Hibernation sites of riparian ground beetles (Coleoptera, Carabidae) in Central and Northern Norway

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In an attempt to detect the winter quarters of Scandinavian riparian carabid beetles, sites at various distances from some rivers and a lake in Central and Northern Norway were investigated with various sampling methods in early spring (April–primo May), in autumn (ultimo September–November) and during the summer (ultimo May–August). *Bembidion bipunctatum* (L., 1761) and species confined to gravelly/stony habitats (*Bembidion prasinum* (Duftschmid, 1812), *B. hyperboraeorum* (Münster, 1923), *B. virens* Gyllenhal, 1827, *B. hastii* (Sahlberg, 1826), *B. petrosum* (Gebler, 1833), *B. saxatile* Gyllenhal, 1827 and larvae of *B. mckinleyi* (Fall, 1926)) hibernate among gravel or under stones (often in grass tussocks) in the most elevated parts of the river banks. Some of these species cluster strongly under stones. Species of fine-grained substratum may hibernate in silty sites in elevated parts of open river banks (e.g. *B. difficile* (Motschulsky, 1844) and larvae as well as adults of *Cicindela maritima* Dejean in Latreille & Dejean, 1822), or close to or in fluvial forest (e.g. *Bembidion schuppelii* Dejean, 1831, *B. semipunctatum* Donovan, 1806 and *Agonum micans* (Nicolai, 1822)). The winter quarters of the subgenus *Bracteon* Bedel, 1879 is still undetected. There is no evidence that riparian beetles migrate far from river banks or lake shores by flight to hibernate. Many riparian beetles are red-listed. Threats to their habitats with special emphasis on their winter quarters are discussed.

Key words: Carabidae, hibernation sites, river banks, red-listed species, conservation value.

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Introduction

Numerous carabid species are confined to banks of running waters in the holarctic region (Lindroth 1961–69, 1985–86, Koch 1989, Lott 2003, Freude et al. 2004, Andersen & Hanssen 2005). The knowledge about the habitat selection of the Scandinavian riparian carabids in their active period (late spring–summer) is fairly comprehensive (e.g. Andersen 1970, 1982, 1983a, 1997, Lindroth 1985–86). However, although the hibernation stages of most of the Scandinavian riparian carabids are known, the published information about their hibernation conditions is fragmentary (Andersen 1968, 1970, 1982, 1983b, Lott 2003).

The purpose of the present study, which is based on studies made in Central and Northern Norway, is to increase the knowledge about the hibernation strategies of the riparian carabids in Scandinavia. Winter quarters were investigated in late autumn and in early spring. Data from these investigations were compared with data obtained during the summer. These latter results have partly been published elsewhere, but in another context (Andersen 1970, 1983a, 1997, 2000).

Material, methods and habitats

Based on the moisture requirements of plants, which were derived from Benum (1958), Lid &

Lid (2005) and Mossberg & Stenberg (2007), the mean moisture content of the soil was calculated as follows (Andersen 2011): α=(H–X)/(H+M+X). α is the moisture index, H the number of plant species requiring moist to wet soils or water, M the number of species demanding mesic or mesic to moist soils and X the species requiring dry or dry to mesic soils. Sites with α-values ≥ 0,28 are usually permanently moist or wet. Sites with α-values of ≤ -0,30 are regarded as dry, whereas those with values between -0,20 and 0,15 are classified as mesic. The moisture content of the soil in the more low-lying zones on river banks fluctuates much and epigeal carabids shift positions correspondingly (Andersen 2008). However, the water level in the rivers was usually low during the present investigations. Some of the habitats ordinarily lack vegetation. The index α has only been estimated in sites where at least twelve plant species were present. The description of the habitats is otherwise based on the same environmental factors as given by Andersen (1970, 1997).

The following sampling methods/procedures were used: *1) Quadrat sampling*. The area of the quadrats was 0,125m^2. The method was used in a silty estuary and in sites where the surface layer consisted of gravel and small stones (area of each stone ≤ 10cm^2). Details of the method are given in Andersen (1970). *2) Investigations under larger stones* (area of each stone ≥ 70cm^2). In those cases where aggregations of beetles were found, the approximate area of the underside of the stones was estimated by means of a graph paper. *3) Ordinary hand collecting within a given time (time-catch)*. The method is described in detail by Andersen (1970). *4) Ordinary hand-collecting without noting of time*. Collecting procedures were otherwise as by time-catch. *5) Sieving of litter on silty sites*. The material was sifted through a sieve with mesh size 5,5mm. The sifted material was examined indoors. The volume of the sifted material was judged subjectively. *6) Digging of sand to a depth of 5–15cm in dry, sandy slopes*. The time was noted. The temperature was 14–26°C during the investigations in summer (second half of May–August) and -0,5–14°C in late autumn or early spring (ultimo September–November, April and primo May). The sampling was conducted during dry weather.

