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Resource partitioning among seven carabid species on Hardangervidda, southern Norway

Kjell Einar Erikstad, Ingvar Byrkjedal & John Atle Kålås

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Resource partitioning is decribed for seven carabid species, viz. *Carabus problematicus*, *Notiophilus aquaticus*, *Miscodera arctica*, *Patrobus septentrionis*, *P. assimilis*, *Cymindis vaporariorum*, and *Amara alpina* in a small study area (of radius 500m) from Hardangervidda, southern Norway. All but two species are well segregated by habitat and/ or body size (differences in size of food items). Only *M. arctica* and *C. vaporariorum* have high habitat overlap and are similar in body size, but these species show the largest segregation in seasonal activity. The observed differences are discussed in relation to the competition hypothesis and a fluctuating and unpredictable environment.

K. E. Erikstad, NINA, Tromsø Museum, University of Tromsø, N9000 Tromsø, Norway.
I. Byrkjedal, Museum of Zoology, University of Bergen, N5007 Bergen, Norway.
J. A. Kålås, NINA, Tungasletta 2, N7000 Trondheim, Norway.

1. Introduction

There are probably more than 40 000 species of Carabid beetles in the world (Thiele 1977). They are to a large extent similar in body size and structure, are found in most habitats, and are with few exceptions ground-living carnivores (Thiele 1977). In Fennoscandia there are about 350 species (Lindroth 1945) and, being among the best known groups of insects, carabids are especially suitable for ecological studies.

Based on a close correlation between the occurrence of different species and light, moisture, habitat structure, etc., it is often stated that abiotic factors are more important than competition and food supply in forming the distribution patterns and community structure of carabid beetles (see Thiele 1977 and Andersen 1986, 1988 for reviews and references).

However, several studies support the competition hypothesis. Lenski (1982a) found a negative effect of population density on body mass in *Carabus limbatus*, and later Lenski (1984) showed that food supplementation increased the body mass of this species and reduced its foraging activity. He also showed that the experimental feeding of *C. limbatus* increased the foraging success of *C. sylvosus* living in the same habitat, presumably because *C. sylvosus* was released from competition for the food items that were shared with *C. limbatus*.

An analysis of body size ratios in carabid communities is also consistent with competition theory. Brandl & Topp (1985) computed the body size structure of *Pterostichus*. spp. associations in central Europe and found that it agreed with the coexistence value put forward by Hutchinson (1959), who stated that closely related species at the same trophic level could not coexist unless their body size ratio exceeded 1.3.

More recent studies on niche differentation and community organization in carabid beetles have also shown that species are not distributed randomly and important niche dimensions are habitat distribution, annual and daily activity patterns and diet (eg. Müller 1985, Loreau 1986, 1988).

This study describes ecological differences between 7 carabid species caught in pitfall traps in a small area (of radius 500m) on Hardangervidda, in southern Norway. We have studied resource partitioning along three dimensions, habitat, body size (an index of food size) and breeding phenology.

2. Study area and methods

The study area was located at Steinbuhei, Eidfjord on the Hardangervidda, at about 1190 m asl. in the middle alpine zone. Pitfall traps (Southwood 1978) (with 4% formalin) were arranged in 6 series. One series was placed in each of the 6 main plant communities (according to the classification of Nordhagen 1943) in the area. The number of traps differed between sites due to the size of the patches studied. The plant communities are as follows:

A) *Juncetum trifidi scandinavicum.* 10 traps. The vegetation was dominated by *Cladonia* and *Cetraria* spp., with scattered stands of *Juncus trifidus*, *Empetrum hermaphroditum*, and *Loiseluria procumbens.* The site lay on top of small (radius about 50 m) moraine, well defined aganist *Nardetum chinophilum* communities on all sides. Snow melted off this site in early May and the site was very dry.

