

# The life cycles of carabid beetles (Coleoptera, Carabidae) in dry, open habitats north of 69°N, Northern Norway

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The life cycle of 23 carabid beetle species of dry and mesic, open habitats in the lowland of Troms was studied by elucidating the reproduction period and the seasonal occurrence of larvae, tenerals and fully hardened adults. Nine species breed in spring–early summer, have summer larvae and hibernate exclusively as adults. Nine species mainly breed in summer/autumn (June–September) and larvae as well as adults hibernate. The latter group of species frequently seems to need more than one, but not two full years to complete their development. However, *Amara bifrons* (Gyllenhal, 1810) which belongs to the group with winter larvae, may exclusively have an annual life cycle. The same also partly applies to *Calathus melanocephalus* (Linnaeus, 1758) in periods with favourable climatic conditions. Third stage larvae of *Amara torrida* (Panzer, 1797) and *A. apricaria* (Paykull, 1790), which overwinter, were unable to fulfill their development at high temperatures ( $\geq 24^{\circ}\text{C}$ ) in the laboratory in autumn and obviously have a larval diapause in Northern Norway. The adults of the species with winter larvae have no aestivation period in summer which is the case for at least some of the species in Central Europe. The species with winter larvae therefore start to reproduce much earlier in the season in Northern Norway than farther south. Eggs and/or pupae as well as larvae and adults of three further species hibernate. Based on marking of larval holes, it was estimated that *Cicindela campestris* (Linnaeus, 1758) needs at least 3 years to fulfil its development in Troms. In the alpine and arctic zones, the proportion of species with summer larvae is significantly lower than that of species with winter larvae indicating that the first group is more dependent on a favourable summer climate. The period 2002–2011 was warm. Earlier reproduction and eclosion of adults was conspicuous in this period. Possible changes in altitudinal and latitudinal distribution and in the life cycles of carabid beetles because of global warming are discussed.

Key words: Carabidae, life cycle, dry, open habitats, Northern Norway.

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## Introduction

Larsson (1939) divided the Scandinavian carabid beetles into two main life cycle categories: a) spring breeders with summer larvae and imaginal hibernation and b) autumn breeders with larval hibernation. Species of the latter category may also hibernate as adults and a few species were assumed to have life cycles lasting more than one year. Later studies of life cycles have documented

a complex pattern among carabid beetles. Thus, several species have two reproduction periods, one in spring and another one in autumn. Furthermore, eggs of some species hibernate and the life cycle traits of a species may vary much with climate (e.g. Lindroth 1945, 1985–86, Refseth 1986, 1988, Butterfield 1996, Sota 1996, Killengren 2002, Hodkinson 2005, Filippov 2006, Matalin 2007). The most important factors regulating annual rhythms are photoperiod and temperature

(Thiele 1977).

Several investigations have focused on life cycles of carabid beetles in relation to altitude, but few seem to have been devoted to studies in latitudinal gradients such as those of e.g. Filippov (2006, 2007). Despite that the temperatures decrease with both altitude and latitude, the environmental alterations are in several ways different. Thus, photoperiodic conditions change with latitude and a lower angle of incidence of sunrays at northern latitudes may create other microclimatic conditions than in similar habitats in more southern areas (Andersen 1993, 1996, Moen 1998).

Lindroth (1945, 1985–86) assumed that some species that have annual life cycles in South Fennoscandia may have biennial life cycles in the northernmost part of their ranges. On the other hand, several riparian *Bembidion* Latreille, 1802 species have the same main life cycles in Northern Norway as in more southern areas (Andersen 1983b). Nevertheless, the knowledge about the life cycles of carabid beetles adapted to other environments such as dry, open habitats is scanty in the northernmost parts of their ranges. The conclusion of Andersen (1984) that the Carabidae species with summer larvae need higher summer temperatures to complete their development than those with winter larvae was therefore based on incomplete knowledge of the life cycle of several species in Northern Norway.

The present investigation examines the life cycle of carabid beetles preferring open and more or less dry habitats in the lowland of Troms County in Northern Norway. A focus is to ascertain whether species with a wide geographical range have the same life cycles in Troms County as further south. The study also re-examines the statement of Andersen (1984) that the proportion of species with summer larvae decreases more with increasing latitude and altitude than the proportion of species with winter larvae.

## Study area

The investigated localities in Troms are situated in coastal (TRY) as well as in fiord and inland districts (TRI) between 69.02–69.77° N. They

are located in the lowland (maximum elevation 78m.a.s.l.) and in the middle boreal zone (Moen 1998). This zone expands further north in Norway than in any other parts of the world (Moen 1998). Some of the investigated sites are naturally open, but most of them are open due to human activity, comprising habitats like fallow fields, road verges, sandpits and arable land. According to a formula compiled by Andersen (2011), the plant composition indicates mesic to dry conditions. The substratum in the sites is sandy/silty or a heterogeneous mixture of silt, sand, gravel and stones. TRI has warmer summers, but colder winters than the coastal districts (Table 1). The period 2002–11 was extraordinarily warm whereas the mean temperature for May–October in the period 1991–2000 was the same as in the normal period 1961–90. The mild springs in 2002–2006 resulted in an exceptionally early flowering of plants (Gamst 2006).

## Material and methods

The material was sampled by pitfall trapping and hand collecting, by far with time notion (time–catch). Andersen (1970, 1995) has described the procedures followed by the two methods. The pitfall trap material stems from the period 2001–2003, in a single site in TRI from 2007–2008. The traps were emptied with half-monthly or monthly intervals. The catches in the traps were given as number of individuals collected per 100 trap days.

Hand collecting was performed without time notion in the period 1986–1989. The time-catch material has been sampled in the periods 1990–2006 and 2009–2012.

In some sites with much litter and moss, the material was sifted through a sieve with mesh size 5.5mm. The sifted material was examined in the laboratory.

A distinction between teneral and fully hardened adults was made. Adults that were classified as teneral, were notably softbodied and pale. The reproduction period of the species was determined by examination of the ovaries of dissected females. Females with ripe eggs (mature ovaries) constituted a distinct group.

**TABLE 1.** Temperature and precipitation at meteorological stations situated on the coast (TRY) and in the inland (TRI) of Troms county. The value for TRY are based on four stations, those of TRI on 7 stations. Years and periods with exceptional temperature conditions are given for Tromsø (TRY). Sources: Aune (1993), Førland (1993), Bjørbæk (1994) and data from The Norwegian Meteorological Institute.

Place, period	Coldest month	Mean temperature (°C)							Precipitation	
		April	May	June	July	August	September	October	April-July	April-October
TRY 1961-90	-3.4	0.9	5.1	9.1	11.8	11.0	7.2	3.5	6.7	565
TRI 1961-90	-7.8	0.2	5.6	10.5	13.1	11.6	6.9	1.8	7.4	432
Tromsø 1961-90	-	0.7	5.1	9.2	11.8	10.9	6.7	3.2	6.7	-
Tromsø 1991-2000	-	0.8	4.6	9.5	11.6	10.9	7.3	2.8	6.6	-
Tromsø 2002-2011	-	2.2	6.2	9.3	12.5	11.5	7.7	3.5	7.6	-
Tromsø 1989	-	3.5	5.5	9.9	10.0	12.1	7.7	2.4	7.2	-
Tromsø 1992	-	0.2	5.7	10.3	10.4	10.5	8.3	-1.4	6.7	-
Tromsø 1993	-	0.5	4.8	7.0	13.8	11.7	5.6	0.9	6.3	-
Tromsø 2000	-	-0.1	5.7	8.6	11.5	10.7	8.0	6.4	6.4	-
Tromsø 2002	-	3.5	5.8	10.7	13.0	11.9	6.4	0.2	8.3	-
Tromsø 2003	-	1.9	6.6	9.3	14.2	11.8	6.9	2.5	8.0	-
Tromsø 2004	-	3.5	6.3	8.5	14.6	11.7	7.8	3.0	8.2	-
Tromsø 2005	-	3.0	4.9	10.1	12.7	11.5	7.3	5.2	7.7	-
Tromsø 2010	-	1.6	7.2	7.2	11.5	9.9	8.1	3.5	6.9	-
Tromsø 2011	-	3.2	6.7	11.1	11.3	12.1	10.0	6.0	8.1	-
Tromsø 2012	-	-0.1	4.3	8.8	10.8	9.8	7.4	2.9	6.0	-

Fully hardened females with immature ovaries, i.e. females with small ovaries without obvious oocytes also usually comprised a well defined category. However, the quality of the preserved material varied much and it has therefore not been distinguished between other developmental stages of the ovaries.