The time-catch method should be used in situations in which most variables are held constant (Greenstone 1979). It was therefore found relevant to compare the relative abundance (number of individuals collected per hr.) of species in the same habitats and sites and with the same sampling methods at different times of the year. The species have mainly contagious dispersions (Andersen 1983a). Differences in the absolute (quadrat samples) and relative abundance between summer and autumn/early spring were therefore tested by means of Mann-Whitney U-tests. The length of each time-catch unit used in the tests varied, but it was always equally large or largest at the time of the year when the caculated abundance values were lowest.

Andersen & Hanssen (2005) restricted the concept riparian species to those mainly or exclusively occurring on river banks with exposed riverine sediments (ERS) N of 58° in Fennoscandia. In the present study, some species that also occur regularly on shores of stagnant freshwaters and sea shores with mineral soils, have been included. Some species that are confined to shores at southern latitudes, are in addition often present in dry or mesic, anthropogenic habitats in Central and Northern Norway (Andersen 1983a, 1997, Andersen & Hanssen 1994). Such species are omitted, except for three species that are rare and red-listed in Denmark. Knowledge about their winter quarters ought to be of interest for that reason.

Characteristics of the investigated habitats are shown in Table 1. The material has been collected in the period 1969–2011.

Results

More than 1770 individuals of 14 riparian species were found in early spring (April–primo May) and autumn (ultimo September). The results are presented in Tables 2–7. Riparian carabids were not encountered under the following circumstances: habitat A1. Rundhaug, October, method 5 (volume 0.5 l): habitat C 2. Andorlia,

TABLE 1. Characteristics of the investigated sites. The α-values are based on the plant species composition. The symbols in brackets refer to the microhabitats described by Andersen (1997). Investigation methods: 1. Quadrat sampling; 2. Investigations under stones with estimated areas; 3. Time-catch; 4. Hand-collecting without time noting; 5. Sieving of litter; 6. Digging of sand; irreg: irregularly flooded; reg: at least flooded during the spring floods; ERS: river banks with exposed riverine sediments; Het: heterogeneous mixture of silt, sand, gravel and stones; O: open; S: shaded by bushes; D: dry; Me: mesic; Mo: moist; W: wet; I: first half of the month; II: second half of the month; * : patches surrounded by snow or ice; **: partly in grass tussocks.

