

The life cycles of carabid beetles (Coleoptera, Carabidae) in wetlands and forests in Northern Norway

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The life cycle of 30 carabid beetle species originating from wetlands and forests was studied by assessing the reproduction period and the seasonal occurrence of larvae, teneral and fully hardened adults in the lowland of Nordland and Troms counties. Thirteen species reproduce in spring and early summer, have summer larvae and hibernate exclusively as adults with immature gonads (summer larvae species). Eggs and perhaps pregnant females of *Dicheirotichus placidus* (Gyllenhal, 1827) hibernate. Sixteen species hibernate as larvae, most of them also as adults (winter larvae species). *Notiophilus biguttatus* (Fabricius, 1779) has been regarded as a species with exclusive imaginal hibernation in Fennoscandia, but in Northern Norway it hibernates as a larva as well. Several winter larvae species have an adult dormancy period in summer in Central Europe, but this does not apply to Northern Norway. Species therefore often start to reproduce at least one month earlier in Northern Norway than in Central Europe. This may be the reason why some winter larvae species may be able to have annual life cycles in Northern Norway, at least in years with high thermal sums. However, *Patrobis atrorufus* (Strøm, 1768) and *Calathus micropterus* (Duftschmid, 1812) have life cycles that may last more than one year in the lowland and the same may be true for several other winter larvae species. Although the winter larvae species constitute a large group, few species seem to hibernate exclusively as larvae. Among the species of the present study this applies to *Leistus terminatus* (Panzer, 1793) and probably also to *Trechus secalis* (Paykull, 1790). It is concluded that many species of a southern origin have the same main life cycle at their northernmost occurrences in Fennoscandia as elsewhere. A majority of them are summer larvae species.

Key words: Carabidae, life cycle, wetland and forest habitats, Northern Norway.

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Introduction

Due to the climate, the southern and middle boreal vegetational zones extend further north in Norway than in any other parts of the world (Moen 1998). Beetles, including many Carabidae species of a southern origin, also frequently have their northernmost occurrences in Fennoscandia in the lowland of Northern Norway (Andersen & Olberg

2003, Andersen 2013). The geographical range of carabid beetles may mainly be determined by their life cycles (Andersen 1984, 2013). This is supposed to apply especially to the species that have life cycles that chiefly are independent of altitude and latitude (Andersen 1983b, 2013, Lindroth 1985–1986, Filippov 2007). However, until now, published data that document the life cycle pattern of carabid beetles at or near their

northernmost occurrences were incomplete, merely treating riparian species and species of open, more or less dry habitats (Andersen 1983b, 2013). The present study treats the life cycle pattern of a number of other carabid beetles occurring in various types of wetlands and forests in Nordland and Troms counties. A main focus of the study was to elucidate whether the species with a wide geographical range have the same life cycle in Northern Norway as elsewhere in their distributional range.

A substantial part of the information about the life cycles of carabid beetles given in Table 7 in Andersen (2013) was based on data quoted in the present paper. Life cycle data of *Bembidion velox* (Linnaeus, 1761) and *B. bipunctatum* (Linnaeus, 1761) in Northern Norway have also been published previously (Andersen 1970, 1983b), but much new information about the two species is given in the present survey.

Study area

The investigated localities are situated in Nordland county in Bodø municipality in the coastal province NSY (67.33° N), in Fauske and Saltdal municipalities in the inland province NSI (67.08–67.25° N), in Troms county in the coastal province TRY (69.5–69.75° N) and the inland province TRI (68.75–69.40° N). All the localities are situated in the lowland (maximum elevation 78 m) and in the southern boreal (some localities in NSY) and middle boreal zones (Moen 1998). The investigated sites comprise moist to dry deciduous forests, clayish slopes, screes, various types of freshwater fringes including bogs and fens, estuaries and open, anthropogenic habitats like sand pits, fallow fields, arable land, meadows etc.

The mean temperature in April–September for five meteorological stations in NSY and NSI in the period 1961–90 was 9.0° C, for seven stations in TRI 8.0°C and for four stations in TRY 7.5°C (Data from Aune 1993, Andersen 2013). Compared with the normal period 1961–90, the period 2002–2014 was extraordinarily warm in Northern Norway. This among others applied to

the years 2002, 2003, 2009 and above all 2013.

Material and methods

Four sampling methods were used: 1) Hand collection without time notion. Performed from 1986 to 1989; 2) Hand collection with time notion. Performed from 1990 to 2015; 3) Sieving. The litter layer from the forest floor and from open, dry or moist sites with luxuriant vegetation as well as turf from bogs and mires was sifted through a sieve with mesh size 5.5 mm. The sifted material was investigated in the laboratory. Sieving was performed from 2004–2015. Larvae of some of the species were exclusively collected by this method; 4) Pitfall trapping. The method was used in the periods 2001–2003, 2007–2008 and in 2014. Methods 1, 2 and 4 were described in detail by Andersen (1970, 1995, 2013).

Criteria for distinguishing between developmental stages of the ovaries (mature and immature) and between fully hardened and teneral adults were according to Andersen (2013). It should be emphasized that beetles that have been classified as teneral always were definitely softbodied (Andersen 2013). The larvae were identified according to Luff (1993) and Kleinwächter & Larink (2006). Larvae of several *Dyschirius* species have been described, but not the larva of *D. nigricornis* Motschulsky, 1844. In the present study, larvae that were regarded to belong to *D. nigricornis* were those that were collected in sites where repeated collecting only gave adults of that species of the genus.

Information about the ecology and distribution of the species is given in Table 1. The original habitats of the species are wetland and/or forests (Lindroth 1985–1986, Andersen 2000). *Amara brunnea* (Gyllenhal, 1810), *Harpalus laevipes* Zetterstedt, 1828 and *Dicheirotichus placidus* (Gyllenhal, 1827) belong to taxa whose members mainly are phytophagous, whereas the rest of the species in Table 1 are carnivorous or mixed feeders (Lindroth 1985–1986, Toft & Bilde 2002, Honek *et al.* 2003, Lövei & Magura 2006, Shearin *et al.* 2007).