Larvae have been identified according to Luff (1993). The larva of *Amara torrida* (Panzer, 1797) is undescribed, but that of the closely allied species *A. alpina* (Paykull, 1790) is described.

These two species are the only ones within subgenus *Curtonotus* occurring in the study area. They have non-overlapping zonal distributions in Troms (the first one not above the treeline, the last one only in the alpine zone). All the larvae of subgenus *Curtonotus* collected in the present study therefore certainly belong to *A. torrida*. The larvae of *Bembidion* could usually be identified to the subgenus level, but not always to species. However, in those cases where repeated collecting yielded adults of a single species of a subgenus of

*Bembidion* in a site for at least two consecutive years, the collected larvae were regarded to belong to the same species as the adults.

The time that *Calathus melanocephalus* (Linnaeus, 1758) and *Cicindela campestris* Linnaeus, 1758 need for their development in the field was tentatively estimated based on the sum of effective air temperatures (SEAT). The SEAT is the number of day degrees above the lower development threshold air temperature (LDAT) needed for complete development of a stage. LDAT is the air temperature at which the development ceases. Information from studies of carabid beetles in the period 1957–61 in Eastern Jutland in Denmark and data from two meteorological stations from the same period and area (Schjøtz-Christensen 1965, data from Danish Meteorological Institute) were used to give an estimate of the SEAT for the whole development of *Calathus melanocephalus*. The calculated SEAT and temperature data from meteorological stations in Troms (Table 1) were used to estimate the time that the species requires for its development in the county.

A study of the development of *Cicindela campestris* was performed in a sand pit in Tromsø municipality. The larvae make burrows with conspicuous mouths. They stay on the same spots during their complete larval life span, but the burrows and holes are widened according to stage. The holes are closed before the winter (Larsson 1968). Based on the diameter of the holes, the larval stages could be identified: holes of first stage: 2mm; holes of second stage: 3mm; holes of third stage: 4.5mm. To estimate the duration of the larval stages of *C. campestris* in 2010–2011, five first stage larval holes (group A) were marked 30 July 2010. Furthermore, six second stage larval holes were marked 24 May 2011 (group B). The holes were checked several times in 2011. They could not be followed up after 7 September 2011 because the markings had disappeared. The calculation of the SEAT of the larval stages of *C. campestris* was based on observations of these holes and the prevailing temperatures in Tromsø in 2010–2011.

To elucidate whether third stage larvae of species with winter larvae are able to develop

to adults without hibernation, a third stage larva of *Amara apricaria* (Paykull, 1790) collected 26 August 2011 and a third stage larva of *A. torrida* collected 8 September 2011 were kept in the laboratory in glasses with somewhat moistened soil and access to dead insects, seeds and bread. The larva of *A. apricaria* was kept at  $14.0 \pm 1.0^\circ\text{C}$  to 6 September, thereafter at  $24.5 \pm 0.5^\circ\text{C}$ , whereas the larva of *A. torrida* lived at  $24.5 \pm 1.0^\circ\text{C}$ . The day length decreased naturally.

The ratio of the frequencies of species of the two life cycle categories established by Larsson (1939) occurring regularly above, versus only below the treeline, was compared. The analysis involved all the carabid beetles that have a regular occurrence in Troms except for arboreal and halophilous (biontic) species. The ratio of the frequencies of species of the two life cycle categories occurring in the arctic zone versus only south of the arctic border line in Northern Norway was also compared. The arctic zone is only represented in Finnmark County in Scandinavia (Moen 1998). Information about the life cycle pattern and altitudinal and latitudinal distribution of species stems from Andersen (1984, 1995, unpublished results), Lindroth (1985–86), Refseth (1986, 1988), den Boer & den BoerDanje (1990), Luff (1993), Butterfield (1996), Olsvik *et al.* (2001), Killengren (2002), Turin *et al.* (2003), Andersen & Olberg (2003), Naujok & Finch (2004), Fillipov (2006, 2007) and Hanssen (2007). A number of species was omitted from the analyses because too little is known about their life cycles in Northern Norway and from other areas with a similar climate. Data about the ecology and distribution of the species are given in Table 2.

Although the present study intends to show the life cycle pattern during average climatic conditions, the high temperatures in spring 1989 and in the period 2002–2011 (Table 1) have been especially considered by the presentation and discussion of the results.

## Results

More than 11,500 adults and 234 larvae of 23 different carabid beetle species were collected

**TABLE 2.** Distribution and ecology of the investigated Carabidae species in Troms and Finnmark counties. The information is based on Lindroth (1945, 1985–86), Andersen (1983a, unpublished data), Vik (1991) and Saurdal (2005). The nomenclature follows Silfverberg (2004). mb: middle boreal zone; nb: northern boreal zone; la: low alpine zone; ma: middle alpine zone; ha: high alpine zone; larc: low arctic zone; 1: mesic-dry, anthropogenic habitats with mineral soil (fallow land, road sides, arable land, sand pits); 2: mesic-dry, anthropogenic meadows; 3: supralittoral, mesic-dry sandy or gravelly areas at the sea, seminatural or natural; 4: river banks, moist-dry; 5: supralittoral, dry sites at the outlet of rivers; 6: supralittoral, steep slopes high above rivers with very dry sand; 7: moist-mesic, clayish slopes, seminatural; 8: dry, gravelly/ stony scree, 9: forest clearings and edges with dry moraine soil; 10: moist-mesic, deciduous forest.; \*: boreal or boreo-montane(arctic) species, typical of the high boreal coniferous region.

Species	Most elevated (Northernmost) vegetation zone, regular occurrence	Habitats in Troms	Provinces in Troms and Finnmark	Northernmost occurrence (latitude)
<i>Cicindela campestris</i>	mb	1, 6, 7	TRY	69.8
<i>Clivina fossor</i>	la	1, 4, 6	TRY, TRI, FV, FI, FN, FØ	70.0
<i>Dyschirius globosus</i>	nb(la?)	1, 2, 3, 4, 5	TRY, TRI, FV, FI, FN, FØ	70.7
<i>Miscodera arctica</i> *	ma	1, 6, 9	TRY, TRI, FV, FI, FN, FØ	71.0
<i>Leistus ferrugineus</i>	larc	1, 2, 3, 8, 10	TRY, TRI, FV	70.7
<i>Notiophilus aquaticus</i>	ha	1, 2, 3, 6, 8, 9	TRY, TRI, FV, FI, FN, FØ	71.0
<i>N. germinyi</i>	la	1, 2, 6, 8, 9, 10	TRY, TRI, FV, FI, FN, FØ	70.7
<i>Bembidion quadrimaculatum</i>	nb	1	TRI, FV, FI, FØ	70.0
<i>B. femoratum</i>	nb	1, 4, 6,	TRY, TRI, FV, FI, FN	70.0
<i>B. bruxellense</i>	nb	1, 2, 4, 7	TRY, TRI, FV, FI, FN, FØ	70.0
<i>B. grapii</i> *	nb	1, 3, 6, 9	TRY, TRI, FV, FI, FN, FØ	70.0
<i>Calathus melanocephalus</i>	la	1, 2, 3, 6, 8, 10	TRY, TRI, FV, FI, FN, FØ	71.0
<i>Pterostichus adstrictus</i> *	nb	1, 3, 4, 5, 6, 9	TRY, TRI, FV, FI, FN, FØ	70.0
<i>Amara communis</i>	nb	1, 2, 6	TRY, TRI	69.7
<i>A. lunicollis</i>	nb	1, 2	TRY, TRI, FV, FN	70.0
<i>A. familiaris</i>	nb	1, 2	TRY, TRI	69.8
<i>A. interstitialis</i> *	nb	1, 2, 3, 6, 9	TRY, TRI, FV, FI, FN, FØ	70.0
<i>A. erratica</i> *	la	1	TRY, TRI, FV, FI, FN, FØ	70.0
<i>A. quenseli</i>	ma	1, 3, 4, 6, 9	TRY, TRI, FV, FI, FN, FØ	71.0
<i>A. bifrons</i>	mb	1, 3	TRY, TRI	69.8
<i>A. apricaria</i>	nb	1, 2, 3, 6	TRY, TRI, FV, FI, FN, FØ	70.7
<i>A. torrida</i> *	larc	1, 2, 3	TRY, TRI, FV, FI, FN, FØ	70.7
<i>Dicheirotichus cognatus</i> *	la	1, 3, 5, 6, 8	TRY, TRI, FV, FI, FN, FØ	71.0

from April to October. About 1850 females were dissected for examination of the ovaries. The results are presented in Tables 3–7. Further data are given below.