Habitats	Elevation above mean water level, spate conditions	Substratum	Moisture α-value	Vegetation coverage, exposion	Investigation method, time	Region, municipality, locality, river or lake
A 1. ERS (3b, 4c, 4d)	Low-moderate reg	Silt/fine sand, often leaf litter on surface	Me- W, -0,05–0.73	1–3, O	3,5; May II–Aug, Sept I, Oct, Nov	STI: Melhus: Melhus, Gaula; TRI: Målselv: Rundhaug and Gullhav, Målselva
A 2. ERS (2a, 3a, 4a)	Low-moderate reg	Silt/fine sand	Mo- W, 0,60	4–5, S–O	3; May II–Aug, Sept, Oct	Melhus
A 3. ERS (7a–b)	Moderate, reg	Medium–fine, loose sand	D-Me, -0,42 0,06	0–2, O	3, 4; May II–Aug, Oct–Nov	Melhus, Rundhaug, Gullhav
A 4. ERS (6a I–III)	Low-moderate, reg	Gravel/stones	Me-W 0,14– >0,58	0–1, O	1, 3; May II–Aug, Oct–Nov	Melhus, Rundhaug; Storfjord: 3 small rivers
A 5. ERS	High, irreg	Silt/fine sand	D-Me -0,50–-0,18	3–5, S	3–5; May II–Aug, Oct–Nov	Melhus, Rundhaug
A 6. ERS	High, irreg	Gravel/ stones**	D-Me, -0,40–-0,10	1–3, O	2–4; April*, May, July, Oct, Nov	Melhus, Rundhaug; Storfjord: 3 small rivers
A7. ERS, Slope	High, irreg	Medium-fine, loose sand	D	0, O	6; May II*	Gullhav, Rundhaug
B 1. Estuary, brackish water (5)	Low, flooded by high tide	Silt	Mo-W, 0,50–0,69	2–3, O	1, 3; June, Sept II	TRY: Tromsø: Tønsvik, Tønsvikelva; TRI: Storfjord: Skibotn, Skibotnelva
B 2. ERS, near outlet (6a I–III)	Low-moderate reg	Gravel/stones	Me-W	0–2, O	1, 3; April–Oct	Tønsvik; Skibotn
B 3. Near outlet	High, not flooded	Gravel/ stones**	D-Me, -0,91– -0,20	0–3, O	1–4; April–Oct	Tønsvik; Skibotn
B 4. Steep slope, 5–10m from B 2. Grass tussock	High, not flooded	Het	D	5, O	4; April*, May I*	Tønsvik
C 1. Shore of lake	Low, often flooded	Pure, medium sand	Mo-W, > 0,54	0–1, O	3; June–Aug, Sept II, Oct	TRI: Balsfjord: Andorlia, Fjellfroskvatn
C 2. Above C 1. Steep slope.	High, not flooded	Pure, medium sand	D, -0,54– -0,43	1–2, O	3, 6; May II, Sept II	Andorlia
D. Fallow fields.	15–500m from open water	Sand or Het	D-Me, -0,43–0,00	1–3 (4), O	3; June–Oct	TRI: Målselv: Olsborg, Rundhaug.

TABLE 2. Relative abundance (number of individuals collected per hour) of riparian carabid beetles in various habitats at Melhus, the Gaula in second half of May–August (Su), first half of September (Sept) and October (Oct). The values from the same habitats at different times of the year are comparable, but too few samples were available for statistical analyses. Characteristics of the habitats are given in Table 1. The nomenclature follows Silfverberg (2004). [D]: redlisted in Denmark (DMU 2007), [N]: redlisted in Norway (Ødegaard et al. 2010), [S]: redlisted in Sweden (Gärdenfors 2010), +: holes (>100) of larvae. Further information and explanations are given in Table 1.

	Habitats											
	A 1. Silt, mesic-wet, sparse-moderate vegetation			A. 2. Silt, moist-wet, dense vegetation			A 3. Fine, loose sand, dry-mesic		A 4. Gravel/ stones, mesic -moist	A 5. Elevated, Silt, dry-mesic, moderate-dense vegetation		A 6. Elevated. Gravel/ stones, dry-mesic
Species	Su	Sept	Oct	Su	Sept	Oct	Su	Sept	Su	Su	Oct	Oct
Agonum micans [D]				2.7							6.9	
Cicindela maritima [D,N,S]							+	+				
Bembidion argenteolum [N,S]							12.2					
B. litorale [D,N]	2.2	5.6										
B. lunatum [D]	2.5	9.2		4.5	15.4					2.4		
B. petrosum [S]							3.9	6.0	8.1			12.0
B. prasinum									22.8			
B. saxatile									14.6			66.0
B. semipunctatum [N,S]	60.4	21.9	2.1	1.4	6.0						1.7	
B. schuppelii [D]	9.5		14.3	37.0	18.9	70.7				1.2	6.9	
Other Carabidae	15.1	16.9	14.3	?	11.1	30.6	0	0	0	26.4	142.3	0
Investigation time (min)	165	85	84	135	70	45	175	50	140	50	35	30

May II, method 6 (40 min).

32 specimens of *Bembidion bipunctatum* (L., 1761) were collected in habitat D between May II and August by method 3 (investigation time: 3215 min, total number of Carabidae specimens collected: 1784). In habitat A 6, *B. petrosum* Gebler, 1833 was usually found alone under larger stones, whereas *B. virens* (Gyllenhal, 1827) and *B. prasinum* (Duftschmid, 1812) mostly occurred singly among gravel or under small stones. The difference in the occurrence between *B. petrosum* and the two other species was highly significant ($X^2 \geq 119.3$, $p < 0.001$, Yate´s correction). The beetles were found under withered leaves or grass or small twigs on the soil surface in habitats A 1, A 2 and A 5 in October and November. The larval holes of *Cicindela maritima* Latreille & Dejean, 1822 in habitat A3 (Table 2) were present in the innermost parts of the sandy areas at places where the substratum consisted of fine sand with a firm top layer of silt. The sites had a sparse and low vegetation. A third stage larva was dug out of its hole in August II at the Gaula.

