On the biology of *Calodromius bifasciatus* and related species in 'De Kaaistoep' (Coleoptera: Carabidae)

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Corticolous species, oak, winter activity, phenology, spheres, pre-oötheca, *Dromius*

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In 'De Kaaistoep', a locality where *Calodromius bifasciatus* is abundant, this and related carabid species were surveyed between 2000 and 2006. Several collecting methods, like pitfall traps, flight interception traps and brown paper wrapped around tree stems, were used in an attempt to learn more about the dispersal and migration of *C. bifasciatus*. Moreover, the stems of 26 oaks were monitored weekly at night for more than two years to observe the behaviour of the beetles. Our data on phenology clearly show that *C. bifasciatus* is active during winter. The species even copulates near freezing point. Some other interesting discoveries were made, for instance about feeding behaviour, the presence of a small sphere at the end of the abdomen, and hiding at low temperatures. Subsequently we obtained similar information about other tree-living *Dromius* s.l. In this article we discuss our results and compare them with recently published information.

Introduction

January 1999 *Calodromius bifasciatus* (Dejean) was discovered for the first time in The Netherlands on the stem of a small oak in De Kaaistoep near Tilburg (Felix & Van Wielink 2000). It is the second Dutch species in the genus *Calodromius*, next to *Calodromius spilotus* (Illiger), a common species in The Netherlands. Later more specimens of *C. bifasciatus* were found in the same area and its surroundings. This species turned out to be abundant in a wide area around Tilburg and it also occurred in Boxtel, a village approximately 20 km east. Specimens were found on trees of several species, like oak (*Quercus*), beech (*Fagus*) and *Robinia* (Van Wielink *et al.* 2002). Except for a single specimen found in May 2007 under the bark of a dead oak at Bekendelle, Winterswijk, about 120 km to the east northeast (Theodoor Heijerman, personal communication), no other records from The Netherlands are available.

Calodromius bifasciatus was thought to be a species of the west Mediterranean. Reports from northern France are scarce; those from Italy, Switzerland, Middle and Eastern Europe as well as from England are highly doubtful (Felix & Van Wielink 2000). In 1995 one specimen was discovered for the first time in Belgium in a pitfall trap (Desender & Maes 1995, Desender & Vanden Bussche 1998) and its presence in Belgium has very recently been confirmed (Van Malderen 2007). In 2004 *C. bifasciatus* was found at several places in Germany in Nordrhein-Westfalen (Hannig & Reissmann 2004). The presence in Hungary (Persohn 2004) is based on old literature (Manfred Persohn, personal communication) and not on collected specimens. No recent records are available from Hungary. All Dutch, Belgian and German places lie roughly between 51-52° N and 3.5-7° E, a rather small area.

Because of the unexpected local abundance of this species in De Kaaistoep we started an investigation on the biology of *C. bifasciatus*. The main topics of our investigation were dispersal, phenology and reproduction. During this research on and near oak trees we also studied related carabid species from the genus *Dromius* s.l. (*Dromius, Calodromius, Paradromius* and *Phylorhizus*), which will be reported here. Information about other beetle families and insect orders will be published later. In subsequent publications we will refer to the boxes in the current paper in which detailed information is presented on the research area (box 1) and collection methods (box 2).

Results

Not all our methods were successful. In pitfall trapping only three *C. bifasciatus* and two *C. spilotus* were collected. The windows did not trap a single *Calodromius*. The results of trapping with rings around the tree stems were also very poor: not a single *C. bifasciatus* was trapped, but few specimens were found on the bark behind the pipe (ring 2). *Calodromius bifasciatus* was not found in the ground at the base of two oak trees. An attempt to rear *C. bifasciatus* in captivity failed: in captivity mating was not observed and eggs or larvae were not found. The results described below are mainly based on the nightly observations.

Box 1

De Kaaistoep: Description and site of research

De Kaaistoep lies immediately west of the urban area of Tilburg, province Noord-Brabant, in the south of The Netherlands. It belongs to the TWM Gronden BV (´Tilburgsche Waterleiding Maatschappij´, the Waterworks Company). Since 1994 the agricultural area has transformed into a more natural landscape (Van Wielink 1999). The western part of De Kaaistoep, the actual site of our research, consists of open grassland on poor sandy soil interrupted by straight rows of deciduous trees and shrubs (figure 1). Four artificial small pools were dug in 1994 and a big one of about 1 ha (Prikven) in 1998. Other measures were the planting of indigenous trees, the removal of exotic ones, such as American black cherry (*Prunus serotina*), and mowing of the grasslands in autumn. In the winter of 2005/2006 the canalized brook at the eastern side (Oude Leij) was partially restored.