Five larvae of *Notiophilus aquaticus* (Linnaeus, 1758) were found in June I–July II. A third stage larva of *Clivina fossor* (Linnaeus, 1758)

was found 18 September 2010 (TRI) whereas two third stage larvae of *Miscodera arctica* (Paykull, 1798) were collected in September I (TRI).

An aggregation of adults (> 77 individuals) of *Calathus melanocephalus* was found hibernating under two large stones 22 September 2000 in TRI.

Females of *Dyschirius globosus* (Herbst, 1784),

**TABLE 3.** Life cycle data of *Bembidion bruxellense* (B bru), *B. femoratum* (B fem), *B. grapii* (B gra), *B. quadrimaculatum* (B qua), *Amara lunicollis* (A lun), *A. familiaris* (A fam), *A. communis* (A com), *A. interstitialis* (A int), *Pterostichus adstrictus* (P ads), *Dicheirotrichus cognatus* (D cog), *Notiophilus germinyi* (N ger), *Leistus ferrugineus* (L fer), *Calathus melanocephalus* (C mel), *Amara quenseli* (A que), *A. apricaria* (A apr) and *A. torrida* (A tor). The numerals give the number of second and third stage larvae (L) and the number of teneral of the total number of adults examined (T). The difference in the ratio of frequencies of teneral between April–first half of July and second half of July–October was tested by means of 2x2 contingency tables with Yates' correction and expected values  $\geq 3.0$ . I: first half; II: second half; ns: not significant; ←: ratio significantly highest in April–July I; →: ratio significantly highest in July II–October; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$

	April		May		June		July		August		September		October		$\chi^2$
	I-II	I	I	II	I	II	I	II	I	II	I	II	I	II	
<i>B bru</i>															
L			1												
T	0/40	0/124	0/219	0/71	0/101	26/97	13/98	14/96	4/85	6/135	0/35	80.35***	→		
<i>B fem</i>															
L					3	14									
T	0/99	0/25	0/52	0/42	7/56	39/133	15/134	18/182	2/134	0/74	3/150	14.94***	→		
<i>B gra</i>															
T	0/39	0/61	0/48	0/56	1/70	12/37	6/25	50/99	8/27	4/51	1/55	91.89***	→		
<i>B qua</i>															
T	0/25	0/25	0/42	0/27	0/1	0/23	2/44	1/32	0/1	0/64					
<i>A lun</i>					1	2									
T	0/18	0/3	0/19	0/15	0/3	0/2	1/1	1/1	2/4	0/2					
<i>A fam</i>						6	5								
L															
T	0/4	0/7	0/19	0/1	0/5	0/17	0/3	4/8	0/1						
<i>A com</i>							3								
L															
T	0/14	0/6	0/18	0/6	0/4	0/4	2/2	1/1							
<i>A int</i>						9	2								
L															
T	0/20	0/33	0/87	0/30	0/12	0/16	9/17	1/12	3/31	1/4	0/27	25.11***	→		
<i>P ads</i>															
L					20	10	1	2	1	1					
T	0/40	0/25	1/59	1/88	1/79	2/11	19/62	20/81	19/56	1/4	0/15	81.07***	→		
<i>D cog</i>															
T	0/41	0/104	0/94	0/105	4/455	27/488	32/224	3/40	1/299	21/300	0/19	41.21***	→		

TABLE 3- continued

	April		May		June		July		August		September		October		$\chi^2$	
	I-II	I	I	II	I	II	I	II	I	II	I	II	I	II		
<i>N ger</i>	L 2	0/23	0/2	0/8	1	7/37	1	6/20	2/11	0/29	0/35	2	0/33	0/1	6	8.62**
	T														0/2	←
<i>L fer</i>	L 24	0/7	2	0/22	0/18	0/19	1/18	1/25	0/31	0/32	0/32	0/10	0/5	1	5	
	T													0/5		
<i>C mel</i>	L 1	0/54	0/5	0/23	0/42	2/82	14/42	29/95	2/77	3/81	2/31	0/100	0/100	0/1	0/1	1.32 ns
	T													0/1		
<i>A que</i>	L 2	0/17	0/13	0/43	0/66	1/46	80/249	107/405	16/90	5/45	2/140	2/140	3/16	2	2	0.01 ns
	T													1		
<i>A apr</i>	L 1	0/19	0/59	0/21	0/109	11/147	46/209	31/168	2/96	5/242	3/54	3/54	0/1	0/1	0/1	2.43 ns
	T													1		
<i>A tor</i>	L 11	0/8	0/19	0/22	0/24	1/18	2/16	5/27	3/67	2/17	0/4	0/4	6	4	0/1	2.22 ns
	T												0/5	0/5	0/1	

*Bembidion bruxellense* Wesmael, 1835, *B. grapii*, Gyllenhal, 1827, *B. femoratum* Sturm, 1825, *B. quadrimaculatum* (Linnaeus, 1761), *Amara familiaris* (Duftschmid, 1812), *A. interstitialis* Dejean, 1828, *A. erratica* (Duftschmid, 1812), *Pterostichus adstrictus* Eschscholz, 1823, *Clivina fossor*, *Leistus ferrugineus* (Linnaeus, 1758) and *Miscodera arctica* had immature ovaries in August/September. The nine firstmentioned species also had immature ovaries in April and/or May. Females of *Amara bifrons* (Gyllenhal, 1810) and *Dicheirotichus cognatus* (Gyllenhal, 1827) were immature in July and August, the last mentioned species also in late September. *Notiophilus germinyi* Fauvel, 1863 had immature ovaries in June/July. Females of *Notiophilus aquaticus*, *Calathus melanocephalus*, *Amara quenseli* (Schönherr, 1806), *A. apricaria* and *A. torrida* had immature ovaries from April or May to July or August/September.

The third stage larva of *Amara apricaria* that was collected 26 August 2011 died 18 September 2011, i.e. after 23 days. The body was swollen, but the back part of the abdomen had shrunk. The third stage larva of *A. torrida* that was collected 8 September 2011 died 20 October 2011, i.e. after 42 days.

Active adults of *Cicindela campestris* have been observed between 27 April and the first half of July. Three of eighteen females from May/June had ripe ovaries. Holes representing the three larval stages were observed in all the months from 18 April to 11 September. Larvae of the three stages were dug out of their burrows 15 August. No larval holes could be seen 19 September 2011, in October 2009 and 2010 because they had been closed before the winter. The observations of the marked larval holes gave the following results: the first stage larvae from 30 July 2010 (group A) were in the same stage 9 June 2011, but had developed to second stage 18 June 2011. Only one hole from group A was

**TABLE 4.** The reproduction period of the carabid beetles. The numerals give the number of females with mature ovaries of the total number of dissected females. The difference in the ratio of the frequencies between April–June II and July I–October was tested by means of 2x2 contingency tables with Yates' correction and expected values  $\geq 3.0$ . Data from TRI and TRY were pooled together in the statistical tests. *D glo*: *Dyschirius globosus*; *A err*: *Amara erratica*; *N aqu*: *Notiophilus aquaticus*; *A bif*: *Amara bifrons*; \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ; ←: ratio significantly highest in April–June II; →: ratio significantly highest in July I–October. For further explanations see Table 3.