The material sampled in anthropogenic habitats in Troms has partly been collected in

the same sites and at the same time as that of the species treated in Andersen (2013), but other species are considered in the present paper.

Results

The material comprises more than 10,000 adults and 305 larvae of 30 Carabidae species that were collected in the period from March to October. More than 2,000 females were dissected for examination of the state of the ovaries. Data about the life cycle of the species are shown in Tables 2–6. Further data and comments are given below (explanation of symbols: I: early part; II: late part).

The species of group a (Table 1) have high relative abundance and activity abundance in May or June at which time they also reproduce. Some species have a new adult abundance peak in August or September. Dissected females of the following species of the group had immature ovaries between July II and September, some of them also in April/May: *Loricera pilicornis* (Fabricius, 1775), *Elaphrus cupreus* Duftschmid, 1812, *Dyschirius nigricornis*, *Bembidion bipunctatum*, *B. velox*, *B. yukonum* Fall, 1926, *Pterostichus oblongopunctatus* (Fabricius, 1787, *P. rhaeticus* Heer, 1837, *P. strenuus* (Panzer, 1796), *P. diligens* (Sturm, 1824) and *Agonum fuliginosum* (Panzer, 1809). Nearly all the larvae of group a were found from June II to August II, but in the warm spring/early summer 2002 a second stage larva of *Dyschirius nigricornis* was found as early as 7 June in NSI (Table 4). Teneral usually emerge between July II and September. It should be noted that the teneral of *Pterostichus strenuus* from September II (Table 3) was collected as late as 18.9 in the warm year 2013.

In addition to the life cycle data for group b given in Tables 1 to 6 the following data about the group was available: Fully hardened adults of *Carabus glabratus* Paykull, 1790 were found from June I to September I. Fully hardened adults of *C. violaceus* Linnaeus, 1758 occurred from May I to August I, whereas a teneral was found in August I (NSY). Fully hardened adults of *Cychrus caraboides* (Linnaeus, 1758) have been collected from June I to August II. Three dissected females

from July I–II had mature ovaries.

Group b is rather heterogeneous. Adults of a majority of the species have the highest activity abundance and relative abundance in July–August, some species in May–June (Tables 5–6). Most species have mature ovaries in the period May II or June to August/September (Table 2). Dissected females of *Asaphidion pallipes* (Duftschmid, 1812), *Notiophilus biguttatus* (Fabricius, 1779), *Patrobus assimilis* Chaudoir, 1844, *Trechus obtusus* Erichson, 1837, *Calathus micropterus* (Duftschmid, 1812) and *Harpalus laevipes* had immature ovaries in July I or II, in August and/or in September/October whereas *Leistus terminatus* (Panzer, 1793) and *Patrobus assimilis* had immature ovaries in June I.

Dicheirotichus placidus was the only member of group c. Table 2 and the following data show that the species has a wide reproduction period: four of five females from 26 October 2014 and two of four females from 15 March 2015 (TRY) had mature ovaries.

Discussion

The sampling methods applied in the present investigation are mainly the same as those used in previous studies of life cycles of carabid beetles and they have been found to be relevant to such studies (Andersen 2013). Although a female-biased sex-ratio of species in catches from pitfall traps is possible (see Yamashita *et al.* 2010) we can not see that this should lead to a serious bias in our results.

Larsson (1939) divided the carabid beetles into two life cycle categories: spring breeders and autumn breeders. den Boer & den Boer-Daanje (1990) found this division inadequate and we are of the same opinion. Instead den Boer & den Boer-Daanje (1990) distinguished between species with summer larvae and such with winter larvae. Nearly all the species of the first group reproduce in spring and early summer. However, the authors also included some species that reproduce from autumn to spring e.g. *Dicheirotichus cognatus* (Gyllenhal, 1827) among those with summer larvae. According to our opinion it is important to

TABLE 1. Distribution and ecology of the Carabidae species. The information is based on Lindroth (1945,1949, 1985-1986), Fjellberg (1972), Andersen (1983a, 2000), Vik (1991), Andersen & Olberg (2003), Naujok & Finch (2004), Saurdal (2005) and Hanssen (2007). The nomenclature follows Silfverberg (2004). Symbols in brackets : occasional occurrence in a zone; mb: middle boreal; nb: northern boreal; la: low alpine; ma: middle alpine; ha: high alpine; 1: mesic- dry, anthropogenic sites, mineral soil; 2: mesic- dry, anthropogenic meadows; 3: supralittoral, mesic- dry sandy or gravelly areas at the sea, seminatural or natural; 4: freshwater fringes, mineral soil; 5: freshwater fringes, soft substratum; 6: fens, bogs; 7: outlet of rivers or brooks at the sea; 8: moist-mesic slopes with moving clay; 9: screes of schist; 10: deciduous forest with mesic - dry soil; 11: deciduous forest with moist soil. Numerals in bold: the material exclusively or mainly originates from the habitat(s) in question. +: Red listed in Norway (Kålås *et al.* 2010). ×: the distribution of the species is incompletely known due to confusion with the sibling species *P. nigrata* Heer, 1837. °: dubious record. *: In Table 7 in Andersen (2013) the species has erroneously been quoted from the alpine zone, but the + -sign for the alpine zone (Alp) concerns *Leistus ferrugineus* (Linnaeus, 1758). The abbreviated species names are those used in Tables 2-6. The life cycle groups are explained in the text.