Discussion

The winter quarters of the beetles. The riparian species had a conspicuos seasonal habitat shift at the localities in Northern Norway (Tables 3–7). The low-lying, mostly moist or wet sites (habitats A1, A4, B1, B2 and C1) were almost

TABLE 3. Relative abundance (number of individuals collected per hour) of riparian carabid beetles at Rundhaug (Ru) and Gullhav (Gu) at the Målselva in second half of May–August (Su) and in second half of September–November (Au). Values from the same habitats at different times of the year are comparable. Values in bold are significantly higher ($p < 0.05$, Mann-Whitney U-test) than those in italics. There was not sufficient available samples to test differences in the relative abundance between Su and Au in A 5. Further information and explanations are given in Tables 1 and 2.

	Habitats								
	A 1. Silt, mesic-wet, sparse-moderate vegetation		A 3. Fine, loose sand, dry-mesic, sparse vegetation		A 4. Gravel/ stones, mesic-moist		A 5. Silt, dry-mesic, moderate-dense vegetation		A 6. Gravel/ stones, dry-mesic
	Ru, Gu		Ru, Gu		Ru		Ru		Ru
Species	Su	Au	Su	Au	Su	Au	Su	Au	Au
Elaphrus riparius	1.5		0.3						
Bembidion lapponicum [N]			**10.7**	*0*					
B. bipunctatum [D]	2.4		3.9				0.5		
B. schuppelii [D]	**47.1**	*2.0*	4.9				16.8	66.7	
B. difficile	0.2	0.3	0.3						
B. prasinum			3.9		**21.1**	*0*			10.6
B. hyperboraeorum					1.6				
B. hastii									
B. virens			1.3	0.4	1.6			0.5	17.3
B. petrosum [S]			3.2		16.5			0.5	2.0
Other Carabidae	4.8	3.0	3.2	0.4	0	0	0	43.5	0
Investigation time (min)	325	180	185	150	185	40	125	125	215

TABLE 4. Relative abundance (number of individuals collected per hour) of riparian carabid beetles at three small rivers in TRI: Storfjord and Andorlia at the lake Fjellfroskvatn in June–August (Su), in second half of September–November (Au) or in second half of September–November and/ or April and May (Au/Sp). Further information and explanations are given in Tables 1–3.

	Small rivers				**Lake**			
	A 4. Gravel/stones, moist- wet		A 6. Gravel/ stones, dry- mesic		C 1. Sandy shore, moist-wet		C 2. Supralittoral. Sandy, dry.	
Species	Su	Au	Su	Au/Sp	Su	Au/Sp	Su	Au
Elaphrus riparius					2.5			
Bembidion velox					**24.6**	*0*		
B. bipunctatum [D]				0.2				0.8
B. hyperboraeorum	**17.5**	*0*		3.1				
B. hastii	**15.9**	*0*		0.5				
B. mckinleyi [N]	2.3							
B. mckinleyi [N] [larvae]				2.2				
B. schuppelii [D]				0.2				0.8
Other Carabidae	0.7	0.8	2.7	1.1	0	0	1.2	1.7
Investigation time (min)	415	120	45	330	95	150	50	145

TABLE 5. Relative abundance (number of individuals collected per hour) of riparian carabid beetles in Tønsvika, the outlet of the river Tønsvikelva (Tø) and in Skibotn, Skibotnelva (Sk) in June–August (Su), in ultimo September, October or in April or primo May (Au/Sp). Values from the same places at different times of the year are comparable, but too few samples were available for statistical analyses. Further information and explanations are given in Tables 1–3.