Species	April		May		June		July		August		September		October		$\chi^2$ test
	II	I	II	I	II	I	II	I	II	I	II	I	II	I	
<i>D glo</i>	TRY		0/6	2/11	13/25		0/4		0/7	0/43					20.23***
<i>B bru</i>	TRI		15/26	11/24	16/32	2/8	1/13	0/4	0/10	0/21	0/2	0/27			64.38***
	TRY	6/7			1/3	2/2			0/4	0/7	0/11				←
<i>B fem</i>	TRI				4/5	4/8	0/5	0/8	0/2	0/24	0/7	0/6			64.13***
	TRY	4/6	2/2	2/2	1/1	4/6	0/4	0/2	0/1	0/14	0/13	0/10			←
<i>B gra</i>	TRI	5/7	5/6	3/5	12/16	1/6	0/4	0/1	0/15	0/13	0/3	0/3			42.98***
	TRY		2/4	4/4	1/5	1/5	0/13	0/1	0/13	0/1					←
<i>B qua</i>	TRI		0/10	4/8	10/20	7/8	0/7	0/4	0/12	0/14					20.26***
	TRY														←
<i>A lun</i>	TRI	TRY	1/1	0/5	4/5	5/5	0/1	0/1	0/1	0/1					
<i>A fam</i>	TRI		2/2	2/2	4/6	1/1	0/6	0/6	0/2						7.61**
<i>A com</i>	TRY		3/3	11/11	8/8		0/2								←
<i>A int</i>	TRI	0/2	0/3	4/7	17/20	4/9	2/3	0/2	0/9	0/1	0/1	0/1			23.87***
	TRY			12/15	1/2	2/2	0/1	0/1	0/7	0/3					←
<i>A err</i>	TRI		0/7	1/9	10/10	0/1	1/2	0/20	0/18						13.54***
	TRY														←
<i>P ads</i>	TRI	4/7		0/1	4/4	4/7	1/2	0/2	0/3	0/5	0/5	0/1			45.97***
	TRY	0/1	11/11	10/12				0/10	0/15	0/4	0/1				←
<i>D cog</i>	TRI		6/13	5/5	8/12	2/2	6/12	2/3	0/2	0/9	1/1	1/1			22.34***
	TRY	3/4	1/1	0/1	1/2	0/40	0/12	11/20	6/20	5/6					←
<i>N aqu</i>	TRI		12/23	2/3	4/12	4/5	2/5	4/18	1/6	2/9	3/8	0/1			1.50 ns
	TRY	0/10	2/3	2/2	1/3	8/19	2/5	0/8	0/8	0/1					



TABLE 4. continued

Species	April		May		June		July		August		September		October		$\chi^2$ -test
	II	I	I	II	I	II	I	II	I	II	I	II	I	II	
<i>N ger</i>	TRI		1/3		2/4	0/1	7/12	1/3							0.00 ns
<i>L fer</i>	TRY	0/2	2/3	2/3	2/2	3/5	5/7	6/6	0/4	0/1					
<i>C mel</i>	TRI		4/4	1/3	4/4	3/3	4/11	0/2							5.88*
<i>A que</i>	TRY	0/5	5/11	2/5	12/15	14/20	7/19	1/11	0/10	0/9	0/1				←
<i>A que</i>	TRI		3/5	1/8	7/11	6/8	5/10	9/13	4/5						3.94*
<i>A bif</i>	TRY				3/18	2/6	22/28	1/1	1/1	7/11					→
<i>A apr</i>	TRI	0/1	2/8	3/7	4/4	1/4	0/1	1/1	0/1						
<i>A apr</i>	TRY		1/1	1/10	1/11	1/5	16/28	23/46	1/7						4.72*
<i>A tor</i>	TRI	0/1	1/10	1/3	1/3	2/5	1/9	0/3	0/7						→
<i>A tor</i>	TRY		1/1	4/7	1/8	2/5	0/3	0/7	0/1						2.09 ns

found 13 August 2011. The larva was still in the second stage. The second stage larvae from 21 May 2011 (group B) were in the same stage 9 June 2011 whereas they had developed to third stage 18 June. All the larvae of group B were in the third stage 7 September 2011.

**Discussion**

*Methods*

Pitfall trapping is a method well suited for very active, large species (Arneberg & Andersen 2003). The period with the highest catches corresponds with the time of the highest activity density and usually, albeit not always, with the reproduction period (Refseth 1980, Makarov 1994). Small, less active species are to a higher degree found by hand collecting and quadrat sampling than by pitfall trapping (Andersen 1995, unpublished results). Lövei & Magura (2011) showed that the components number of traps and length of operation do not contribute to the final catch in the same way. However, in the present study, the same traps were used in the same spots through the season. The catches at different times of the year are therefore considered comparable.

Within given sites, the yields per unit time at different times of the year (Table 5) give a reliable estimate of the relative abundance of species during the season (Andersen 2011). The sampling methods used in the present study were therefore considered to be relevant to study the life history of the species.

The thermal constants lower development threshold (LDT) and sum of effective temperatures (SET) are based on laboratory experiments and therefore give a measure of the direct thermal requirements of species (Saska & Honek 2003) whereas SEAT and LDAT are founded on air temperatures. Obviously, the temperatures in the microhabitats of *Calathus melanocephalus* and *Cicindela campestris* deviate from those of the air, but a correlation between the temperatures at microclimatic and macroclimatic levels exists (Andersen 1984).

**TABLE 5.** Seasonal relative abundance (number of specimens collected by hand per hour) and activity abundance (number of individuals per 100 trap days) of the carabid beetles. The activity abundance is given with monthly intervals, the relative abundance with half-monthly intervals. Act: Activity; Rel: relative; *C fos*: *Clivina fossor*; N: total number of individuals. For further explanation of symbols see Tables 3 and 4.

Species	April		May		June		July		August		September	October	N
	II	I	II	I	II	I	II	I	II	I	I-II		
<i>B bru</i>		5.1	7.5	9.5	3.8	4.9	0.9	2.1	6.3	11.4			553
		10.5		3.6		0		0.2					28
<i>B fem</i>	4.9	3.1	0	2.8	2.7	3.0	3.2	5.2	4.5	5.7	13.5		391
<i>B gra</i>		13.0	18.2	12.4	6.2	3.8	3.9	2.6	11.3	7.2	14.4		310
		2.5		1.4		1.6		1.0					36
<i>B qua</i>			23.0	6.3	4.6		4.3	2.9	12.0	9.4			174
<i>A lun</i>			1.9	1.4	1.7	0.3	0.3	0	0	0	0		27
<i>A com</i>		3.8	8.6	21.3	2.7	0	1.0	0	1.0	0.4			87
<i>A int</i>		10.5	2.1	4.3	0.2	0.2	0.5	1.9	0.5	1.4			148
		14.4		6.9		1.1		0.9		1.1			66
<i>A err</i>			2.9	1.6	1.3	0.3	0	0.8		1.2			23
<i>P ads</i>		1.7	4.6	3.5	4.4	5.5	2.9	6.6	3.5	4.6			464
		20.1		9.0		5.4		12.9		3.9			243
<i>D cog</i>		3.0	8.9	5.7	18.6	18.3	13.4	14.1	11.7	23.5			1679
<i>C fos</i>			1.1	1.1		6.7	2.1	1.0	0	0			45
<i>N aqu</i>		2.0	4.7	4.0	5.9	5.2	7.3	8.0		3.8			537
		0.7		0.9		2.7		1.8		0			73
<i>N ger</i>		3.7	2.8	3.3	0.8	8.1	6.3		4.3	9.6			131
<i>C mel</i>		0.5	0	1.4	2.9	1.5	3.1		3.6	1.0			242
		4.2		16.0		6.6		8.9		5.0			146
<i>A que</i>		0.9	1.5	2.2	2.6	8.0	6.4	7.9	6.9	2.4			703
		2.9		10.9		4.4		3.0		2.3			186
<i>A bif</i>		0		0	0	4.4	4.3	1.0	1.5	0			33
<i>A apr</i>		5.1	4.7	9.2	13.5	11.6	7.1	27.8	15.7	10.5			1176
		0.7		9.8		29.7		21.4		15.7			84

TABLE 5. continued

Species	April		May		June		July		August		September		October		N
	II	I	II	I	II	I	II	I	II	I	II	I-II			
<i>A. tor</i>		0.7	0		2.8	1.6	3.5	1.6	0	1.6	0	0.1			58
Act abundance		0.9		4.3		1.4		0.7		0.7		0.5			62
<i>L. fe</i>		0.6		2.6		13.2		12.1		12.1		3.9			237

Although the LDAT of the various stages of *Calathus melanocephalus* is unknown, a calculation based on data from laboratory studies of five carabid beetle species occurring in Troms gave a mean LDT of 9.3°C (extremes 5.5 and 11.8°C) (Saska & Honek 2003). The temperatures in the uppermost layers of dry soil where *C. melanocephalus* mostly lives, are 2–7°C higher than the air temperatures during the summer (Andersen 1986). The LDAT of the various stages of *C. melanocephalus* is therefore supposed to lie somewhere between 0–7°C and the calculated SEAT of the species was therefore based on these two LDAT values. The same values were used for *Cicindela campestris*.