B) *Nardetum chinophilum.* 5 traps, in the middle of a patch covering about 200 × 400 m, diffusely bordered by *Juncetum trifidi scandinavicum*, *Anthoxantho - Deschampsietum flexuosae* and *Caricietum rigidae - lachenalii.* The vegetation was dominated by *Nardus stricta.*

C) *Anthoxantho - Deschampsietum flexuosae.* 10 traps. The vegetation was dominated by the grasses *Anthoxanthum odoratum*, and *Deschampsia flexuosa*, and flowering plants e.g. *Alchemilla spp*, *Ranunculus acris*, *Pedicularia lapponum*, and *Bartsia alpina.* The patch was about 40 × 60 m in size and relatively sharply defined against *Nardetum chinophilum* on one side, less sharply against *Caricetum rigidae lachenalii* on the other.

D) *Caricetum rigidae - lachenalii.* 5 traps. The patch measured 30 × 40 m, gradually merging into *Nardetum chinophilum* on all sides. The vegetation was mainly characterized by *Carex bigelowii.*

E) *Salicetum herbaceae boreale.* 5 traps. A well defined patch of almost pure *Salix herbacea*, covering about 30 × 50 m. Neighbouring plant communities were mainly *Nardetum chinophilum* and *Phyllodoco - Vaccinium myrtilli.*

F) *Phyllodoco - Vaccinium myrtilli.* 5 traps. Well defined against the previous site on one side and diffusely bordered by *Anthoxantho Deschampsietum flexuosa* on the other. The patch measured about 50 × 50 m. *Vaccinium myrtillus* dominated the vegetation, but plants of the *Anthoxantho - Deschampsietum flexuosae* community and *Cladonia* spp. were also found.

The communities on sites B and E were typically *chinophilous* communities, while that on site A was *chinophobic.*

In each series the distance between the traps was 5–6 m and the 6 trapping sites were situated within a radius of about 500 m. The traps were run from the time of the snow melt; 19, 18 and 18 May on site A, 11, 13 and 11 June on site B, C and D, and 7 July, 13 June and 13 July on site E and F in 1980, 1981 and 1982 respectively. The traps were run until 11 August in 1980 and until the snow covered the ground on 4 and 3 October in 1981 and 1982 respectively.

Seasonal activity patterns were studied in 1980 and 1981 on sites A, B and C. The traps were emptied regularly and the catches were converted to the number of individuals per 100 trap days. The breeding season of the various species was determined from the variation in the trapping frequency (cf. Larsson 1939, Greenslade 1965, Refseth 1980, 1988). Combined data for all three years at each site were used to calculate habitat utilization.

Ambient temperatures recorded at Finse (about 25 km NNW of the study area) in 1980 and 1981, when seasonal activity patterns were studied, were provided by the Meterological Institute in Oslo.

The trapping frequency of carabids is not only a measure of their population size, but also a result of differences in activity ('effective abundance', Den Boer 1977). We have therefore not attempted to estimate the population density of species, but only their seasonal activity and distribution in different habitats. Differences in vegetation cover in the different habitats was not thought to have influenced the trapping frequency of species (Greenslade 1964) as the vegetation was scattered and sparse in all 6 habitats.

While it is difficult to obtain data on food ecology in Carabid beetles, body size is commonly used as an indication of differences in food selection. Although this method has been questioned by many others (Hespenheide 1973, Wilson 1975, Turner & Polis 1979, Wiens 1982), a correlation between carabid body size and what they eat has been documented (Hengeveld 1980, 1981). Dawson (1965), Spencer (1979), Pearson & Murphy (1979) and Andersen (1988) have further shown that

Table 1. Relative abundance (%) (proportion of individuals of a given species caught per unit time in pitfall traps) at Hardangervidda, southern Norway, 1980–82. — Habitats according to Nordhagen 1943: A: *Juncetum trifidi scandinavicum.* B: *Nardetum chinophilum.* C: *Anthoxantho - Deschampsietum flexuosae.* D: *Caricetum rigidae - lachenalii.* E: *Salicetum herbaceae boreale.* F: *Phyllodoco - Vaccinium myrtilli.*