	Habitats								
	B 1. Estuary, Silt, moist- wet		B 2. Gravel/stones, mesic-wet			B 3. Elevated, Gravel/stones, dry-mesic			
	Tø	Sk	Tø	Sk	Sk	Tø	Tø	Sk	Sk
Species	Su	Su	Su	Su	Au/Sp	Su	Au/Sp	Su	Au/Sp
Elaphrus riparius	0.3	0.6							
Bembidion bipunctatum D	22.2	25.2	3.0	2.2			26.7		12.4
B. hastii			26.3						
B. hyperboraeorum			0.3						
B. mckinleyi N			0.3						
B. virens				13.7					16.4
B. schuppelii D		0.6						0.8	
Other Carabidae	10.6	5.4	4.6	0.9	0	15.4	0	1.2	3.6
Investigation time (min)	210	100	237	70	50	70	72	100	150

devoid of individuals in late autumn and early spring (September II–November, April and May I) whereas riparian species were abundant in the same habitats during the summer (May II–August). On the other hand, the elevated sites (A5, A6, B3 and B4) had a rich riparian fauna in early spring and/or in autumn. These elevated sites no doubt represent the winter quarters of the species. Hence, the beetles were inactive or little active (patches often surrounded by ice or snow in early spring) and some species aggregated strongly under stones. Although riparian carabid beetles mainly have contagious distribution (Andersen 1983a), obvious aggregations have not been observed among such species in summer, whereas ground beetles frequently form clusters during hibernation (Thiele 1977). In addition, at least habitats A6 and B3 seemed to lack riparian species during the summer.

Individuals of the silt-living species *Bembidion semipunctatum* (Donovan, 1806) and *B. schuppelii* Dejean, 1831 were still present in moist or wet sites at the Gaula as late as in October (A1 and A2, Table 2). Although a few carabid beetle species are known to hibernate in wet surroundings (Lindroth 1985–86), there are indications that *B. semipunctatum* selects somewhat drier sites in fluvial forests before hibernation (Andersen 1970). It is also likely that *Bembidion schuppelii* mainly leaves the wet sites at the Gaula and hibernates in elevated parts of the river banks like at Målselva (habitat A5, Tables 3 and 7). Larvae of *Bembidion lunatum* (Duftschmid, 1812) occurred in fluvial forest in October at the Gaula (Andersen 1968). This species hibernates exclusively on the larval stage (Andersen 1970, 1983 b) so the whole riverine population undoubtedly spend the winter on river beds. The silt species may therefore generally hibernate in elevated, exposed or semiexposed, silty sites on river banks and/or in the fluvial forest behind.

Bembidion bipunctatum and the lithophilous species, i. e. those confined to gravelly/stony bars (*Bembidion petrosum, B. saxatile* Gyllenhal, 1827, *B. virens*, *B. hastii* Sahlberg, 1827, *B. prasinum, B. hyperboraeorum* Munster, 1923 and larvae of *B. mckinleyi scandicum* Lindroth, 1943) hibernate under stones or among gravel (often in grass tussocks) in elevated parts of river banks (habitats A 6, B 3 and B 4, see also Andersen 1968). Central European lithophilous species such as *Bembidion tibiale* (Duftschmid, 1812) (also present in Norway), *B. ascendens* K. Daniel, 1902, *B. conforme* Dejean, 1831 and

TABLE 6. Number of individuals per m² of riparian carabids in Tønsvik, at Tønsvikelva in May–August (Su) or in ultimo September (Au) estimated by means of quadrat sampling. B3 is situated at the same place as in Table 5. Differences in abundance between Su and Au in B1 and between B2 (Su) and B3 (Au) were tested by means of Mann-Whitney U-tests. Values in bold are significantly higher than those in italics. Further information and explanations are given in Tables 1–3.

	Habitats			
	B 1. Estuary, silt, moist-wet		B 2. Gravel/stones, mesic-wet	B 3. Gravel/stones, dry-mesic
Species	Su	Au	Su	Au
Bembidion bipunctatum D	**3.7**	*0*	*0.1*	**7.7**
B. hastii			5.8	4.4
B. hyperboraeorum			**9.7**	*0.3*
B. mckinleyi N		0.5		
Other Carabidae				
Number of samples of 0,125m²	24	20	72	24

TABLE 7. Number of individuals of *Elaphrus riparius* (*El riparius*) and species of Bembidion (B.) collected by various sampling methods at Melhus (Me), Gullhav (Gu), Rundhaug (Ru), Tønsvik (Tø) and Olsborg (Ol). Months are given as numerals. Min: investigation time in minutes; Quad: number of quadrat samples of 0.125 m²; Vol: approximate volume of sample (litre); Stones cm²: approximate surface area (cm²) of underside of stones. Further information and explanations of symbols are given in Table 1.