Spring breeders with summer larvae

A majority of the species could be placed in either of the two life cycle categories established by Larsson (1939): a) spring breeders with summer larvae and exclusive imaginal hibernation and b) autumn (summer) breeders with winter larvae. The first group consists of *Dyschirius globosus*, *Bembidion bruxellense*, *B. grapii*, *B. femoratum*, *B. quadrimaculatum*, *Amara lunicollis* Schiødte, 1837, *A. communis* (Panzer, 1797), *A. familiaris* and *A. interstitialis*. These species are generally most abundant, have the highest activity density and reproduce in May and June (Tables 4–5). Some species reproduce as early as in April in years with mild springs. The new generation of adults with teneral usually appears from end of July and the *Bembidion* spp. are abundant in August–October (Tables 3 and 5). Fully hardened females with immature ovaries are found in April/May and August–

October. This life cycle pattern coincides with that found for a number of riparian *Bembidion* species with spring breeding, summer larvae and exclusive imaginal hibernation in Northern Norway (Andersen 1983b).

Hence, the spring breeders of dry and mesic, open habitats accomplish their development from eggs to teneral in the course of a summer in Troms like in the southern parts of their distributional ranges (Lindroth 1945, Thiele 1977, Shilenkov 1978, den Boer & den Boer-Danje 1990). The main pattern in the life cycles of the current species is therefore independent of latitude. They are termed species with summer larvae.

If larvae of the species with summer larvae were able to survive the winter and develop to adults after hibernation, teneral would be expected to emerge earlier than usual after years with cold summers the preceding year. However, the earliest occurrence of teneral of any species with summer larvae was 10 July 2003 (*Bembidion femoratum*, Table 6) after an exceptionally warm spring and summer in 2002 (Table 1). The early occurrence of teneral of *Bembidion femoratum* in 2003, of *B. grapii* in 2002 and of *B. bruxellense* in 2005 (Table 6) was obviously due to the warm weather in spring and early summer these years (Table 1). Therefore, it is unlikely that larvae of the species with summer larvae are able to survive the winter (see also discussion in Andersen 1983b).

All the available data indicate that *Amara erraticata* has imaginal hibernation in the lowland of Troms. Above the treeline, however, larvae as well as adults may hibernate since this is the case in the alpine zone in Central Europe (Lindroth 1986).

**TABLE 6.** Additional information about the life cycle of the species. Numerals in brackets give the total number of individuals or the number of individuals with the actual feature of the total number of individuals examined. The dates are based on hand-collecting. I: first half of the month, II: second half of the month; +: TRY; \*: TRI. *M arc*: *Miscodera arctica*. For further abbreviations of species names see Tables 3 and 4.

Species	Adults		Tenerals		Ripe	
	Total period, months	Total period, months	First (early) record(s), date, month, year	Latest record, date, month, year	First record, date, month, year	Latest record, date, month, year
<i>D glo</i>	4 II-9 I (344)	8 I-9 I (2/184)	10.8-89(1/1)	10.9-08(1/4)	19.5-11(2/10)+	12.6-12(7/13)+
<i>B bru</i>			17.7-05(1/1)+	18.9-10(6/11)*	27.4-04(6/7)+	8.7-05(1/12)*
<i>B fem</i>			10.7-03(7/14)+	8.10-05(1/18)+	15.4-89(4/6)+	25.6-10(4/4)+
<i>B gra</i>			15.7-02(1/1)+	20.9-10(1/5)+	29.4-02(5/7)*	24.6-12(1/3)*
<i>B qua</i>			15.8-11(1/10)*	25.8-11 (1/23)*	22.5-11(1/3)*	24.6-12(3/3)*
<i>A lun</i>				10.9-92 (1/1)*	4.5-03 (1/1)+	25.6-12(4/4)*
<i>A fam</i>			26.8-11(1/2)*	30.8-11 (1/2)*	29.5-11 (1/1)*	20.6-11(1/1)*
<i>A com</i>			27.8-11(2/2)+	17.9-10(1/1)+	15.5-03(3/3)+	11.6-10(1/1)+
<i>A int</i>			5.8-04(3/4)*	26.9-87(1/4)+	19.5-10(3/5)*	12.7-93(1/1)*
<i>A err</i>	5 I-9 II (179)*	7 II-9 II(12/95)*	30.7-89(1/1)*	21.9-10(1/1)*	19.5-10(1/1)*	2.7-91(1/2)*
<i>P ads</i>			24.5-92(1/6)*	20.9-10(1/1)*	29.4-02(4/7)*	12.7-93(1/4)*
			2.6-00(2/2)+			
			21.6-93(1/1)+			
<i>D cog</i>			10.7-89(6/23)*	24.9-90(2/32)*	15.4-89(3/4)+	2.10-12(5/6)+
<i>C fos</i>	4 II-9 I (69)+*	5 II (1/1)*	22.5-92(1/1)*		14.6-93 (1/1)*	12.7-93(1/2)*
<i>M arc</i>	4 II-9 II (56)+*	7 I (1/1)*	10.7-89(1/1)*		4.6-12 (1/1)*	25.6-10(1/1)*
<i>N aqu</i>	4 II-10 I (631)	6 II- 7 II (75/341)	28.6-02(1/4)	25.7-91(2/13)+	23.5-11(2/3)+	19.9-91(3/8)+
<i>N ger</i>			29.6-94(1/3)*	24.7-92(1/6)*	1.6-01(1/3)+	28.8-06(1/1)*
<i>C mel</i>			26.6-01(1/4)+	3.9-94(1/1)+	23.5-11(1/3)*	29.8-12(1/6)+
<i>A que</i>			20.6-02(1/7)*	19.9-91(3/13)+	23.5-11(2/5)*	19.9-91(7/11)+
<i>A bif</i>	4 II (1) * 7 I-9 I (33)+	7 I- II (7/24) +	11.7-92(5/16)+	20.7-91(1/3)+		29.8-12(1/1)+
<i>A apr</i>			29.6-91(1/1)+	11.9-89(3/46)+	23.5-11(3/6)*	12.9-12(1/1)+
<i>A tor</i>			20.6-91(1/4)+	28.8-12(1/10)+	5.6-89(1/7)*	9.8-89(1/9)+

#### *Autumn (summer) breeders with winter larvae*

The autumn (summer) breeders with winter larvae consist of the following species: *Miscodera arctica*, *Notiophilus germinyi*, *N. aquaticus*, *Leistus ferrugineus*, *Calathus melanocephalus*, *Amara quenseli*, *A. apricaria*, *A. torrida* and *A. bifrons*. These species are usually most abundant and have the highest activity density in June to August at which time they reproduce, but females of some species have mature ovaries already in

May in years with mild springs (Tables 4–5). Tenerals emerge from the second half of June or the first half of July whereas the larvae hibernate since they mainly are found in autumn (September/October) and spring (Table 3). They are therefore termed species with winter larvae.

The highest known threshold temperature for development (LDT) of third stage larvae of any *Amara* species with summer larvae is 12.1°C with a sum of effective temperatures (SET) varying between 118.9 and 155.6 day degrees (Saska &

**TABLE 7.** Presence/absence in the alpine zone(Alp) and the arctic zone (Arc) in Scandinavia of the two life cycle categories of carabid beetles that occur regularly in Troms county. Arboreal and halobiontic (philous) species as well as such with accidental occurrences (single specimens) or with unknown life cycles in Troms are not considered. SL: exclusively summer larvae; WL: at least in part hibernation as eggs and/or larvae; \* : only regularly present in the alpine zone in Troms.