Habitat:	A	B	C	D	E	F	N
Carabus problematicus Hbst.	87.8	12.2					163
Amara alpina Payk.	100						68
Miscodera arctica Payk.	100						218
Cymindis vaporariom L.	100						163
Patrobus septentrionis Dej.		27.7	17.9	24.1	13.5	16.8	3579
Patrobus assimilis Chaud.		24.3	22.9	19.2	12.2	21.2	2179
Notiophilus aquaticus L.	0.8	8.3	26.9	17.5	14.0	32.5	427
Nebria nivalis	4.1	68.5	27.4				14
Amara praetermissa Sahlb.		81.1	18.9				6

large species of Carabids and the closely related Tiger Beetles (Cicindelidae) take larger prey than small ones. As a measure of body size, we used the length of the elytra (which is strongly correlated with total body length and mandible size (cf. Bengtson 1980)). The individuals in a sample of each species caught in 1980 were grouped in 0.1 mm size groups of elytra length and overlap in body size between males and females of the same species was calculated according to the formulae given by Pianka (1975). The overlap values range from 0 (no overlap) to 1 (complete overlap).

3. Results

3.1. Species composition and habitat utilization

6817 individuals of 9 species were caught in the 6 habitats during the 3 years (Table 1). *Patrobus septentrionis* and *P. assimilis* were the dominant species in the area and made up 52.5 and 32.0% respectively of the total number of specimens caught. Only 6 (0.09%) and 14 (0.2%) specimens of *Amara praetermissa* and *Nebria nivalis* were caught and these species were excluded from further calculations.

All specimens of *Miscodera arctica*, *Amara alpina* and *Cymindis vaporariorum* and 88% of all *Carabus problematicus* were caught in one habitat only. (A: *Juncetum trifidi scandinavicum*). *Notiophilus aquaticus* was found in all 6 habitats, while *P. septentrionis* and *P. assimilis* were caught in 5 habitats (B–F).

3.2. Seasonal activity

For all but one species (*Cymindis vaporariorum*), there was a peak in the trapping frequency during early June in 1980, only a few days after the snow melt (Fig. 1) which suggests spring breeding. The largest difference in activity occurred between *C. vaporariorum* and *M. arctica* in habitat A, *M. arctica* having an activity peak about a month earlier than *C. vaporariorum*. For all species it was evident that the activity peak occured later in 1981 than in 1980, probably because of the low temperatures in late May and June in 1981 (Fig. 2). This was most evident for *A. alpina* and *N. aquaticus*, which were most active nearly two months later in 1981 than in 1980. However, the seasonal trends in activity patterns between species observed in 1980 were also evident in 1981.

Newly hatched imagines of three species (*P. septentrionis* (*n*=7), *P. assimilis* (*n*=15) and *M. arctica* (*n*=7)) were trapped in 1981. All were caught late in the season, mainly in September and October, and the hatching and emergence of these callows probably explains the increased trapping frequency of these species at the end of the season (Fig. 1).