	Habitats											
	A3	A3	A4	A5	A5	A6	A6	A7	B3	B3	B4	D
Place	Me	Ru	Ru	Ru	Ru	Ru	Ru	Gu,Ru	Tø	Tø	Tø	Ol,Ru
Month	9 I	9 I	7	10, 11	10	10	10, 11	5 II	4	4, 9 II	4, 5 I	9 II, 10
Method	4	3	1	4	5	2	4	6	2	4	4	3
Min		50						55				600
Quad			37									
Vol					1.5							
Stones cm²						225			420			
El. riparius		1									1	
B. argenteolum S,N	3											
B. lapponicum N	27	3										
B. bipunctatum D		2						1	75	>90	34	10
B. difficile								1			13	
B. schuppelii D				>200	21			5				
B. petrosum S		10	43		1	230	>300					
B. virens					1		27					
B. prasinum							>165					
B. hastii									3	15		
Other Carabidae												431

B. variocolor Fabricius, 1803 also hibernate on gravel bars at the rivers (Kurka 1975, Dietrich 1996). Most likely, the same is the case with the lithophilous, red-listed click beetle *Fleutiauxellus maritimus* (Curtis, 1840) which seems to hibernate exclusively in the larval instar (Andersen 1982). Lithophilous species may therefore generally hibernate in more or less dry, gravelly/stony parts of river banks.

The tendency to form clusters seems to vary with species. *Bembidion petrosum*, for instance, shows a strong aggregation need in its winter quarter. Thus, 230 specimens of this species were found under two stones that had an estimated area of 225cm^2 at Målselva in late autumn (habitat A6, Table 7). This corresponds with >10,000 individuals per m^2. Since the abundance of *B. petrosum* at Målselva is below 10 individuals per m^2 in its optimal habitat (A4, Table 7) during the summer, this means that the beetles under the two stones probably represented the population over an area of more than 20m^2 of the summer habitat. Likewise, the 75 individuals of *Bembidion bipunctatum* that were found under three stones with an estimated area of 421cm^2 at Tønsvikelva (habitat B3, Table 7) may have aggregated from an area of about 20m^2 of the summer habitat (see habitat B1 in Table 6). *B. saxatile* also tends to form clusters during hibernation (Andersen 1968). Other lithophilous species like *Bembidion virens* and *B. prasinum* seem to have less tendency to aggregate. The mechanisms involved in the shift of *Bembidion petrosum* between the reproduction and hibernation habitat have been dealt with by Andersen (2006).

Third instar larvae of *Cicindela maritima* were found at the Gaula in August. They probably develop to adults in the course of the autumn and spend the winter in their pupal chambers (Direktoratet for naturforvaltning 2009). Since larvae also hibernate (Lindroth 1945, Saurdal 2005), the whole population of *Cicindela maritima* most likely spend the winter in the transition between the sandy and silty sites in the elevated parts of river banks.

The winter quarters of *Bembidion argenteolum* Ahrens, 1812, *B. velox* (L., 1761), *B. lapponicum* Zetterstedt, 1828 and *B. litorale* (Olivier, 1790), all belonging to subgenus *Bracteon* (Löbl & Smetana 2003), are undetected. Three of these species were still active in their summer habitats in primo September, but later in autumn and/or in spring, all the species were searched for in vain there (habitats A1, A 3 and C1, see also Andersen 1970). Andersen (1968) and Meissner (1983) postulated that riparian carabids may hibernate far away from open water, migrating by flight. However, in view of the existing knowledge, this seems unlikely. Thus, riparian species were not encountered in mesic or dry habitats more distant from water (habitat D) in autumn. The only exception was *Bembidion bipunctatum* (Table 7), but this species was also present in open, anthropogenic habitats in summer. Riparian species have neither been found in mesic or dry forest farther from open water in autumn (unpublished data). Furthermore, several records of flying individuals of *Bembidion* species have been made in the period May–August, but not later in the year (Lindroth 1945, Andersen 1970, 1997). Generally, the flight activity of littoral carabid beetles is high (e.g. Zulka 1994, Lott 2003, Rothenbücher and Schaefer 2006), but it seems to be very low in September and later in the year (Andersen 2011).