Life cycle group	Species	Most elevated vegetation zone in Scandinavia	Habitats in Northern Norway	Provinces in Northern Norway	
a	<i>Pelophila borealis</i> (<i>Pel bor</i>)	la	4, 5	NS, NN, TR, F	
	<i>Loricera pilicornis</i> (<i>Lor pil</i>)	nb	1, 2, 3, 4, 5, 7, 10, 11	NS NN TR F	
	<i>Elaphrus cupreus</i> (<i>Ela cup</i>)	nb	4, 5, 6, 7, 8	NS, NN, TR, FV, FN, FØ	
	<i>E. riparius</i> (<i>Ela rip</i>)	la	1, 4, 5, 7	NS, NNØ, TR, F	
	<i>Dyschirius nigricornis</i> (<i>Dys nig</i>)	nb	1, 4, 7, 8	NS, NNØ, TR, F	
	<i>Bembidion velox</i> (<i>Bem vel</i>)	nb	4	TRI, FI, FN, FØ	
	<i>B. bipunctatum</i> (<i>Bem bip</i>)	nb (la)	1, 3, 4, 5, 7, 8, 9	NS, NN, TR, F	
	<i>B. yukonum</i> (<i>Bem yuk</i>) ⁺	nb	8, 9	TR, F	
	<i>Pterostichus oblongopunctatus</i> (<i>Pte obl</i>)	mb(nb)	1, 2, 4, 9, 10, 11	NS, NNV, TR, FV	
	<i>P. rhaeticus</i> (<i>Pte rha</i>) [×]	nb?	6	TR, FØ	
	<i>P. strenuus</i> (<i>Pte str</i>)	mb	1, 2, 4, 9, 11	NS, NN, TR	
	<i>P. diligens</i> (<i>Pte dil</i>)	la	1, 2, 6	NS, NNV, TR, F	
	<i>Agonum fuliginosum</i> (<i>Ago ful</i>)	nb	1, 2, 4, 5, 6, 11	NS, NN, TR, F	
	b	<i>Asaphidion pallipes</i> (<i>Asa pal</i>)	nb	1, 4, 8	NS, NNØ, TR, F
		<i>Leistus terminatus</i> (<i>Lei ter</i>)	nb*	1, 2, 4, 10, 11	NS, NNØ, TR, FV, FN
<i>Nebria rufescens</i> (<i>Neb ruf</i>)		ma(ha)	1, 2, 3, 4, 9, 10, 11	NS, NN, TR, F	
<i>Notiophilus biguttatus</i> (<i>Not big</i>)		la	1, 2, 4, 9, 10, 11	NS, NN, TR, F	
<i>Carabus glabratus</i> (<i>Car glab</i>)		ma	1, 2, 10, 11	NS, NN, TR, F	
<i>C. violaceus</i> (<i>Car vio</i>)		la	1, 8, 10	NS, NN, TR, FV, FN	
<i>Cychrus caraboides</i> (<i>Cyc car</i>)		la	1, 2, 10, 11	NS, NN, TR, FV, FN, FØ	
<i>Patrobus septentrionis</i> (<i>Pat sep</i>)		ha	1, 2, 5, 6, 11	NS, NN, TR, F	
<i>P. assimilis</i> (<i>Pat ass</i>)		la	1, 2, 4, 5, 6, 10, 11	NS, NN, TR, F	
<i>P. atrorufus</i> (<i>Pat atr</i>)		nb	1, 11	NS, NN, TRY	
<i>Trechus secalis</i> (<i>Tre sec</i>)		mb	1, 2, 10, 11	NS, TRI °	
<i>T. rubens</i> (<i>Tre rub</i>)		nb	1, 4, 7, 8, 9, 11	NS, NN, TR, FV, FØ	
<i>T. obtusus</i> (<i>Tre obt</i>)		la (nb)	1, 2, 10, 11	NS, NN, TR	
<i>Calathus micropterus</i> (<i>Cal mic</i>)		nb	1, 2, 3, 4, 7, 10, 11	NS, NN, TR, F	
<i>Amara brunnea</i> (<i>Ama bru</i>)		la	1, 2, 4, 8, 10, 11	NS, NN, TR, F	
<i>Harpalus laevipes</i> (<i>Har lae</i>)		nb	1, 2, 9, 10	NS, NN, TR, FV, FN, FØ	
c		<i>Dicheirotrichus placidus</i> (<i>Dic pla</i>)	nb	1, 2, 4, 7, 10, 11	NS, NN, TR, FV

TABLE 2. The reproduction period of the carabid beetles. The fractions give the number of females with mature ovaries of the total number of dissected females. Some data are taken from Andersen (1983 b, 1995). For abbreviations of species names see Table 1. I: first part; II: second part. The differences in the ratio of the frequencies between May–July I and July II–October (Oct I–II) were tested by means of 2x2 contingency tables with Yate’s correction and expected values ≥ 3.0 . ns: not significant ($p > 0.05$); *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. \leftarrow : ratio significantly highest in May–July I; \rightarrow : ratio significantly highest in July II–October.