Our main research object consists of 26 pedunculate oaks (*Quercus robur*). These oaks are part of two rows with trees and shrubs (figure 1). One of the rows is about 80 m long and directed from SSE to NNW (row A). We studied seven oaks from the northern part of the row. Between these oaks there are no other shrubs or trees and the ground beneath is densely covered with grass and small accumulations of dead leaves and moulded branches. In the southern part of row A smaller trees occur such as birch (*Betula*), alder buckthorn (*Rhamnus frangula*), rowan (*Sorbus aucuparia*) and many blackberries (*Rubus*). The other row (row B, figure 2) is about 150 m in a SW to NE direction and consists of 19 oak trees, bordered at the west end by bushes of European elder (*Sambucus nigra*) and blackberry, and at the east end by many European elders, American black cherries, some birches and blackberries. Under the oak trees at row B there are many shoots of European elder and American black cherry. The oaks of row B have lower branches than those of row A, shading most of the ground, and a more open vegetation of grass clumps. Near these oaks much leaf litter is deposited and debris of dead branches.

An artificial pool lies to the southwest of rows A and B and to the west extends an open grassland of about 300 m. In this grassland on poor sandy soil various herbs are abundant (*Rumex acetosella*, *Senecio jacobaea* and *Plantago lanceolata*). At the western side the open grassland is bordered by a straight row of trees, mainly oak. At this side insects are studied by means of light from 1996 onwards. A biological cereal field (C, figure 1) lies at a short distance southeast of row B. North of row B and east of A there is another grassland on poor sandy soil. It has a greater variety of herbs: apart from the abundant ones (*S. jacobaea* and *R. acetosella*) also many others (i.e. *Urtica dioica*, *Cirsium vulgare*, *C. arvense*, *Arabidopsis thaliana*, several species of *Geranium* and *Cerastium* and *Holcus lanatus*). In all grasslands rabbit digging result in patches of bare soil and abundant holes.

The oak trees in both rows are healthy and undamaged and, on average, stand about 4 m apart. They are 15-22 m tall, have a crown of about 10-20 m in diameter and a stem girth of 90-230 cm. In row A the branches of the trees intertwine. In row B only the twigs of tree B1, B17 and B18 (counting from the west) intertwine, whereas B19 is completely isolated. Under or near the oaks of row B many rabbit holes are present whereas there are much fewer in row A.

1. An overview of the western part of De Kaaistoep. Map made by Jaap van Kemenade.
1. Een overzicht van het westelijk gedeelte van de Kaaistoep.

2. View on the oaks of row B from the west (April 5, 2006). Photo: Paul van Wielink.
2. De eiken van rij B gezien vanuit het westen (5 april 2006).

Epiphytes on the oaks of rows A and B consist of algae and lichens. On row A 26 species of lichens were found, 22 on row B, e.g. *Evernia prunastri*, *Lecanora expallens* and *Amandinea punctata*. Only at the foot of some trees two species of mosses were found: mainly *Hypnum cupressiforme* but also *Dicranoweisia cirrata*. The oaks of row A are much more densely covered by lichens than those of row B, probably due to the much greater exposure of row A to wind, rain and sun.

Box 2

Methods used for invertebrate studies in De Kaaistoep

From the discovery of *C. bifasciatus* onwards, we used several methods to study the insect fauna on or near 26 oaks of rows A and B (figures 1 and 2). The methods and their period of use are depicted in a diagram (figure 3).

Pitfall traps

From April 8, 2000 until May 22, 2001 pitfall traps were functioning around oak 5 (from the north) in row A (A5) and oak 6 (from the west) in row B (B6). These oaks were about 16 and 20 m tall and had a stem girth of 1.45 and 1.80 m, respectively. The traps were placed in three circles of four pitfalls each. One circle as close as possible against the foot of the stem, the second circle at 1.5-2 m distance and the third at about 6 m from the stem (just beneath the edge of the crown of the tree). The vegetation contained some dead wood of barren twigs, especially near B6. The outer circle of pitfalls at the south side of B6 was close to a biological cereal field (figure 1).

All pitfalls were made of 1.5-l cups, placed in pvc tubes, of 11 cm wide and 15 cm deep. They were filled with 4% formaldehyde and a few drops of detergent. Hardboard plates covered the pitfalls at a height of at least 2 cm above the opening. The pitfalls were emptied every two weeks. Occasionally a pitfall was damaged by vehicles or lifted by moles.

Window traps

From April 19. 2002 until July 3, 2004 three window traps were used (figure 4). The transparent acrylate screens were 1 × 2 m each and intercepted flying insects at a height of 1.25 until 2.25 m above the soil. A PVC gutter, 20 cm wide and 7 cm deep, sampled the falling insects. Water with 4% formaldehyde and a few drops of detergent, was used as conservation liquid. The gutter was emptied by a tube with a tap, on which a piece of nylon stocking was bound. The liquid was recycled and used again for several times if possible. Insects were collected from both flight directions. The traps were inspected and emptied every week.

