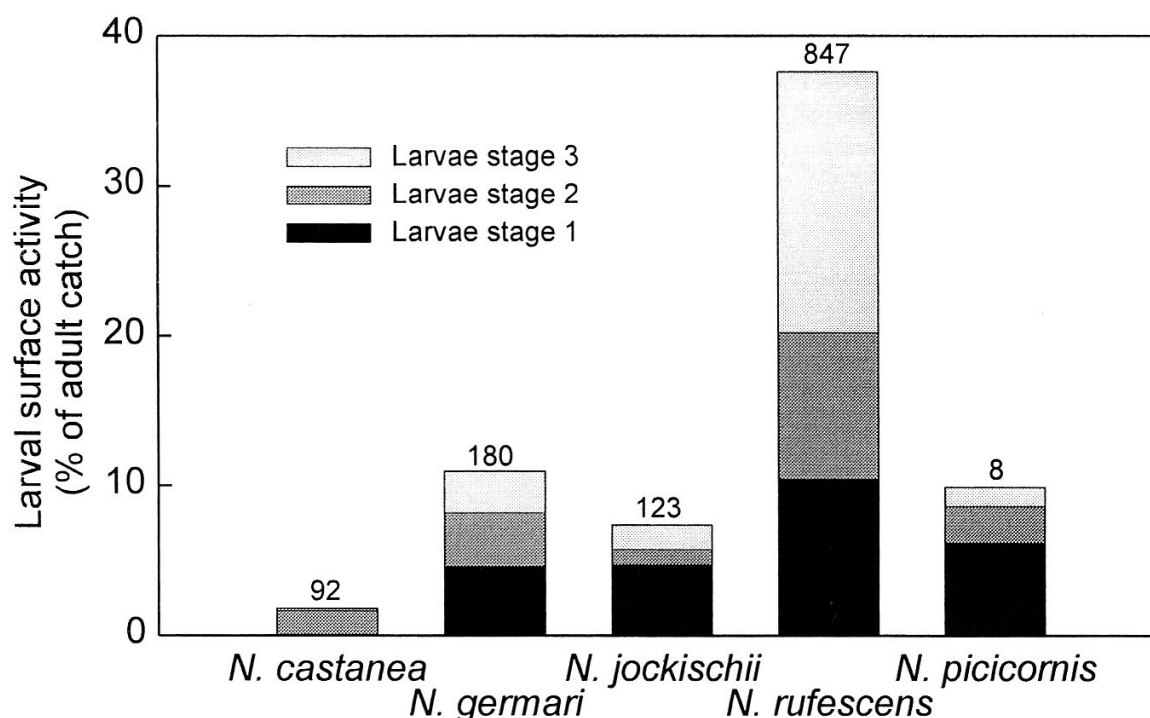


Fig. 6. Relative surface activity of *Nebria* larvae. Given are larval catches in relation to adult numbers (total catches 1995–1998). Numbers denote total larvae caught.

caught. Thus there was no indication that different localities were used for adult foraging and for breeding.

Larval surface activities are shown in Fig. 6 as the ratio of larval to adult individuals caught over the years 1995 to 1998. *N. castanea* instar 1 larvae seemed to live underground (confirming findings of HUBER 1993); but stage 2 and, in minimal quantities, also stage 3 larvae were caught in the pitfall traps. In relation to adults, this species exhibited the lowest larval surface activity. Of the other species all three larval instars were present. Surface activity was by far the highest in *N. rufescens*, particularly in stage 3 larvae. The results for *N. germari* and *N. jockischii* larvae were similar, on a lower level, whereby mainly stage 1 was surface active in the latter. The proportions of the larval instars caught on the surface were significantly different between species (all $p < 0.001$ except *N. picicornis*, χ^2 -tests). No reliable estimates can be given for the rarely caught *N. picicornis*, nonetheless all three larval stages were present superficially.