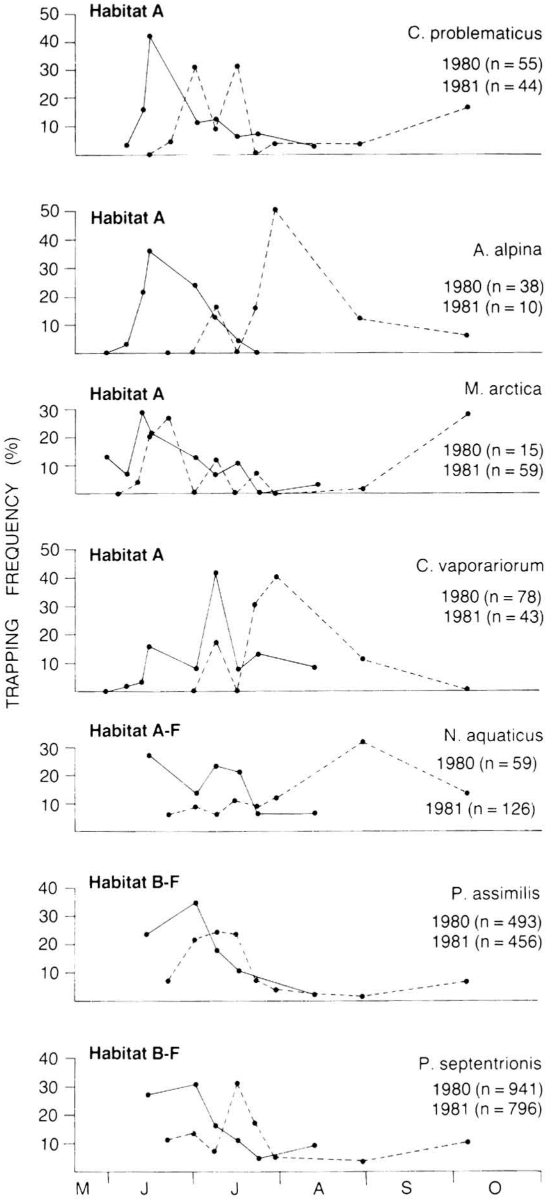

Fig. 1. The seasonal activity patterns of Carabid beetles from Hardangervidda in 1980 (solid line) and 1981 (dotted line).

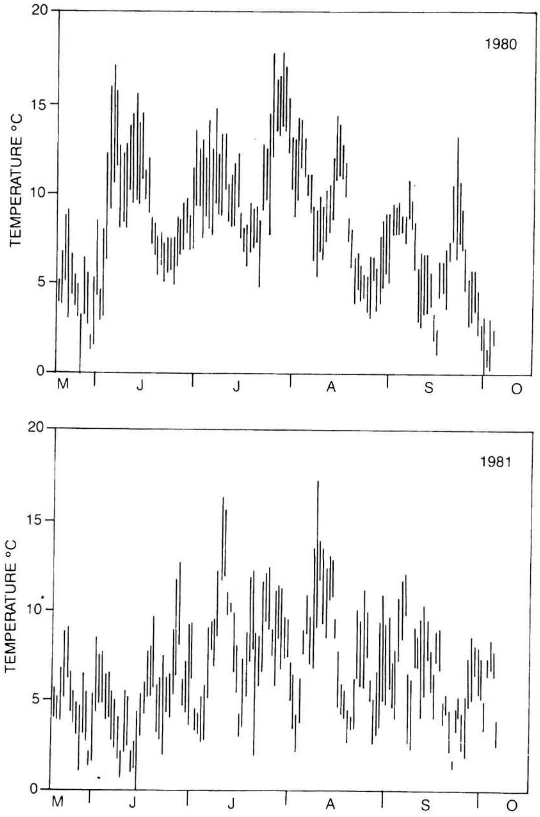

Fig. 2. Air temperatures (°C) at Finse Meteorological Station in 1980 and 1981, calculated as mean (±1*SD*) of max. and min. temperatures measured at 0100, 0700, 1300 and 1900.

3.3. Body size

The length of the elytra ranged from 3.1 mm for *N. aquaticus* to 12.9 mm in *C. problematicus* (Table 2), while the 5 other species ranged in size from 3.98 to 5.98 mm. Although the females of all species were larger than the males, the differences were not large (approx. 9%). The overlap in size between the sexes was small in all species (0.03–0.40), except *A. alpina* for which the overlap between sexes was 0.95.

3.4. Resource partitioning

The relationship between habitat utilization and body size is shown in Fig. 3. The size range of *M. arctica*, *C. vaporariorum* and *A. alpina* which occur together in habitat A is very similar to that of *P. septentrionis* and *P. assimilis* which were found in the 5 other habitats (BF). *N. aquaticus* was much smaller than any other species in the area, while *C. problematicus* (not included in Fig. 3) was over twice the size of any species in the study area (Table 2). The only two species which overlapped both in size and habitat were *M. arctica* and *C. vaporariorum*, but these two species exhibited the largest segregation in annual activity pattern.

4. Discusssion

4.1. Habitat segregation

Of the 7 species studied, only *A. alpina* and *M. arctica* are alpine species not distributed elsewhere.