The first trap was positioned between A5 and A6 beneath the crowns of the trees. On the top it was covered by a screen to prevent insects falling from above into the device. This trap functioned with small intervals from April 19, 2002 until January 30, 2004. The second and third window traps were placed in the open field at a distance of about 50 m from both row A and B (figure 4). Trap 2 intercepted insects flying from the south and the north, whereas trap 3 intercepted the east and west direction of flight. Traps 2 and 3 functioned from April 19, 2002 until May 23, 2003 and from May 24, 2002 until May 23, 2003, respectively. After a year trap 2 was also placed in an east west interception direction, but it was placed as low as possible with an interception height of about 60 cm just above the top of the dominant vegetation, whereas trap 3 was placed as high as possible (interception 1.50 until 2.50 m). In this way trap 2 functioned from May 23, 2003 until July 3, 2004, and trap 3 from May 23, 2003 until March 12, 2004, with intervals.

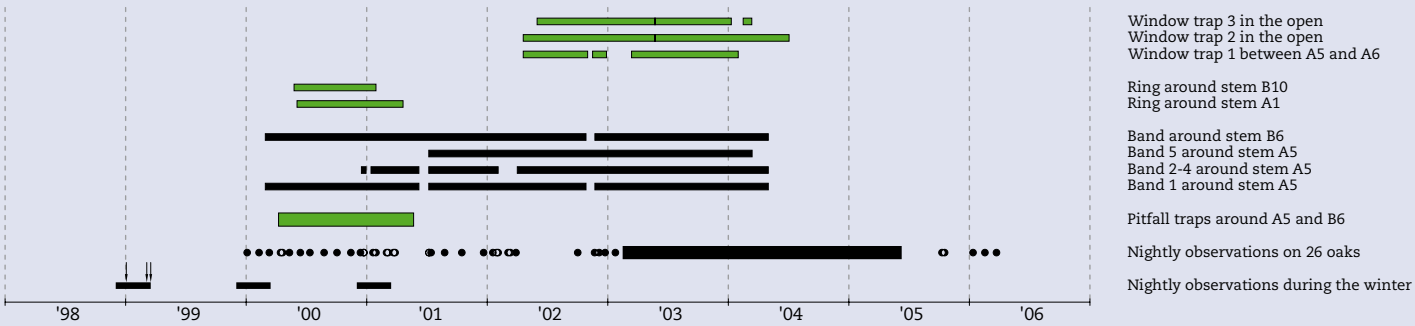
Three times storm winds broke the windows to pieces which gave rise to intervals with non-functioning traps. Especially the highest screen was susceptible to damage by wind.

Bands and rings

From February 27, 2000 until December 27, 2003 bands were used on oaks A5 and B6, the same trees around which the pitfalls were placed. These bands were made of brown paper. After some experiments, for instance with corrugated cardboard as used by Casale *et al.* (1996), we choose a simple strip of packing paper of about 60 cm wide, longitudinal rumpled and wrapped around the stem (figures 4 and 5). Insects hiding in and underneath the paper were easily collected by carefully opening and shedding the paper bit by bit over a big white plastic tray. These bands were attached to the trees at about 1.60 m above the ground.

Starting December 15, 2000 we installed three bands more on tree A5: one at the stem at 4 m and two others at branches at about 6 and 7 m. On July 5, 2001 a fifth band was installed on a branch about 4 m from the stem. The specifications of all these bands, including depth of the clefts beneath the bands, are summarized in table 1. The numbers and species in or behind the bands were noted during inspection and replaced carefully behind the top of the lower band. The bands were inspected every 6-8 weeks on average (figure 5). Sometimes they were destroyed by strong winds and band 4 on A5 was several times destroyed by jackdaws (in Dutch: kauwen). If wet the bands could not be inspected, but this happened only occasionally.

Two kinds of pipe were used as stem embracing bands. One was made of rather thick rubber (inner width 3 cm), cut longitudinally and attached to the stem of tree B10. The open side was directed outwards and the side that contacted the tree was



3. Methods used for research on *Calodromius bifasciatus* in De Kaaistoep. Green: devices that did not trap *C. bifasciatus*. The small interruptions in the bars refer to short periods of malfunctioning. Arrows: discovery of the first three specimens of *C. bifasciatus* in De Kaaistoep (Felix & Van Wielink 2000). Dots in the nightly inspection of 26 oaks refer to single observations; the bar refers to systematic observations with intervals of a week. Drawing by Peter M. van Wielink.