Sex ratios were similar in all species, with 53–61% females; a slightly higher value of 69% for *N. picicornis* was only marginally significant ($p' \approx 0.05$, χ^2 -test BONFERRONI corrected for 25 comparisons). There was no change in sex ratios with season (Fig. 7). In the outwash area of the glacier brook a shift towards males (43–45% females) was significant in *N. jockischii* and *N. castanea* ($p' < 0.001$), and was present as a tendency in *N. rufescens* ($p' = 0.085$, χ^2 -tests BONFERRONI corrected for 10 comparisons). Local changes of sex ratios on the barren moraine till near the glacier snout showed no uniform trend among species.

Phenologies found by pitfall trapping are shown in Fig. 7A and Fig. 7B for all species except *N. picicornis* for which catches were insufficient for making reliable estimates. Daily catches are totalled over the whole area; data from 1995 were corrected for the smaller number of traps according to proportions found in these traps in other years. Adults newly emerged within the past few days were recognisable by their still soft elytra and pale colour (THIELE 1961). No data for these are

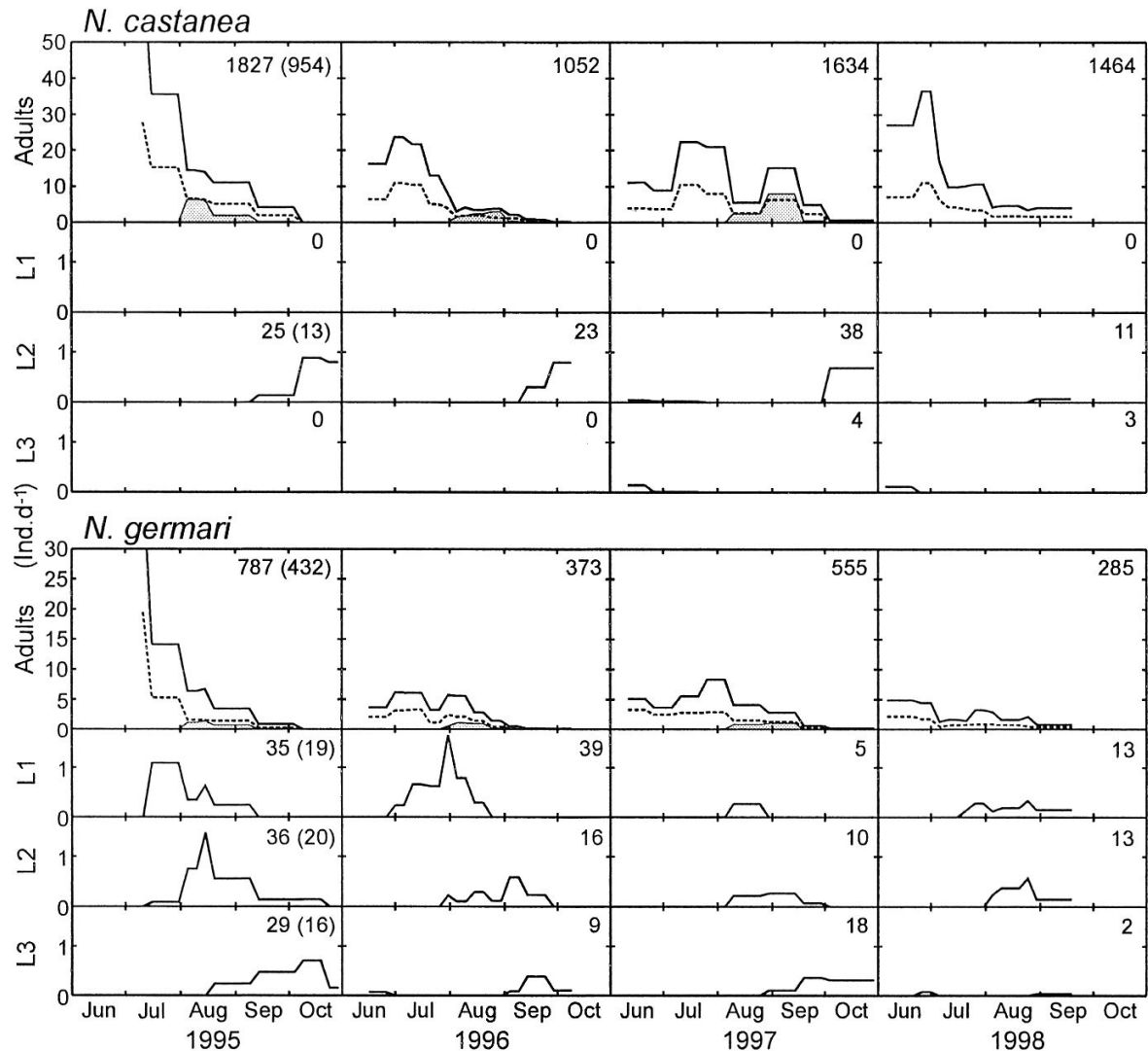


Fig. 7A. Phenology of the high alpine species *Nebria castanea* and *N. germari* in Rotmoos glacier foreland 1995–1998. Daily catches (total of all pitfall traps) are given for adults (top panel, solid line: total adults, broken line: males, shaded area: teneral adults, not available for 1998) and for the three larval instars L1, L2, and L3 (lower panels). Numbers indicate total individuals caught per year, 1995 data were corrected for the reduced number of traps according to their proportion of the total catch in other years (original catch numbers in brackets).

available for 1998. The basic pattern was similar in these species and indicated a two-year life-cycle. Typically, reproduction coincided with the period of highest activity, which followed immediately on snow melt in late June and July.

N. germari larvae were the first to hatch in early July, followed by *N. rufescens* which exhibited a very similar pattern. *N. jockischii* did not hatch before August and *N. castanea* possibly appeared still later as deduced from the late appearance of instar 2 larvae. Accordingly, *N. germari* and *N. rufescens* overwintered at instar 3, *N. castanea* and *N. jockischii* at instar 2 and 3. Adults emerged in August and September of the following year, which in some cases resulted in a second activity maximum at this time. These adults again overwintered to start reproduction in the second year. No decisive diagnosis of life cycles can be given for *N. picicornis* which reaches the limits of its distribution at these altitudes, but is common on riparian gravel bars in lower regions (MARGGI 1992). No activity of adults was observed in early summer, but was high from July to August and may last into September. Reproduction is possibly delayed until the heavy flooding of their habi-