Species	SL		Species	WL		$\chi^2$	p
	Alp	Arc		Alp	Arc		
<i>Pelophila borealis</i>	+	+	<i>Cicindela campestris</i>	-	-		
<i>Elaphrus lapponicus</i>	+	-	<i>Cychrus caraboides</i>	+	+		
<i>E. riparius</i>	+	-	<i>Carabus glabratus</i>	+	-		
<i>E. cupreus</i>	-	-	<i>C. violaceus</i>	+	-		
<i>Diacheila arctica*</i>	+	+	<i>C. problematicus</i>	+	+		
<i>Loricera pilicornis</i>	-	-	<i>Leistus terminatus</i>	+	-		
<i>Dyschirius nigricornis</i>	-	-	<i>L. ferrugineus</i>	-	+		
<i>D. angustatus</i>	-	-	<i>Nebria rufescens</i>	+	+		
<i>D. globosus</i>	-	-	<i>N. nivalis*</i>	+	-		
<i>Bembidion velox</i>	-	-	<i>Notiophilus biguttatus</i>	+	-		
<i>B.lapponicum</i>	-	-	<i>N.aquaticus</i>	+	+		
<i>B.bipunctatum</i>	+	-	<i>N.germyni</i>	+	-		
<i>B. difficile</i>	-	-	<i>Clivina fossor</i>	+	-		
<i>B. prasinum</i>	-	-	<i>Miscodera arctica</i>	+	+		
<i>B. hyperboraeorum</i>	+	+	<i>Trechus obtusus</i>	+	-		
<i>B. virens</i>	-	-	<i>Patrobus septentrionis</i>	+	+		
<i>B. quadrimaculatum</i>	-	-	<i>P. assimilis</i>	+	+		
<i>B. schuppelii</i>	-	-	<i>P. atrorufus</i>	-	-		
<i>B. yukonum</i>	-	-	<i>Asaphidion pallipes</i>	-	-		
<i>B. grapii</i>	-	-	<i>Bembidion fellmanni</i>	+	+		
<i>B. femoratum</i>	-	-	<i>B. hastii</i>	+	+		
<i>B. bruxellense</i>	-	-	<i>B. scandicum</i>	-	-		
<i>B. petrosum</i>	-	-	<i>Pterostichus adstrictus</i>	-	-		
<i>B. saxatile</i>	-	-	<i>Calathus melanocephalus</i>	+	+		
<i>Agonum fuliginosum</i>	-	-	<i>C. micropterus</i>	-	+		
<i>A. consimile</i>	+	+	<i>Amara quenseli</i>	+	+		
<i>Amara communis</i>	-	-	<i>A. bifrons</i>	-	-		
<i>A. lunicollis</i>	-	-	<i>A. brunnea</i>	+	+		
<i>A. familiaris</i>	-	-	<i>A.praetermissa</i>	+	-		
<i>A. interstitialis</i>	-	-	<i>A. erratica</i>	+	-		
<i>Pterostichus oblongopunctatus</i>	-	-	<i>A. apricaria</i>	-	-		
<i>P. strenuus</i>	-	-	<i>A. torrida</i>	-	+		
			<i>A. alpina*</i>	+	+		
			<i>Dicheirotichus cognatus</i>	+	+		
			<i>D. placidus</i>	-	-		

TABLE 7. continued

Species	SL		Species	WL		$\chi^2$	p
	Alp	Arc		Alp	Arc		
			<i>Cymindis vaporariorum</i>	+	+		
In Alp/not in Alp	7/25 (21.9%)			25/11 (69.4%)		13.54	< 0.001
In Arc/not in Arc	4/28 (12.5%)			18/18 (50.0%)		9.24	< 0.01

Honek 2003). Converted to temperature sums with a LDT of 12.1°C, the third stage larvae of *A. apricaria* and *A. torrida* that were kept in the laboratory in autumn 2011, had been exposed to at least 164 and 480 day degrees, respectively, without pupating. Thus, the two larvae had been exposed to a higher thermal sum than the *Amara* species with summer larvae need for their whole development in the third larval stage. Third stage larvae of *Amara apricaria* and *A. torrida* therefore seem to be unable to pupate at high temperatures. *Amara apricaria* is a species of southern origin whereas *A. torrida* has a northern distribution in Fennoscandia. The northern species *Miscodera arctica* and two species of *Bembidion* with winter larvae also seem to be unable to pupate before hibernation in Central and Northern Norway (Andersen 1968, 1970, 1983b). Contrarily, among riparian *Bembidion* species with summer larvae, third stage larvae were repeatedly reared to adults during the summer (Andersen 1970, 1983b). Northern as well as southern species with winter larvae may therefore have larval dormancies in Northern Norway.

It is likely, therefore, that other species that have larval dormancies in Central Europe, such as *Calathus melanocephalus* and *Amara quenseli* (Dijk 1972, Hurka 1986), also have a larval diapause in Northern Norway. Teneralis of *Calathus melanocephalus*, *Amara apricaria*, *A. torrida* and *A. quenseli* that were found in ultimo August and in September, were therefore probably the descendants of a generation that had bred one year earlier. The teneralis of *C. melanocephalus* from September were certainly unable to breed before the winter since none of the dissected females were gravid and the adults were in the hibernation phase at that time (large aggregation of individuals). Furthermore, the last teneralis of *Amara quenseli* emerged so late

in autumn (19 September) that they hardly were able to reproduce before the winter. The actual individuals of *C. melanocephalus* and *A. quenseli* therefore obviously had a life cycle lasting more than one year.

Some individuals of *Notiophilus aquaticus*, *Calathus melanocephalus*, *Amara apricaria* and *A. quenseli* reproduce already in May, i.e. at the same time as the species with summer larvae. These beetles have undoubtedly hibernated because the females were gravid long before the appearance of the first teneralis (second half of June or first half of July). Since the three latter species seem to have a larval diapause in Troms, the larvae originating from the eggs laid in May obviously hibernate and continue the development to adults the following summer, i.e. the individuals use more than one year to fulfill their development.

The species with winter larvae therefore often have a development lasting more than one year in the lowland of Troms such as is the case with *Calathus melanocephalus* in the northern taiga in Russia (Filippov 2006).

However, in periods with favourable climatic conditions, a part of the population of *Calathus melanocephalus* probably has an annual life cycle in the lowland of Troms like the whole population of the species in Denmark (Schjøtz-Christensen 1965). In Eastern Jutland in Denmark, gravid females of *C. melanocephalus* were found as late as 27 October, whereas teneralis emerged between 29 May and 15 June in the period 1957–1961. Reasonably, the teneralis from mid June originated from eggs laid in end of October. The highest thermal sum between 27 October and 15 June in Eastern Jutland in the years 1957–1961 was in the period 1960–1961. The number of day degrees at a LDAT of 7° and 0°C was 260 and 1375 day degrees, respectively. In Denmark, the main reproduction period of *C. melanocephalus*

is delayed to August/September, whereas the species soon enters the reproduction phase after the eclosion in Troms. Teneral of *Calathus melanocephalus* that emerged as early as 26 June in Troms were therefore probably able to reproduce before 16 July because the highest fraction of pregnant females was found in the first part of July (Table 4). In the climatically favourable period 2002–2011, the number of day degrees between 16 July and 26 June was 312 in TRY and 393 in TRI at a LDAT of 7° and about 1415 in both areas at a LDAT of 0°C. These values are higher than those for Eastern Jutland between 27 October–15 June 1960–1961. At least in periods with a favourable climate, the thermal sums therefore seem to be high enough to realize an annual life cycle for parts of the populations of *C. melanocephalus*. This conclusion ought to be taken with reservation because the low angle of incidence of sunrays may lead to lower temperatures in the habitats of the species in Troms than in Denmark (see Andersen 1993, 1996). In addition, the thermal effect of differences in number of sun hours and precipitation is obscure.

*Amara bifrons* hibernates exclusively as a larva in South Sweden (Lindroth 1945) and the same is nearly the case in Troms. Thus, a single female was found in April, but all the other adults were collected in the period July to September (Table 6). Although the data are incomplete, they suggest that *A. bifrons* has an annual life cycle in Troms.

It is likely that the other species with winter larvae may have annual life cycles in Troms, at least in warm periods. However, this cannot be convincingly demonstrated with the present knowledge.

To summarize, larvae as well as adults of the species with winter larvae hibernate. *Amara bifrons* may exclusively have an annual life cycle, but the other species probably have annual life cycles as well as such lasting more than one year in the lowland of Troms.

### *Species with special life cycles*

Most of the data indicate that *Pterostichus adstrictus* is a spring breeder with summer larva.

Hence, the activity density is highest in May and the species reproduces between May and the first half of July (Tables 4–5). Furthermore, most larvae occur in summer and teneral from end of July (Table 3). Yet, the finds of a larva in second half of September and a teneral in late June indicate that larval hibernation is possible as also stated by Lindroth (1955). The occurrence of teneral 24 May 1992 and 2 June 2000 (Table 6) is much earlier in the season than for any other species (except for *Clivina fossor*, see below) despite normal temperature conditions in spring these years (Table 1). Such individuals have therefore probably hibernated as pupae. That pupal hibernation is possible among Carabidae is supported by the fact that pupae of *Carabus nemoralis* Müller, 1764 and *C. cancellatus* Illiger, 1798 sometimes overwinter (Lindroth 1945). The females of *P. adstrictus* are able to reach maturity when they are exposed to short as well as long day (Paarmann 1994). The species therefore has a flexible life cycle contrary to the species with summer larvae. The latter species need short day conditions followed by long day to ripen the ovaries (Paarmann 1994). Thus, the females of *P. adstrictus* originating from hibernating larvae or pupae are probably able to lay eggs in the course of the summer.