Species	County	May I–II	June I	June II	July I	July II	Aug I	Aug II	Sep I	Sep II	Oct I–II	χ^2
<i>Pel bor</i>	TR	1/3	8/12	3/4	26/37	1/1				0/1		
<i>Lor pil</i>	TR, N	17/22	23/27	3/7	1/2	1/2	0/9	0/11	0/4	0/1		35.66*** \leftarrow
<i>Ela cup</i>	TR, N	2/5	11/16	2/2	15/23	2/8	0/2					5.14* \leftarrow
<i>Ela rip</i>	TR, N	1/1	11/14	9/11	0/1	2/4	0/1	0/2				
<i>Dys nig</i>	TR	6/9	6/9	1/5	3/4	0/4	0/12	0/2				14.07*** \leftarrow
<i>Bem vel</i>	TR		7/7	3/3	11/17	2/2	0/2	0/14				16.63*** \leftarrow
<i>Bem bip</i>	TR, N	15/18	5/13	11/14	20/36	3/18		0/14				24.29*** \leftarrow
<i>Bem yuk</i>	TR		2/2		0/5			0/1	0/1	0/3		
<i>Pte obl</i>	TR, N	35/42	42/42	11/17	0/1	0/10	0/1	0/2		0/1		45.44*** \leftarrow
<i>Pte rha</i>	TR	6/8	10/12	2/2		0/1	0/4	0/2	0/2	0/1		15.53*** \leftarrow
<i>Pte str</i>	TR, N	3/3	7/9	6/13		0/2	0/2	0/2		0/3	0/1	9.35** \leftarrow
<i>Pte dil</i>	TR, N	7/7	10/14	7/7	0/5	0/4	0/1	0/2	0/4		0/2	16.95*** \leftarrow
<i>Ago ful</i>	TR, N	2/20	58/70	22/25	3/7	3/8	0/8	0/9	0/4	0/7	0/1	41.07*** \leftarrow
<i>Asa pal</i>	TR	5/9	4/9	5/8	12/17	6/8	1/2	5/9	0/3			0.04 ns
<i>Lei ter</i>	TR, N		0/6	0/3	14/16	13/14	14/16	5/6	2/2			7.56** \rightarrow
<i>Neb ruf</i>	TR, N	0/1	0/7	3/9	1/1	3/5	3/5	1/3				2.06 ns
<i>Not big</i>	TR, N	3/4	6/7	4/8	8/14	4/8	32/34	12/16	8/14	3/4	0/2	1.12 ns
<i>Car gla</i>	TR			1/1	1/2	0/1	2/3					
<i>Car vio</i>	TR, N			0/4		0/2	1/2					
<i>Pat sep</i>	TR	0/1	2/2	4/4	1/3	0/1	0/1					
<i>Pat ass</i>	TR	0/13	1/3	19/21	9/16	6/12	0/7	0/7	0/4			8.10** \leftarrow
<i>Pat atr</i>	TR	0/16	41/51	55/68	48/76	58/71	57/70	32/75	0/1			<0.01 ns
<i>Tre sec</i>	N				2/6	1/1	25/30					
<i>Tre rub</i>	TR	0/3	0/1		1/1		0/2					
<i>Tre obt</i>	N, TR	0/6	3/5	3/8	14/19	10/20	5/30	3/25	1/5		0/2	8.97** \leftarrow
<i>Cal mic</i>	TR, N	3/6	24/36	40/50	45/59	33/44	17/23	5/6	0/2		0/3	0.19 ns
<i>Ama bru</i>	TR, N	5/6	1/17	0/12	2/6	0/3	1/1					
<i>Har lae</i>	N, TR		0/2		2/3		1/2					
<i>Dic pla</i>	TR, N	2/5	11/16	0/3	3/14	0/9	0/8	19/48	4/8	8/20	10/11	0.01 ns

distinguish between such species and species that breed only in spring and early summer and hibernate exclusively as adults with immature gonads. Matalin (2007) divided the life cycle of carabid beetles in the western Palearctic in 30 variants. Among others he distinguished between 11 types regarding time of reproduction in the course of the

year. We could not apply this detailed grouping to our data from Northern Norway because the time of reproduction of one and the same species may vary considerably from one year to another (Andersen 2013). For practical purposes, we found it relevant to operate with three main life cycle groups. They constitute a modification of

TABLE 3. Seasonal occurrence of teneral of the carabid beetles. The fractions give the number of teneral of the total number of individuals examined. The differences in the ratio between April–July I and July II–October I–II were tested by means of 2x2 contingency tables with Yate’s correction and expected values ≥ 3.0 . Values from TR and NS were pooled together by the statistical treatment. For explanation of symbols see Tables 1 and 2.

Species	County	Apr II, May I	May II	June I	June II	July I	July II	Aug I	Aug II	Sep I	Sep II	Oct I-II	χ^2 -test
<i>Pel bor</i>	TR	0/1	0/5	0/42	0/42	0/398	0/9		3/8		0/4		
<i>Lor pil</i>	TR	0/23	0/69	0/104	0/127	0/39	0/30	6/21	5/67	0/32	0/20	0/3	20.39*** →
	NS			0/3	0/1			1/8	0/12				
<i>Ela cup</i>	TR		0/11	0/36	0/8	0/38	1/5	0/1	1/1		2/2		
<i>Ela rip</i>	TR, NS		0/2	0/70	0/58	0/42	1/9	1/1	2/8		0/1		
<i>Dys nig</i>	TR, NS	0/21	0/31	0/113	0/55	0/73	1/55	2/29	0/68	0/6	1/6	0/13	
<i>Bem vel</i>	TR		0/2	0/21	0/22	0/17	7/33	0/3	9/22				17.42*** →
<i>Bem bip</i>	TR	0/23	0/92	0/198	0/91	1/232	15/178	0/22	11/106	1/25	0/37	0/5	41.13*** →
<i>Bem yuk</i>	TR	0/5	0/4	0/6	0/4	0/19	1/2	1/1	1/4	0/8	0/12		
<i>Pte obl</i>	TR, NS		0/88	0/99	0/56	0/22	0/19	5/20	13/27	6/16	1/2	1/4	80.28*** →
<i>Pte rha</i>	TR		0/14	0/6	0/2		1/2	3/8	0/6	1/6			
<i>Pte str</i>	TR, NS		0/7	0/30	0/27	0/4	0/2	1/4	1/6		1/4	0/2	
<i>Pte dil</i>	N, TR		0/13	0/10	0/12	0/2	0/4	1/5	1/4	0/8			
<i>Ago ful</i>	TR, NS	0/4	0/9	0/160	0/117	0/35	0/23	0/34	4/19	2/5	6/29	2/3	48.01*** →
<i>Asa pal</i>	TR	0/69	0/17	0/198	2/46	47/229	3/94		0/92	0/41	0/8	0/18	17.90*** ←
	NS			0/7		1/14	0/13	0/10	0/11				
<i>Lei ter</i>	TR			1/2	1/17	0/38	0/27	0/45	0/11	0/2			9.81** ←
	NS			8/33			0/2	0/15					
<i>Neb ruf</i>	TR, NS		0/8	3/28	0/41	7/38	3/150	1/31	0/43	0/4	0/1		7.77** ←
<i>Not big</i>	TR	0/44	0/19	0/38	0/34	5/60	12/105	2/115	1/89	0/37	0/24	0/8	1.33 ns
	NS			0/1	0/1		0/13	7/54	0/7				
<i>Pat sep</i>	TR		0/5	0/5	0/16	1/11	1/8	0/2	0/3	0/2	0/2		
<i>Pat ass</i>	TR		0/29	0/34	0/124	0/102	5/59	2/17	0/13	0/5			
<i>Pat atr</i>	TR, NS	0/2	0/43	0/90	0/88	0/113	1/139	2/117	2/206				
<i>Tre sec</i>	NS			6/15		0/9	0/17	0/254					
<i>Tre rub</i>	TR, NS		0/11	0/13	0/5	0/6	1/12	5/7	2/23	1/2	0/3		5.69* →
<i>Tre obt</i>	TR	0/8	0/11	0/23	0/65	0/41	7/80	9/48	3/36	0/2	0/1	0/1	17.87*** →
	NS			0/9		1/2	1/3	6/28					
<i>Cal mic</i>	TR	0/4	0/85	0/106	0/72	0/99	1/203	3/133	13/106	3/20	0/4	1/7	15.36*** →
	NS			0/14	0/1	0/3	1/12	0/19	0/2				
<i>Ama bru</i>	TR	0/1	0/39	0/37	0/26	1/41	8/56	0/16	0/4	0/4			9.08** →
	NS			0/2	0/2	0/1	0/1	0/3					
<i>Har lae</i>	TR	0/3			0/6	0/14	0/5	1/2	0/1	0/1			
	NS			0/1		0/26	0/13	0/8	4/11				
<i>Dic pla</i>	TR	0/37	0/45	0/43	0/75	0/135	9/210	6/102	9/92	1/38	5/32	1/18	22.51*** →
	NS			0/26	0/24	0/4	0/41	3/64	2/4				