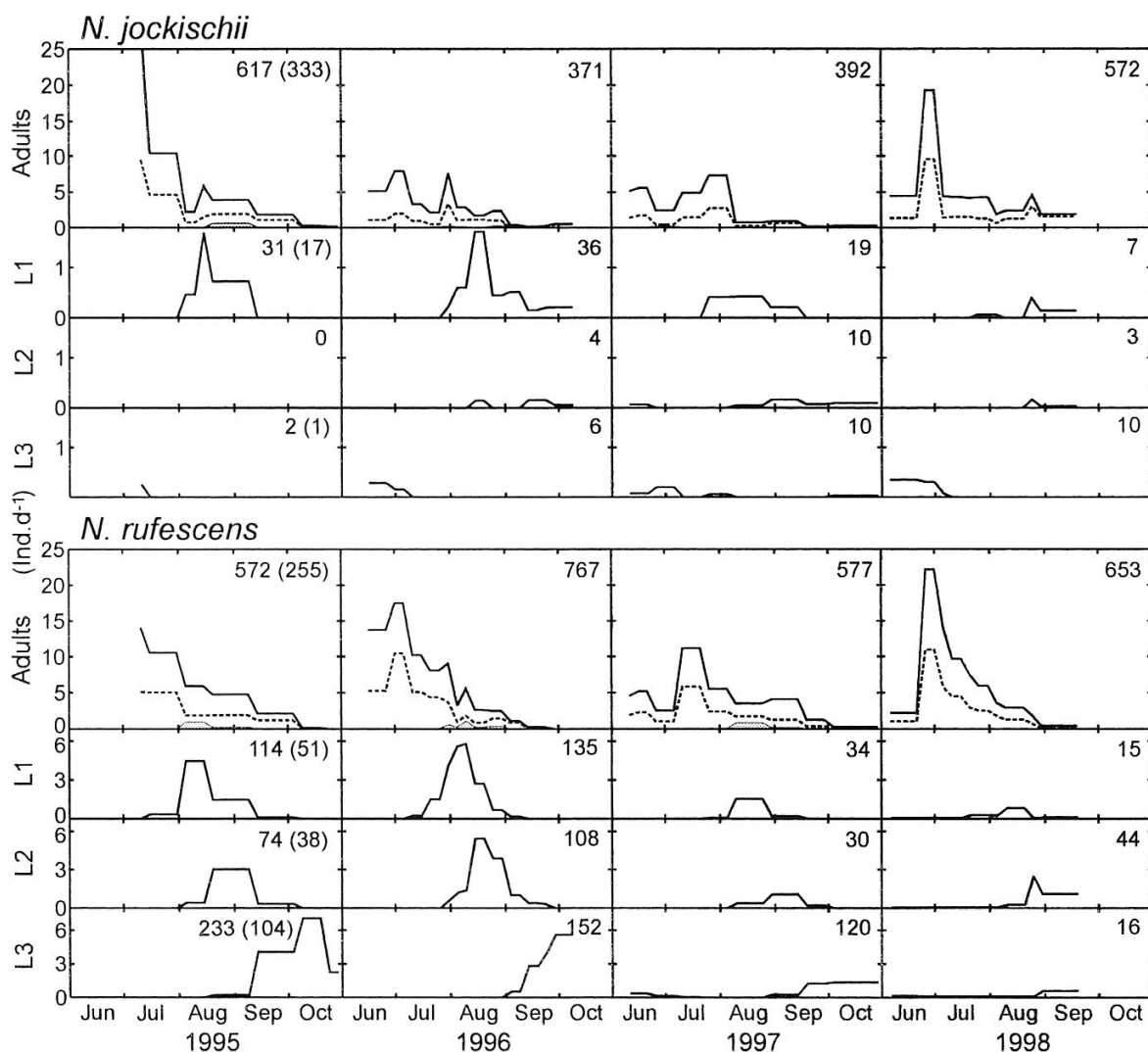


Fig. 7B. Phenology of the ripicolous species *Nebria jockischii* and *N. rufescens* in Rotmoos glacier foreland 1995–1998. All calculations and notation as in Fig. 7A.

tat in the outwash plain by glacier ablation is over; occasional larvae were caught in September.

There were quite pronounced fluctuations between years with no obvious relation to climate and without synchronicity among species. Only in early summer 1995 did *N. castanea*, *N. germari*, and *N. jockischii* simultaneously exhibit unusually high activities; in both 1997 and 1998 reproduction was poor in all species, as indicated by the low numbers of larvae caught.

DISCUSSION

Spatial patterns and environmental factors

Although overlapping, the five *Nebria* species coexisting on a glacier foreland had clearly distinct distribution patterns. Areas of high abundances had extensions of 200–500 m, the patterns remained stable over 4 years. Such patterns have been observed before (GEREBEN 1994, 1995) and required explanation. Considering the high mobility of these species, the stability of the small scale spatial patterns should indicate habitat preferences. Sites preferred for adult foraging were also used for reproduction and larval development. Interpretations may be sought in

terms of niche segregation by environmental factors and limiting resources, or, alternatively, in the context of species interactions and competitive advantages.

In general, habitat preferences of the *Nebria* species found here agreed with previous findings. They are typical and often dominant carabids of alpine habitats and favour scarcely vegetated areas and moist sites or sites near running water. *N. picicornis*, *N. jockischii* and *N. rufescens* have been characterised as ripicolous with a wide altitudinal range, *N. germari* and *N. castanea* as alpine species present from the treeline to the nival zone. There is general agreement that *N. castanea* is the most euryoecious species (DE ZORDO 1979a, 1979b; KOCH 1989; MARGGI 1992 and citations therein; BRANDSTETTER et al. 1993).