In Britain, *Clivina fossor* reproduces in early summer as well as in autumn suggesting larval as well as imaginal hibernation (Jones 1979). The following facts indicate that *C. fossor* may hibernate in most stages in the lowland of Troms: a larva was found as late as in second half of September which suggests larval hibernation. The find of a teneral 22 May 1992 (Table 6) shows that hibernation on the pupal stage is probable (see discussion of life cycle of *Pterostichus adstrictus* above). Since fully hardened beetles are present already in April, adults also hibernate.

*Dicheirotichus cognatus* seems to have two reproduction periods in TRY, one from April to June and another one in September/October (Table 4). Two reproduction periods are also evident in Central Europe (den Boer & den Boer-Daanje 1990). If the larvae develop to adults without parapause in Troms which seems to be the case in Central Europe (den Boer &

den Boer-Daanje 1990), eggs from the first egg laying period are probably those emerging as teneral in August/September. Females having mature ovaries in autumn may partly deposit the eggs the same year, but it is doubtful whether this applies to individuals with ripe eggs as late as in October (Table 6). The life cycle pattern in TRI is not evident. In conclusion, eggs, females with immature, probably also with mature ovaries, and perhaps even larvae of *Dicheirotrichus cognatus* seem to hibernate in Troms.

The development of *Cicindela* species lasts 2–2.5 years at southern latitudes (Lindroth 1945, Luff 1993, Pineda & Kondrathieff 2003). In Troms, however, the development of *C. campestris* lasts at least three years according to the facts presented below (the estimations are based on a LDAT of 0°C and the assumption that the development ceases 15 September since the holes are closed between 11 and 19 September). The observations show that larvae of all stages as well as adults hibernate. The larvae of group A had certainly been in the first stage some time before their holes were observed 30 July 2010 because the eggs are deposited in spring and early summer. Based on the prevailing air temperatures in Tromsø 2010–2011, this means that the first stage larvae require >800 day degrees before moulting (the larvae were in the first stage before 30 July 2010 to at least 9 June 2011). A single larva of group A was still in the second stage 13 August 2011, indicating that the second stage larvae require >620 day degrees before moulting. The larvae of group B were in the third stage before 18 June 2011 and in the same stage 7 September. The third stage larvae therefore require >940 day degrees before pupation. To realize a 2-year life cycle with reproduction in spring–early summer 2012, the larvae of group A would have <1160 day degrees (between 9–18 June and 15 September) to develop from second stage larvae to adults. This value is far too low since the observations indicate that the 2+3 stages alone require a thermal sum of >1560 day degrees. The larvae of group A therefore certainly continued their development in 2012, probably with adult eclosion in late summer and reproduction in spring or early summer 2013, i.e. the life cycle lasts at least three years. The

conclusion is the same when a LDAT of 7°C is used as a limit. Since the mean temperature from April to September in 2010–2011 was about 1°C above that in the normal period 1961–1990, a development lasting at least three years is the normal situation for the species in Troms where it reaches its northern limit.

#### *Life cycle, climate and distribution*

Insects cope with climatic changes and variations in several ways (Hodkinson 2005). Species may produce smaller or fewer eggs, smaller adults, switch from an annual life cycle to one lasting more than one year, develop faster or reproduce earlier in the season in areas with colder climates (Refseth 1988, Paarmann 1994, Sota 1996, Ernsting & Isaaks 1997, 2000, Killengren 2002, Khobrakova & Sharova 2005, Filippov 2006). The last possibility was evident for *Calathus melanocephalus* and *Leistus ferrugineus*. Hence, the two species reproduce in autumn in South Scandinavia whereas their reproduction period is from May or June to August in Troms.

*C. melanocephalus* and *L. ferrugineus* have an imaginal aestivation period in summer in Central Europe (Dijk 1972, Thiele 1977). The gonadal development is suppressed by continuous long day in such species, but egg ripening is triggered by changeover to short day (Thiele 1977). Nonetheless, the ripening of the ovaries of *C. melanocephalus* and *L. ferrugineus* takes place during long day (mainly midnight sun) conditions in Troms. Therefore, there may be genetical differences between the populations of the species in Central Europe and Central/Northern Norway (see also Refseth 1986).

A common way of coping with short and cold summers is to change from an annual life cycle to one lasting more than one year (Sømme 1995, Sota 1996). Thus, even in the lowland of Troms, *Calathus melanocephalus*, *Amara apricaria* and *A. quenseli* have life cycles that seem to last more than one, but hardly two full years. However, in warm years, parts of the population of *C. melanocephalus* may have an annual life cycle in the county. The lowland of Troms, which is situated in the middle and northern boreal zones,



may therefore constitute a transitional zone between one where the species mainly have annual life cycles and one where most species need more than one year to fulfill their development.

The proportion of species occurring in the alpine and arctic zones was significantly lower among those with summer larvae than among those with winter larvae (Table 7). Sømme (1995) also quoted that the frequency of species that occur in the alpine zone is much lower for univoltine species than for those with prolonged life cycles. The thermal sums are lower in the alpine and arctic zones than elsewhere in the country. As stated by Andersen (1984), the species with summer larvae therefore generally seem to depend on warmer summers than the species with winter larvae.

Species with summer larvae probably make up more than 50% of the total number of the Carabidae species in Norway. One of the main reasons why so many carabid beetle species are absent in northernmost Europe may therefore be that the summers are too cool and short to realize an annual life cycle there.

Mean temperatures have risen over a more or less long period dependent upon area. This global warming is predicted to continue (Begon *et al.* 2006). According to Butterfield (1996) carabid beetles are more likely to respond to climate change by changing distributions than by physiological adaptations. Thus, many animal species have changed their distributions in recent time (e.g. Parmesan *et al.* 1999, Begon *et al.* 2006, Chen *et al.* 2011). Nevertheless, with a warmer climate, changes in the life cycle pattern of carabid beetles could be expected. For example, *Calathus melanocephalus* partly seems to have an annual life cycle in periods with favourable climatic conditions in the lowland of Troms. As temperatures rise, a complete changeover to annual life cycles of the species with winter larvae may be possible. In addition, it cannot be ruled out that climatic changes may lead to the selection of genotypes with a changed response to photoperiod. Species with summer larvae and exclusive imaginal hibernation may also to some extent change phenology. Hence, the warm springs in Troms in the period 2002–2011 led to early reproduction and emergence of teneral of

some of the species with summer larvae such as *Bembidion femoratum* and *B. bruxellense*.

## References

- Andersen, J. 1968. The larva of *Miscodera arctica* Payk. (Col. Carabidae). *Norsk entomologisk Tidsskrift* 15, 71–74.
- Andersen, J. 1970. Habitat choice and life history of Bembidiini (Col., Carabidae) on river banks in central and northern Norway. *Norsk entomologisk Tidsskrift* 17, 17–65.
- Andersen, J. 1983a. The habitat distribution of species of the tribe Bembidiini (Coleoptera, Carabidae) on banks and shores in northern Norway. *Notulae Entomologicae* 63, 131–142.
- Andersen, J. 1983b. The life cycles of the riparian species of *Bembidion* (Coleoptera, Carabidae) in northern Norway. *Notulae Entomologicae* 63, 195–202.
- Andersen, J. 1984. A re-analysis of the relationships between life cycle patterns and the geographical distribution of fennoscandian carabid beetles. *Journal of Biogeography* 11, 479–489.
- Andersen, J. 1986. Temperature response and heat tolerance of riparian Bembidiini species (Coleoptera: Carabidae). *Entomologia Generalis* 12, 57–70.
- Andersen, J. 1993. Beetle remains as indicators of the climate in the Quaternary. *Journal of Biogeography* 20, 557–562.
- Andersen, J. 1995. A comparison of pitfall trapping and quadrat sampling of Carabidae (Coleoptera) on river banks. *Entomologica Fennica* 6, 65–77.
- Andersen, J. 1996. Do beetle remains reliably reflect the macroclimate in the past? – a reply to Coope & Lemdal. *Journal of Biogeography* 23, 115–121.
- Andersen, J. 2011. Winter quarters of wetland ground beetles (Coleoptera, Carabidae) in South Scandinavia. *Journal of Insect Conservation* 15, 799–810.
- Andersen, J. & Olberg, S. 2003. New records of Coleoptera from Northern Norway. *Norwegian Journal of Entomology* 50, 57–67.
- Arneberg, P. & Andersen, J. 2003. The energetic equivalence rule rejected because of a potentially common sampling error: evidence from carabid beetles. *Oikos* 101, 367–375.
- Aune, B. 1993. *Air temperature normals, normal period 1961–1990*. Det Norske Meteorologiske Institutt – klimaavdelingen, Oslo.