TABLE 4. Seasonal occurrence of larvae (number of individuals) of the carabid beetles. Numerals without signs concern second and third stage larvae. •: first stage; °: second stage; *: third stage. For further explanations of symbols see Tables 1 and 2.

	Province or county	May I	May II	June I	June II	July I	July II	Aug I	Aug II	Sep I	Sep II	Oct I	Oct II
<i>Pel bor</i>	TRI					1•2°2*	1* 7° 15*	1*	1*				
<i>Lor pil</i>	TR				1•	2•	2• 27	1° 8*			1*		
	NS					1°		2°					
<i>Ela cup</i>	TRI					1°	3*						
<i>Ela rip</i>	TRI				1	3	1• 17		7*				
<i>Dys nig</i>	TRi				1	2°	2	1*	1*				
	NSI			1°									
<i>Bem vel</i>	TRI						8*						
<i>Bem bip</i>	TR				4	2* 9	7	1	4*				
<i>Pte obl</i>	TR				1•	7	1°	1*					
<i>Pte rha</i>	TRI					1°	2*		1*				
<i>Pte str</i>	TRI, TRY						1° 4*						
<i>Pte dil</i>	TRI						3*						
<i>Ago ful</i>	TRI					2	4*	2*	2*				
<i>Asa pal</i>	TRY	1**		1*									
<i>Lei ter</i>	TR	3*		1*					6	3	2*	1°	
<i>Neb ruf</i>	TR	1*						1	2• 27	3*	4*	5*	2*
<i>Not big</i>	TR			3*	7*	1	2						
<i>Pat sep</i>	TRI			1*						1*			
<i>Car gla</i>	TR			1		2	1°	2°	6*	1°		1*	
	NSY							2°					
<i>Car viol</i>	TRY					4				2*	1*	1*	
	NSY							1*					
<i>Cyc car</i>	TRY									4•°	1°		
<i>Cal micr</i>	TR		1*	1*							1*		
<i>Ama brun</i>	TR						1	2*		1	1*		
<i>Dic pla</i>	TRY						6*						

the division made by den Boer & den Boer-Daanje (1990) and are as follows: a) species with summer larvae and exclusive hibernation as adults with immature gonads; b) species where larvae and usually also adults hibernate; c) species with other types of life cycles. According to this division, some of the species that den Boer & den Boer-Daanje (1990) have categorized as summer larvae species, are included in group b or c in the present study and in Andersen (2013). Group b and c are

heterogeneous compared with group a and may be divided into subgroups.

By assessing the life cycle of the species, it has been considered that there seems to be a connection between phylogeny and life cycle type (Hurka 1986). It has also been borne in mind that small carabid beetles generally seem to develop faster than larger, especially phytophagous species (Andersen, unpublished data).

TABLE 5. Number of individuals collected by hand per hour (hand collection) of the carabid beetles during the season. N: number of individuals. For each species, the same sites have been investigated at different times of the year. For further explanation of symbols see Tables 1 and 2