The detailed small scale analysis of a glacier foreland, however, indicated more specific associations with certain habitats, not all of which can be readily explained. Some inconsistencies with previous species characterisations were also revealed. The spatial patterns found could partly be associated to local conditions, the most important being a combination of temperature and substrate quality, and by the moisture regime. The greatest similarities in the Rotmoos glacier foreland were found between ripicolous and high-alpine species (*N. castanea* – *N. rufescens*, *N. germari* – *N. jockischii*) rather than within the same group. On a regional scale *N. castanea* and *N. rufescens* were separated by their different altitudinal range with only little overlap.

Association with moist sites was detected only for *N. rufescens* and to a lesser extent for *N. castanea*, whereas in the literature all the five species found have been described as hygrophilic (KOCH 1989; BRANDSTETTER et al. 1993). JANETSCHKE (1949) observed that *N. castanea* is hygrophilic only at lower altitudes. Possibly this shift in habitat preferences also occurs in other species, or, as an alternative interpretation, such characterisations insufficiently describe the relevant conditions over wide altitudinal ranges. It should be added that the moisture regime is particularly difficult to assess in the heterogeneous alpine ground. According to GERESEN (1995) the ripicolous species are more tolerant to desiccation and prefer higher temperatures. In contrast, *N. jockischii* occurred at the coolest sites in the glacier foreland.

It is believed that substrate texture and a system of viable subterranean cavities are among the most decisive factors for both adults and larvae. Except for *N. jockischii*, adults are nocturnal, spending most of the day below ground (OTTESEN 1985; GERESEN 1995). Larvae remain active below the snow cover (DE ZORDO 1979b) which may help them to escape waterlogging during snow-melt. Preliminary tests with below-ground traps in the Rotmoos glacier foreland yielded rare catches of *N. rufescens* (adults and larvae), *N. castanea* (adults) and *N. germari* (larvae) down to a depth of 50 cm. Similarly, DIETERICH (1996) found *Bembidion* adults down to 75 cm in gravel. Using subterranean living space may be an advantage in barren alpine habitats with extreme fluctuations of surface temperature. In our study larvae of the species typical for such habitats were rarely caught on the surface, whereas *N. rufescens* with a high larval surface activity occurred mainly at moist sites with a less severe temperature regime. However, *N. castanea* with the least surface active larvae occupied similar areas, and our results are at variance with a study where *N. jockischii* larvae were found to be much more surface active than *N. rufescens* (GERESEN 1995).

Life cycle and population dynamics

The flexibility to extend life-cycle and larval overwintering have been proposed as key adaptive features for carabids in high alpine environments (SOTA

1996). Shifts from an annual to a biennial life-cycle with increasing altitude have been repeatedly reported for *Nebria* (DE ZORDO 1979a, 1979b; JUNG 1980; HUBER 1993; BUTTERFIELD 1996). A biennial life cycle was found in all species of the Obergurgl area above 2000 m (Figs. 7A, 7B). *N. picicornis*, the life-cycle of which could not be determined, is known to be annual in lower regions (MANDERBACH & PLACHTER 1997) and according to present results is the only real autumn-breeder (see also BURMEISTER 1939); in the Obergurgl area it was restricted to altitudes below 2450 m.

It is impossible to decide whether there is an adaptive value in commencing reproduction immediately after snow-melt, in order to maximise the time available for larval development during the first year. It is difficult to believe that this should be meaningless in habitats with 3 months or less of snow-free period. However, there was no clear relationship between life-cycle timing and altitudinal range of the species. *N. germari*, the earliest to breed, is one of the high alpine species extending up into the nival zone. But so, too, is *N. castanea* which obviously emerges later.

Even if climatic correlates are impossible to infer from the 4-year data sequence, the pronounced year to year fluctuations may still indicate a diminished reproductive success in unfavourable years. Possibly long-lived iteroparous adults can compensate for reproductively poor summers such as that of 1997. But local extinction and recolonisation have also been repeatedly discussed for carabid assemblages (DEN BOER 1981; DESENDER 1996; DE VRIES et al. 1996) and remain a conceivable scenario over longer time spans for high alpine habitats.