Elaphrus spp. hibernate in sites not far from water. The species may dig rather deep in the soil before hibernation (Bauer 1974) and the individuals are therefore rarely discovered by means of the usual sampling methods. It is likely that the *Bracteon* species also dwell buried in the soil during the winter. Thus, three of them are psammophilous and show a great burrowing capacity even during the summer, while the fourth species (*B. litorale*) has been observed to make burrows in sand at low temperatures in captivity in autumn (Andersen 1970, 1978, 1997, Kleinwächter & Burkel 2008). However, no specimens of the *Bracteon* species were found by method 6 (digging of sand) in elevated, sandy parts of river banks or a lake shore in spring or autumn. This may be because the beetles stay deep in the soil during hibernation.

There seems to be two main reasons why the riparian species usually hibernate in more or less dry sites: 1. The beetles may avoid to be trapped by cold water if the water level in the river rises;

2. *Bembidion* species depend on supercooling to survive the winter (unpublished data). For such species, there is less risk of lethal inoculative freezing in dry surroundings because the probability of contact with ice is reduced (Sømme 1995).

Conservation aspects. Riverine habitats are influenced negatively by various human activities, and a considerable number of the riparian species are red-listed (Tables 2–6, Andersen & Hanssen 2005, Moen et al. 2010). It is therefore of decicive importance to protect the reproduction habitats as well as the winter quarters of the riparian species. Threats to these species with special emphasis on their winter quarters are discussed in the following.

Reduced floodings due to flow regulations are supposed to have the most serious effects in the elevated parts of river banks. Such sites become overgrown (Berglind et al. 1997) and in years without evident spring floods, it has been observed that the soil in parts of the river banks may be transformed due to invasion of Lumbricidae and Formicidae. Highly transformed soils seem to be avoided by riparian species (Andersen 1978, unpublished observation). In addition, ants have a more direct, negative effect on riparian beetles (Berglind et al. 1997). Consequently, reduced floods probably lead to shortage or absence of suitable winter quarters for many riparian beetles such as the lithophilous species, *Cicindela maritima*, *Bembidion difficile* Motschulsky, 1844 and perhaps also species of subgenus *Bracteon*.

More elevated sites close to or in fluvial forest serve as winter quarters for riparian species. Hence, larvae of *Bembidion lunatum* and adults of *Bembidion schuppelii*, probably also of *B. semipunctatum* and *Agonum micans* Nicolai, 1822, hibernate in such habitats (Table 2–3, Andersen 1968, 1970). Fluvial forest is a near threatened nature type in Norway and also constitutes the reproduction habitat of some rare and red-listed beetles belonging to other families than Carabidae (Strand 1957, Andersen & Hanssen 1994, 2005, Ødegaard et al. 2010, Lindgaard & Henriksen 2011). The protection of this forest type therefore ought to have high priority.

Flood-prevention walls and canalizations are serious threats to the riparian fauna in Norway (Andersen & Hanssen 2005). Such impacts destroy the summer habitats as well as the winter quarters of the species. Small, low-lying gravel bars may develop in rivers even at places where flood-prevention walls are present. The bars may harbour low populations of some lithophilous species, e.g. *Bembidion hyperboraeorum* (personal observation), but it is questionable whether the beetles are able to exist permanently there, i.e. because of the scarcity of suitable winter quarters.

It is important to be aware that although impacts such as wear and tear, removal of sediments and other types of exploitations have a negative effect on riparian species in their reproduction habitats (Andersen & Hanssen 2005, Bates et al. 2006, 2007), the effect is supposed to be even worse when the beetles have settled in their winter quarters. Hence, the beetles are mainly inactive during the winter and if their winter quarters are destroyed, they are therefore unable to find new, intact sites. If such impacts involve clusters of beetles under large stones, populations over larger areas may be swept out.

A recent, but serious threat to the flora and fauna of river banks in Norway is the introduced plant *Lupinus polyphyllus* which is on the Norwegian Black list (Gederaas et al. 2007, Moen et al. 2010). From gardens, road sides, fallow land etc. this species has now invaded river banks in Central Norway with alarming speed. Especially in the elevated parts of the river bars, the plant forms dense stands. This changes the soil type as well as the moisture, temperature and light conditions of the original habitats and probably leads to uninhabitable conditions for riparian species. In this way summer habitats as well as winter quarters may be destroyed.

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