Species	Province	Apr II	May I	May II	June I	June II	July I	July II	Aug I	Aug II	Sep I	Sep II	N
<i>Pel bor</i>	TRY				9.60	7.20		0.43		3.0		0.86	24
<i>Lor pil</i>	TR	0.48	0	0.68	0.59	0.29	0.31	0.04	0.65	0.36	0.26		47
<i>Ela cup</i>	TRI			1.32	1.41	0.19	0.11	0.17	0.39	0.60			23
<i>Ela rip</i>	TRI				5.50	6.88	3.08	0.43	0.46	0	0		38
<i>Bem vel</i>	TRI			2.67	42.00	37.71	15.60	2.79	12.0	15.00	0		107
<i>Bem bip</i>	TR		3.40	6.49	3.38	4.77	0.71	6.53	2.88	7.05	4.50	3.20	266
<i>Bem yuk</i>	TRY		6.00		0.86	2.12	0		0		7.00	8.00	38
<i>Pte obl</i>	TRI			1.76	0.49	1.14	0	0.40	0.36	1.36	0		40
<i>Pte str</i>	TRI			0.94	1.02	0		0	0.55			1.92	15
	NSY				6.55	3.90		0	0.38				46
<i>Pte dil</i>	TRI				2.34	2.00		0.95		1.00	2.50		30
<i>Ago ful</i>	TRI			5.05	4.29	1.30	0.49	0.59	0	0		13.71	70
	NS			1.53	5.33			1.33					25
<i>Asa pal</i>	TR			9.45	17.60	33.33	24.00	28.30	31.63	24.40	7.43		615
<i>Lei ter</i>	TRI		0	0	0.11	1.86	1.46	0.09	0.59	0.29	0		38
	NSY				4.38			1.00	0.59				31
<i>Neb ruf</i>	TR	0	0	0.88	0.34	2.71	4.11	6.31	1.15	1.84	0	0	183
<i>Not big</i>	TRI		0	2.40	0.42	0.61	1.89	3.07	3.03	1.92	1.0		130
	NS				1.19	2.40		2.74	3.45				49
<i>Pat ass</i>	TRI	0	0	0.36	0.67	1.10	1.60	0.83	0.62	0.60	0		46
<i>Pat atr</i>	TRY			10.2	4.29	4.36		64.00	10.00				64
<i>Tre sec</i>	NS				2.18	3.00	2.84	1.50	3.46				103
<i>Tre rub</i>	TR		0	2.03	2.15	0.52	0.44	0.92	1.20	2.10	1.50		45
<i>Tre obt</i>	TRI	4.00		5.14	0.41	0.59	0.86	3.91	4.31	7.50	0		105
<i>Cal mic</i>	TRI		0	2.36	0.92	2.29	7.88	8.86	4.53	2.05	15.10		657
	NS					1.53	5.33			1.33			36
<i>Ama bru</i>	TRI	0		4.55	0	2.52	0.78	1.08	0.43	0.62	0.95		100
<i>Har lae</i>	TRY	1.57	3.43			5.53	11.20	4.67	6.00	2.00	0		36
<i>Dic pla</i>	TR	4.00	7.71	1.64	2.40	3.74	6.48	7.82	4.29	4.80	2.88		515
	NS				2.63	3.56	2.55	1.50	5.69	2.77			113

The summer larvae species (group a)

The available data about the life cycle of group a indicate that the species have summer larvae and hibernate exclusively as adults with unripe gonads. The larvae occur during the summer whereas teneral usually emerge from July II (Tables 3 and 4). Adults are abundant in May or

June at which time they also reproduce (Tables 2, 5 and 6, Hanssen 2007). A few females of several summer larvae species have mature ovaries as late as in July II and teneral of some summer larvae species, e.g. *Pterostichus strenuus*, are found as late as in September II even after very warm summers. Furthermore, a third stage larva of *Loricera pilicornis* was found in September

TABLE 6. Catches of carabid beetles in pitfall traps given as number of individuals per 100 trap days. For explanation of symbols see Tables 1, 2 and 5.

Species	Province	May II	June I	June II	July I	July II	Aug I	Aug II	Sep I-II	N
<i>Lor pil</i>	TRI	3.2	6.4	3.0	1.6	0.7	3.0	1.8	9.4	242
<i>Ela cup</i>	TRI		20.0	2.0	4.7	2.5	0.9	0	0	31
<i>Pte obl</i>	TRI	8.3	5.4	1.6	1.0	0.3	0.3	0		214
<i>Pte rhae</i>	TRI		4.4	0	0	2.5	2.4	0.6	0.8	21
<i>Ago ful</i>	TRI	0	8.3	7.2		1.5		1.7		177
<i>Lei ter</i>	TRI	0	0	0.4	0.6	4.4	2.8	0	0.4	106
<i>Neb ruf</i>	TRY	2.0	2.1	3.2	5.7	6.0	2.2	0.7	0	87
<i>Not big</i>	TRI	0.3	2.1	4.9	1.5	1.0	2.4	5.5	8.5	147
<i>Pat ass</i>	TRI	0.6	2.2	3.0	4.7	2.2	1.8	0	0.8	308
<i>Pat atr</i>	TRY		195.0	209.0	223.0	184.0	149.0	153.0		693
<i>Tre obt</i>	TRI	2.2	3.1	10.9	7.9	7.2	4.3		4.1	179
<i>Cal mic</i>	TRI	1.5	6.8	4.0	5.5	6.0	0.3	1.8	1.8	561

II (Table 4). It is likely, therefore, that not all the larvae of the summer larvae species are able to develop to adults before the winter in years with average or low thermal sums. Nevertheless, there are no indications that such larvae survive the winter and continue the development the subsequent year. If this had been the case, early occurrence of teneral the year after a year with a low thermal sum would have been expected (Andersen 2013). However, this is not the case. Early occurrence of larvae and teneral of species with summer larvae seems to be associated with warm springs and summers the same year like those in 1972 and 2002–2014 (Andersen 1983 b, 2013). Accordingly, a second stage larva of *Dyschirius nigricornis* was found as early as 7 June in NSI in the warm year 2002 (Table 4). Furthermore, a teneral of *Bembidion bipunctatum* emerged 11 July in the comparatively warm year 2009 (TRI). This was at the same time of the year as the first occurrences (10 July) of *Bembidion femoratum* Sturm, 1825 in the warm year 2003 (Tables 1 and 6 in Andersen (2013). *B. femoratum*, which is slightly larger than *B. bipunctatum*, hibernates exclusively as an adult like most other species of the genus. Therefore, the same most likely also applies to *B. bipunctatum*.