- Begon, M., Townsend, C.R. & Harper, J.L. 2006. *Ecology. From individuals to ecosystems*. Blackwell, Malden.
- Bjørnbæk, G. 1994. *Norsk vær i 100 år*. Teknologisk Forlag, Drammen.
- Butterfield, J. 1996. Carabid life-cycle strategies and climate change: a study on an altitude transect. *Ecological Entomology* 21, 9–16.
- Chen, I.-C., Hill, J.K., Ohlemmüller, R., Roy, D.B. & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026.
- den Boer, P.J. & den Boer-Daanje, W. 1990. On life history tactics in carabid beetles: are there only spring and autumn breeders? Pp. 247–258 in: Stork, N. E. (ed). *The role of ground beetles in ecological and environmental studies*. Intercept, Andover.
- Dijk, T.S.van. 1972. The significance of the diversity in age composition of *Calathus melanocephalus* L. (Col., Carabidae) in space and time at Schiermonnikoog. *Oecologia (Berlin)* 10, 11–136.
- Ernsting, G. & Isaaks, A. 1997. Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus*. *Ecological Entomology* 22, 32–40.
- Ernsting, G. & Isaaks, A. 2000. Ectoterms, temperature, and trade offs: size and number of eggs in a carabid beetle. *American Naturalist* 155, 804–81.
- Filippov, B.Y. 2006. Seasonal aspects of life cycles in the ground beetles *Calathus melanocephalus* and *C. micropterus* (Coleoptera, Carabidae) in the northern taiga. *Zoologiceskij Zhurnal* 85, 1196–1204 (in Russian with an English abstract).
- Filippov, B. Y. 2007. Seasonal patterns of life cycle of ground beetle *Carabus nitens* (Coleoptera, Carabidae) in southern tundra. *Biology Bulletin* 34, 577–582.
- Førland, E.J. 1993. *Precipitation normals. Normal period 1961–90*. DNMI – Klimaavdelingen, Oslo.
- Gamst, U.R.B. 2006. Flowering and fruit-set in Tromsø – new data from 2003–2006. *Polarflokken* 30, 123–138.
- Hanssen, V.G. 2007. Livssyklus hos løpebiller (Coleoptera, Carabidae) i en temperaturgradient i NordNorge. Cand Scient Thesis, University of Tromsø, Tromsø.
- Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80, 489–513.
- Hurka, K. 1986. The developmental type of Carabidae in the temperate zones as a taxonomic character. Pp. 187–193 in: den Boer, P.J., Luff, M.L., Mossakowski, D. & Weber F. (Eds) *Carabid beetles: Their adaptations and dynamics*. Fischer, Stuttgart.
- Jones, M.G. 1979. The abundance and reproductive activity of common Carabidae in a winter wheat crop. *Ecological Entomology* 4, 31–43.
- Khobrakova, L.S. & Sharova, I.K. 2005. Life cycles of ground beetles (Coleoptera, Carabidae) from the mountain taiga and mountain forest steppe in the eastern Sayan. *Biology Bulletin* 32, 571–575.
- Killengren, S.T. 2002. *Flexibility in life history traits of Amara brunnea and Calathus micropterus, two species of the family of Carabidae*. Cand Scient Thesis, University of Tromsø, Tromsø.
- Larsson, S.G. 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. *Entomologiske Meddelelser* 20, 277–560.
- Larsson, S.G. 1968. Løbebillernes larver. *Danmarks Fauna* 76, 282–433.
- Lindroth, C.H. 1945. Die fennoscandischen Carabidae. I. Spezieller Teil. *Göteborgs Kungliga Vetenskaps och vitterhet Samhälles Handlingar* B 4, 1–709.
- Lindroth, C.H. 1955. The carabid beetles of Newfoundland. *Opuscula Entomologica*. Suppl. 12, 1–160.
- Lindroth, C.H. 1985–86. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna entomologica scandinavica* 15, 1497.
- Lövei, G.L. & Magura, T. 2011. Can carabidologists spot a pitfall? The non-equivalence of two components of sampling effort in pitfall-trapped ground beetles (Carabidae). *Community Ecology* 12, 18–22.
- Luff, M.L. 1993. The Carabidae (Coleoptera) larvae of Fennoscandia and Denmark. *Fauna entomologica scandinavica* 27, 1–187.
- Makarov, K.V. 1994. Annual reproduction rhythms of ground beetles: a new approach to the old problem. Pp. 177–182 in Desender, K., Dufréne, M., Loreau, M., Luff, M.L. & Maelfait, J.P. (eds). *Carabid beetles: Ecology and evolution*. Kluwer, the Netherlands.
- Matalin, A.V. 2007. Typology of life cycles of ground beetles (Coleoptera, Carabidae) from western Palearctic. *Zoologiceskij Zhurnal* 86, 1196–1220 (in Russian with English summary).
- Moen, A. 1998. *Nasjonalatlas for Norge: vegetasjon*. Statens kartverk, Hønefoss.
- Naujok, J. & Finch, O.-D. 2004. Communities and spatio-temporal patterns of epigeic beetles (Coleoptera) in high mountain habitats of the Central Norwegian Scandes, with special emphasis on carabid beetles. *Norwegian Journal of Entomology* 51, 31–55.

- Olsvik, P.A., Ødegaard, F. & Hanssen, O. 2001. The beetle fauna (Coleoptera) of the arctic mainland of Norway. *Fauna norvegica* 21, 17–24.
- Paarmann, W. 1994. Temperature and photoperiodic influence in developmental stages and adults of the subarctic carabid beetle *Pterostichus adstrictus* (Coleoptera). Pp. 201–205 in Desender, K., Dufrene, M., Luff, M. L. & Maelfait, J. P. (eds). *Carabid beetles: Ecology and evolution*. Kluwer, the Netherlands.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.M. & Warrens, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583.
- Pineda, P.M. & Kondrathieff, B.C. 2003. Natural history of the Colorado great Sand Dunes tiger beetle, *Cicindela theatina* Rotger. *Transactions of the American entomological Society* 129, 333–360.
- Refseth, D. 1980. Differences in seasonal activity pattern and breeding time of *Patrobus atrorufus* (Carabidae) in central Norway. *Holarctic Ecology* 3, 87–90.
- Refseth, D. 1986. Phenological adaptations in *Patrobus atrorufus* and *P. assimilis* (Col., Carabidae). *Fauna norvegica* B 33, 57–63.
- Refseth, D. 1988. Annual patterns of activity, reproduction and development in some Norwegian Carabidae (Col.). *Fauna norvegica* B 35, 21–30.
- Saska, P. & Honek, A. 2003. Temperature and development of central European species of *Amara*. *European Journal of Entomology* 100, 509–515.
- Saurdal, G. 2005. *A survey of the riparian Coleoptera fauna along the river Altaelva after 15 years with regulation*. Master thesis, University of Tromsø.
- Schjøtz-Cristensen, B. 1965. Biology and population studies of Carabidae of the Corynephoretum. *Natura Jutlandica* 11, 1–173.
- Shilenkov, V.G. 1978. Biological characteristics of abundant species of Carabidae (Coleoptera) in South Cisbaikalia. *Entomological review* 57, 202–209.
- Silfverberg, H. 2004. Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae. *Sahlbergia* 9, 1–111.
- Sømme, L. 1995. *Invertebrates in hot and cold arid environments*. Springer, Berlin.
- Sota, T. 1996. Altitudinal variation in life cycles of Carabid beetles: life cycle strategy and colonization in alpine zones. *Arctic and alpine research* 28, 441–447.
- Thiele, H.U. 1977. Carabid beetles in their environment. *Zoophysiology and Ecology* 10, 1–369.
- Turin, H., Penev, L. & Casale, A. (eds). 2003. *The genus Carabus in Europe. A synthesis*. Pensoft, Sofia and European Invertebrate Survey, Leiden.
- Vik, A. 1991. *Catalogus Coleopterorum Norvegica*. Stig Otto Hansen, Larvik.

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