Possibility of interspecific interactions

Interspecific interactions cannot be ruled out *a priori* as structuring forces for *Nebria* assemblages. However, it is generally believed that biotic interactions are of minor importance in environments with severe abiotic constraints such as in high alpine areas. There has been a long going debate about competitive effects in carabids, but little conclusive evidence has emerged so far (reviewed by NIEMELÄ 1993). On the other hand, on barren moraines and most likely also in other oligotrophic alpine habitats, several *Nebria* species coexist in high abundance, together with other predatory species (Tab. 2). The supporting food chain of this community remains unclear (KAUFMANN 2001). Therefore, not only food availability, but also suitable microhabitats and living space are possibly limiting resources inducing competition. Additionally, predation pressure on larvae may be relevant, as proposed by CURRIE et al. (1996). *Nebria* might gain competitive advantage from specific prey preferences and feeding habits. Generally they are considered opportunistic predators or scavengers (SPENCE & SUTCLIFFE 1982; HERING 1995; KIELTY et al. 1996), but more detailed knowledge would be highly desirable. The most likely diet in the glacier foreland are collembolans and dwarf spiders.

Obviously it is impossible to infer interspecific interactions from distribution patterns alone. Coexistence in low but not in high densities of species with similar habitat requirements, as was observed in the species pairs *N. castanea* – *N. germari* and to a lesser extent *N. castanea* – *N. jockischii*, might suggest competition. There were also some inconclusive, but statistically significant sex-ratio shifts in *N. castanea* correlated to densities of *N. jockischii* and *N. rufescens*. However, we found no negative interactions among any of the *Nebria* species, making strong competition unlikely.

Tab. 2. Preferred site conditions and influence of environmental factors. Rotmoos glacier foreland: conditions at sites with highest abundances (range for 75% of total catch), influential effects (PCA analysis) are given as none, positive or negative (0; +/- moderate, + +/- – pronounced).

Condition	<i>N. castanea</i>	<i>N. germari</i>	<i>N. jockischii</i>	<i>N. rufescens</i>	<i>N. picicornis</i>
1. Rotmoos glacier foreland					
Successional site age (yr)	20–45	< 35	< 20	35–110	—
Presence in glacial outwash	sometimes	sporadic	frequent	frequent	exclusive
Vegetation cover (%)	20–85	< 35	< 20	15–85	< 5
Cover of organic soil (%)	< 40	< 5	0	< 40	0
Temperature / sun	–	– –	– –	0	0
Moisture / snow cover	+	0	0	++	–
Structured substrate / interstitial cavities	+	++	++	0	0
2. Surrounding high alpine areas and neighbouring valleys					
Altitudinal range (m a.s.l.)	> 2400	> 2400	1900–3000	< 2450	< 2400
Vegetation	accepted	tolerated	avoided	accepted	strictly avoided
Preferred substrates	scree boulders gravel	scree boulders gravel moraine till	scree gravel moraine till	gravel	gravel (riparian banks)
Presence at moist sites	typical	sometimes	rare	rare	no
Presence in riparian beds and banks	rare	frequent	frequent	frequent	exclusive
Pioneer species near glacier snouts	sometimes	typical	frequent	no	no

Conclusions and outlook

Carabids of the genus *Nebria* in alpine habitats and in particular in glacier forelands provide an almost perfect model system for studying niche segregation among ecologically similar and closely related species. In these habitats several *Nebria* species coexist as dominants in an otherwise simple community. The present study documented the highly structured small-scale patterns and clarified relations with environmental factors and life cycles. It remains unclear, however, to what extent larval or adult traits are important in this respect. Future research would seem worthwhile (1) to assess the subterranean habitat requirements of larvae, (2) to establish whether species specific exploitation of limited food resources is important, (3) to investigate experimentally the role of interspecific interactions, both congeneric or with other taxa, and, (4) on a larger spatial scale, whether biogeographic and historical constraints have been limiting to reach suitable habitats, either for ripicolous species dispersing along streams or for species spreading from high alpine refugia.

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