By and large, other information (e.g. Larsson

& Gigja 1959, Shilenkov 1978, Wasner 1979, Lindroth 1985–1986, den Boer & den Boer-Daanje 1990, Luff 1993) confirm that the species of group a are spring breeders with summer larvae and exclusive imaginal hibernation. The only controversial case seems to be *Loricera pilicornis*. In Scandinavia, Siberia and Northern America, the species hibernates exclusively as an adult (Lindroth 1955, 1985, Luff 1993, Shilenkov 1978). Ulrich & Zalewski (2006), on the other hand, mentioned that the species has a complex life cycle and Loreau (1985) concluded that it may hibernate both as larvae and adults since it breeds both in spring and in late summer (July/August) in Belgium. However, Belgium has an oceanic climate with high temperatures in late summer and autumn. It can not be excluded, therefore, that eggs that are deposited in July/August are able to develop to adults before the winter. A dormancy period for the current larvae seems unlikely since this does not apply to the larvae developing during spring/summer.

Lindroth (1945) assumed that as an exception, some summer larvae species may hibernate as larvae because in Northern Sweden teneral (unreife Käfer) have been found quite early (about mid July). However, the lowland of Northern Sweden have warm summers, mainly

appreciably warmer than those in Northern Norway (data in Alexanderson *et al.* 1991) so the time of occurrence of these teneral hardly prove larval hibernation. Occurrences of single or a few individuals of what has been termed teneral or immature beetles of spring breeders (e.g. *Pterostichus oblongopunctatus*, *P. diligens* and *Agonum fuliginosum*) in spring have been taken as an indication that such species now and then may hibernate as larvae (Lindroth 1945, Loreau 1985, Refseth 1988). As pointed out by den Boer & den Boer-Daanje (1990), adult carabid beetles may stay lightly coloured for a long time after eclosion, especially at low temperatures. In fact, Lindroth (1945) also emphasized that not all pale individuals of some species need to be immature. In the present study, for example, a female of *Pterostichus diligens* with mature ovaries in June I was brownish, but with a very hard cuticle. As pointed out previously, only definitely soft bodied beetles have been termed teneral in the present study and only such individuals indicate recent eclosion of beetles.

The summer larvae species have different habitat requirements, several occurring in open, wet or moist sites, others in open, mesic to dry environments whereas some species prefer forests (Table 1, Andersen 2013). These habitats have quite different thermal conditions (Andersen 1986). Reasonably, this influences the duration of the development of the species, but the data from the present investigation and Andersen (2013) can not document this.

The winter larvae species (group b)

Larvae of a majority of the species of life cycle group b (Table 1) are found in autumn and/or in spring and early summer (Table 4). They therefore hibernate as larvae and are termed winter larvae species. In addition, most species also hibernate as adults.

In fact, data for one of the winter larvae species, *Trechus rubens* (Fabricius, 1792), suggest a species with summer larva (Tables 2–3 and 5). However, a full grown larva has been found in May in Iceland indicating that larval hibernation

is possible (Larsson & Gigja 1959). Since the climate in Iceland is quite similar to that in the most oceanic parts of Northern Norway, it is likely that adults as well as larvae also hibernate in our country.

Notiophilus biguttatus has been regarded as a typical spring breeder with imaginal hibernation in Scandinavia and Central Europe (Larsson 1939, Lindroth 1945, den Boer & den Boer-Daanje 1990). However, in Northern Norway the species reproduces in the whole period from May to September and third stage larvae are found already in the first part of June (Tables 2 and 4). *N. biguttatus* therefore no doubt also hibernates as a larva. This is also the case in Belgium (Loreau 1985) and according to Luff (1993) the species reproduces at any time of the year.

The life cycle of *Patrobus assimilis* probably deviates from that of a majority of the other species with winter larvae since the reproduction period seems to cease before August (Table 2). The species hibernates both as larvae and adults in subalpine areas in Central Norway and probably has a biennial life cycle even in the lowland of that part of the country (Refseth 1986). It is likely that the same is true in Northern Norway.

A number of winter larvae species are known or supposed to have a thermic hibernation parapause at the larval stage. This characteristic seems to apply within the whole distributional area of such species (Andersen 2013). Among the species treated in the present study this at least applies to *Carabus glabratus*, *C. violaceus*, *Patrobus atrorufus* (Ström, 1768) and *Calathus micropterus* (Thiele 1977, Hurka 1986, Turin *et al.* 2003). The two latter species have a life cycle that obviously lasts more than one year in the lowland of Nordland and Troms counties. Thus, eggs are deposited as early as in May/June (Table 2, Killengren 2002). These eggs originate from females that have hibernated (from year 1 to 2) because in year 2 they have ripe ovaries long before the first teneral emerge in July II. The larvae originating from these eggs hibernate since they have a thermic parapause. They fulfil the development the following year (year 3). *Carabus glabratus* and *C. violaceus* reproduce as late as in August I in Nordland and Troms (Table

2). Most likely, the two species also reproduce in spring in these counties since this is the case in the climatically quite similar subalpine areas in Central Norway (Refseth 1988). This implies that the two species also have life cycles that may last more than one year in Northern Norway.

Despite that the carabid beetles with winter larvae are a species-rich group, few of them seem to hibernate exclusively as larvae. According to Lindroth (1945) *Leistus terminatus* hibernates only as a larva in South Scandinavia and the present study confirms that this also applies to the species in Northern Norway. Hence, adults have never been found before June I, whereas the adults of all the other winter larvae species, except for *Trechus secalis* (Paykull, 1790) were present already in April or May (Tables 3, 5, 6 and Table 3 in Andersen 2013). In addition, second and third stage larvae of *L. terminatus* have only been found from autumn to spring/early summer, but never in the middle of the summer (June II–August I) (Table 4).