Table 2. Body size (mm, length ± *SD* of elytra and (*n*)), sex dimorphism and sex overlap in Carabidae beetles caught in pitfall traps on Hardangervidda, southern Norway.

	Males		Females		Mean		Dimorph.[a)]	Overlap[b)]
C. problematicus	12.91±0.54	(21)	14.55±0.90	(35)	13.95±1.11	(56)	88.7	0.13
N. aquaticus [c)]			3.13±0.11	(95)				
M. artica	3.98±0.08	(5)	4.24±0.10	(14)	4.17±0.15	(19)	93.9	0.13
C. vaporarorum	4.46±0.15	(20)	4.85±0.10	(37)	4.72±0.22	(57)	92.0	0.03
A. alpina	5.98±0.22	(32)	6.09±0.24	(51)	6.05±0.24	(83)	98.2	0.95
P. septentrionis	5.28±0.26	(267)	5.73±0.30	(408)	5.73±0.38	(675)	83.7	0.27
P. assimilis	4.09±0.17	(167)	4.38±0.19	(315)	4.23±0.20	(482)	93.4	0.40

a) The mean size of the males as percent of the mean size of the females.
b) Calculated according to Pianka (1975).
c) Only females were present in the sample.

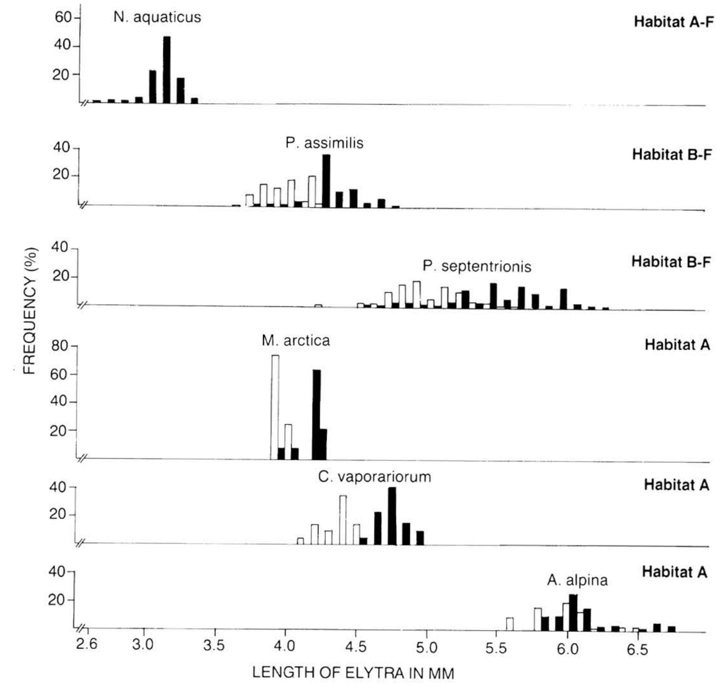

Fig. 3. Body size (length of elytra in 0.10 mm classes) of male (open bars) and female (solid bars) carabid beetles from Hardangervidda.

A. alpina is a Palearctic species and *M. arctica* has a northern distribution (Lindroth 1945). *Cymindis vaporariorum* and *Carabus problematicus* are common species in most dry habitats in Europe and in mountain habitats they often occur together with *A. alpina* and *M. arctica* on dry lichen heath (Lindroth 1945, Solhøy et al. 1975). This is consistent with the result in this study where these 4 species only were found in the dry heath habitat (A) and exhibited almost no habitat overlap with the other 3 species studied (*P. assimilis*, *P. septentrionis* and *N. aquaticus*).

P. assimilis (European species) and *P. septentrionis* (circumpolaric distribution) are common in both open and forest habitats throughout most of their range (Lindroth 1945). In mountain habitats they are confined to wet areas, as shown by their absence from habitat A in this study (see also Solhøy et al. 1975). However, Lindroth (1945) claimed that *P. assimilis* and *M. arctica* frequently occur together in mountain habitats. This is in direct contrast to this study where there was no overlap.