Trechus secalis is also emphasized as an exclusive larval hibernator by Lindroth (1945). The life cycle data of the species from Nordland, where it has its northernmost occurrences, are somewhat incomplete. However, a substantial material of *T. secalis* from the province STI in Central Norway shows that the species exclusively hibernates as a larva there (Refseth 1988, Andersen, unpublished data). Since the temperature conditions in Nordland and some of those parts of STI where *T. secalis* occurs are rather similar, it is likely that the species also has an annual life cycle in the northernmost part of its distributional range.

The winter larvae species often start to reproduce much earlier in the season at high latitudes than further south (Refseth 1988, Andersen 2013). Thus, according to data in Thiele (1977) and den Boer & den Boer-Daanje (1990) *Patrobus atrorufus*, *Trechus obtusus* and *Amara brunnea* start to reproduce at least one month later in Central Europe than in Northern Norway. *Calathus melanocephalus* (Linnaeus, 1758) and *Leistus ferrugineus* (Linnaeus, 1758) also start to reproduce later in the season in Denmark and Central Europe than in Northern Europe (Schjötz-

Christensen 1965, Andersen 2013). In Central Europe adults of *Patrobus atrorufus* and *Leistus ferrugineus* have an aestivation dormancy period in summer (Thiele 1977), but this is obviously not the case in Central and Northern Norway (Refseth 1988, Andersen 2013). Similar differences between the populations in Central and Northern Europe may exist for the other species mentioned above as well. However, according to den Boer & den Boer-Daanje (1990) and contrary to what is stated by Andersen (2013), *Calathus melanocephalus* should be an autumn breeder without dormancy of young adults in summer also in Central Europe.

The early reproduction without adult aestivation dormancy in summer may be the reason why a number of species with winter larvae are able to have annual life cycles even in Northern Norway, at least in warm years.

Species with special life cycles (group c)

Dicheirotrichus placidus has a life cycle deviating from all the other species treated in the present study. Thus, it reproduces from August II through the winter months to July I (Table 2). The reproduction period is similar in Central Europe (den Boer & den Boer-Daanje 1990). Since individuals with mature ovaries are found in late autumn and winter, some females obviously hibernate in this state in Northern Norway. Eggs and adults with immature as well as mature ovaries therefore hibernate, but it is uncertain whether this also applies to the larvae since they never have been found in autumn or spring (Table 4, see also data in Larsson (1939) and den Boer & den Boer-Daanje (1990)). *D. placidus* seems to have a similar life cycle as *D. cognatus* (Andersen 2013).

Life cycle, climate and geographical distribution

Previously, there was no published data about the life cycle of *Pterostichus diligens* and *P. rhaeticus* in the northernmost part of Fennoscandia. Inclusion of them in Table 7 in Andersen (2013) only gives minor changes in the numerals and no changes in significance levels in the table. The conclusion that in the alpine and arctic zones, the

percentage of species with summer larvae is much lower than among species with other types of life cycles is therefore still valid. One of the main reasons for this pattern is that the thermal sums in the actual zones are too low to realize annual life cycles for most species with summer larvae there. Species with winter larvae, on the other hand, often have a long reproduction period (Table 2) and according to data in Refseth (1986, 1988), they are able to hibernate both as second and third stage larvae, usually also as adults. Hence, the species with winter larvae generally have more flexible life cycles and are therefore better adapted to climates with a cold, short summer than those with summer larvae (Andersen 1984, 2013).

Adult carabid beetles often live more than one year and may have more than one breeding season. It has been argued that this may buffer population extremes of summer larvae species in marginal areas (Andersen 1983b). A check of literature (Lindroth 1985–1986, Schjötz-Christensen 1965, Jones 1979, Andersen 1983b, Sharova & Denisova 1997, Turin *et al.* 2003) suggests that it mainly is the larger carabid beetles (length > 7.5 mm) that have more than one reproduction period. At least 70 % of the summer larvae species occurring in Nordland and Troms counties are small (≤ 7.5 mm) and the current trait has therefore probably a quite limited importance among the summer larvae species. This is also supported by the fact that in July/August the relative abundance of the adults of nearly all the species with summer larvae only amounted to 0–11% of that in May/June (Table 5). This indicates that the individuals of the generation that have reproduced once mainly succumb before the winter.

Biennial life cycles are not unusual among carabid beetles within the temperate zone (Matalin 2008), but according to den Boer & den Boer-Daanje (1990) the winter larvae species normally seem to have annual life cycles in Central Europe. Among those species that have a wide geographical range, several switch to a biennial life cycle at northern latitudes (Filippov 2006, 2007, Andersen 2013). However, as is indicated by the present study, some winter larvae species do not switch to a biennial life cycle. Such species are probably equally dependent upon sufficiently

high thermal sums within a single year as the summer larvae species. This above all applies if the species should be unable to abolish an adult summer dormancy period.

Based on the present study as well as Andersen (1983b, 2013) it is concluded that many carabid beetles of a southern origin have the same main life cycles at their northernmost occurrences as elsewhere. A majority of them are summer larvae species with exclusive hibernation as adults with unripe gonads, but *Leistus terminatus*, *Bembidion mckinleyi* Fall, 1926, *B. lunatum* (Duftschmid, 1812) and probably also *Trechus secalis* have annual life cycles and hibernate exclusively as larvae. However, several or a majority of the winter larvae species at least partly switch to a biennial life cycle in northernmost Fennoscandia.

Obviously, further studies of the life cycle, behaviour, autecology and geographical distribution of carabid beetles are needed to give an adequate explanation of their geographical distribution in Scandinavia. This above all applies to the winter larvae species. Further studies of life cycle patterns and distribution of carabid beetles are also worthwhile because of the global warming, which is predicted to continue. This have already lead to geographical range expansions and phenological changes among carabid beetles (Pozgai & Littlewood 2011, Andersen 2013), but in the future the changes may be more comprehensive and concern many species.

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