N. aquaticus was the only species found in all 6 habitats studied. This species is circumpolaric and, according to Lindroth (1945), eurytopic and common both in wet and dry habitats.

4.2. Seasonal segregation

The short vegetative growth period in the area (3–4 months (Østbye et al. 1975)) allows little scope for seasonal segregation, and all species found had an activity peak in June and July, suggesting spring breeding (cf Larsson 1939, Greenslade 1965, Refseth 1980). This is a common pattern in northern and high mountain habitats (Thiele 1977, Refseth 1980, 1988).

However, *M. arctica* and *C. vaporariorum* which were the two species most similar in body size and with a complete habitat overlap, did exhibit some seasonal segregation, with *M. arctica* being most active about 1 month earlier than *C. vaporariorum*. The sample size of *M. arctica* was small in 1980, but the same trend in seasonal patterns of these two species was observed in both 1980 and 1981. *C. vaporariorum* is described as an autumn breeder in other parts of Europe (Lindroth 1945, De Zordo 1979). We do not know if this is the case in this study area as some species have been shown to vary from autumn to spring breeding according to habitat altitude (eg. Refseth 1980, 1986).

A fourth possible segregation dimension is the diel activity pattern. Some species are nocturnal, others are diurnal (Thiele & Weber 1968, Thiele 1977) and some vary in their activity pattern according to habitat or latitude (Erikstad 1989)

From Hardangervidda the diel activity patterns are known for 5 of the 7 species in this study (Ottessen 1985). *C. vaporariorum*, *A. alpina*, *P. septentrionis* and *P. assimilis* are all strictly nocturnal and only the small *N. aquaticus* is diurnal. Thus, the potential for resource segregation along this dimension is small. Unfortunately the diel activity pattern of *M. arctica*, which is very similar to *C. vaporariorum* both in habitat selection and body size, is unknown.

4.4. Resource partitioning

This study shows that all the species involved are segregated by at least one of the 3 niche dimensions investigated. Moreover, there is a low overlap between sexes in body size (0.03–0.40), except in *A. alpina* (0.95), which, in contrast to the other species, is mainly herbivorous (Thiele 1977).

Niche segregation caused by competition presumably involves some degree of specialization. In the fluctuating and unpredictable environment of Hardangervidda very little specialization should be possible, unless the Carabid populations are frequently well below carrying capacity (cf. Pyke et al. 1977) e.g. due to harsh and varying weather conditions. However, if that is the case, a less perfect and regular niche segregation than that brought about by interspecific competition should be expected, despite the fact that the different species may be confined to well defined and narrow niches.

Predation is another factor which can keep carabid populations below carrying capacity and minimize competition (den Boer 1986, Parmenter & MacMahon 1988). On Hardangervidda several bird species are known to prey heavily upon carabids (Hågvar & Østby 1976, Byrkjedal 1980, Byrkjedal et al. 1986) and Ottersen (1985) suggested that the high frequency of nocturnal carabids on Hardangervidda was an adaptation to lower predation pressure at night, because birds in the area feed mainly on the ground during daytime.

Den Boer (1986) recently questioned the validity of the competitive exclusion principle and the usefulness of looking for ecological differences among closely related species. This statement was strongly refuted by others (Abrams 1986, Giller 1986, Roughgarden 1986), who pointed out that a large number of experiments and field studies have shown that competition is widespread. According to Giller (1986) the right question to be asked is how different do species need to be to coexist? There are also numerous, both field and experimental, studies of Carabid beetles which suggest that competition is frequent (Murdoch 1966, Grum 1971, Heessen 1980, Lenski 1982a, 1982b, 1984, Baars & Dijk 1984a, 1984b, Brandl & Topp 1985, Loreau 1986, 1988, Müller 1987).

The results in this study are consistent with the competition theory, and support the conclusion made by Müller (1987) that differences with respect to body size, spatial distribution and seasonal activity are important niche dimensions among carabid beetles. However, before any final conclusion can be reached more field experiments are needed. Species assemblages in small and well defined patches such as those found in this study are especially suitable for testing the competition hypothesis through the removal of one or several species by extensive trapping.

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