3. Methoden van onderzoek aan *Calodromius bifasciatus* in de Kaaistoep. groen: met deze methoden werd *C. bifasciatus* niet waargenomen/verzameld. De onderbrekingen in de balken geven korte perioden van disfunctioneren aan. Pijlen: de ontdekking van de eerste drie exemplaren van *C. bifasciatus* in de Kaaistoep (Felix & Van Wielink 2000). Stippen in de weergave van de nachtelijke observaties op 26 eiken zijn data van afzonderlijke waarnemingen; de balk is een reeks van observaties met een interval van een week.

4. Window traps in the snow on February 1, 2003. In the foreground oak A5 (with a band) and A6/A7, in between a window trap. In the background the two other window traps (white by hoar-frost) and the oaks of row B. Photo: Paul van Wielink.
4. Raamvallen in de sneeuw op 1 februari 2003. Op de voorgrond eik A5 en A6/7, met daartussen een raamval. Op de achtergrond de andere twee raamvallen (berijpt) en de eiken van rij B.

6. A ring with the opening against the bark of A1. Animals follow the ring and at the opening they drop in a small bottle with 70% alcohol (July 2000). Photo: Paul van Wielink.
6. Een ring met de opening tegen de stam van A1. De vangst komt uiteindelijk in een flesje met 70% alcohol (juni 2000).

5. Ron Felix on ladder, inspecting band 3 on oak A5, on February 28, 2003. The bands A5-1, A5-2 and A5-4 as well as the window trap near A5 are visible. Photo: Paul van Wielink.
5. Ron Felix inspecteert op 28 februari 2003 verband 3 op eik A5. De verbanden A5-1, A5-2 en A5-4 zijn goed te zien evenals de raamval bij A5.

Table 1. Characteristics of the trees at the site of the bands and rings, period of sampling.
Tabel 1. Kenmerken van de bomen op plaats van de verbanden en ringen, verzamelperiode.

band/ring	height (m)	circum-ference (cm)	depth of cleft (mm)	sampling period	times inspected
A5 band 1	1.6	145	12.5	27.ii.00-27.xii.03	35
A5 band 2	4	124	11	15.xii.00-7.xii.03	28
A5 band 3	6	76	5	Idem	28
A5 band 4	7	42	2	Idem	28
A5 band 5*	6	27	< 1	7.vii.01-27.xii.03	19
B6 band 1	1.6	180	14	27.ii.00-27.xii.03	35
A1 ring 1	1.6	170	12	3.vi.00-20.iv.01	21
B10 ring 2	1.6	195	17	25.v.00-28.i.01	11

* Band 5 on a branch, about 4 m from the stem.
* Band 5 om een zijtak op ongeveer 4 m van de stam.

kitted. A T-pipe with a bottle containing 70% ethanol was attached to an opening and served as a collecting device. The other band on A1 was made in the same way but a smaller pipe (1 cm diameter) was used and the open side was turned towards the stem (figure 6). The first type of ring was used from June 3, 2000 until April 20, 2001, the second type from May 25, 2000 until January 28, 2001 (table 1, figure 3).

Monitoring the tree stems at night

More than 6 years, from January 2000 until March 2006, we monitored 144 times all 26 oaks (27 stems) at night from the foot up to about 2.5 m. In the period from February 14, 2003 until June 9, 2005 the inspection was carried out nearly every week on a Thursday (104 times). We started at 1.5-6 hours after sundown (in winter relatively later) and each inspection took 35-90 minutes (depending on the number of observations; in winter relatively longer). For illumination we initially used torches (90 V), but later LEDs were used. The position of all *Dromius* s.l. on the stem (height and direction) was registered, as well as mating and other behaviour. Already in the first year of our study we noticed some specimens with a sphere of small particles at the end of their abdomen. Although we did not know anything about spheres or their function we started to register the absence or presence of spheres during our observations. Weather conditions (temperature, direction and strength of the wind, humidity, presence of fog, etc.) were registered too. We sampled very few beetles because we could identify the specimens to species level *in situ* and we wanted to disturb as little as possible. The beetles were disturbed by the light when we started our research (they acutely stopped their normal activities, tried to get away fast, seek shelter in the clefts, or even dropped themselves). The use of LEDs limited the disturbances and they gave a better and more directed light.

The circumference of each tree, as well as the depth of the clefts in the bark, were measured at about 1.60 m height. On several occasions video-recordings were made of the behaviour of *C. bifasciatus* and other *Dromius* s.l.

Other methods

We dug away the ground at the base of two oak trees in search for *C. bifasciatus*. We also attempted to breed this species in captivity.

Table 2. *Calodromius bifasciatus* and other Carabidae seen or sampled.
Tabel 2. *Calodromius bifasciatus* en andere Carabidae die zijn waargenomen of verzameld.

soort	Nightly observations total	Nightly observations weekly	Pitfall series	Bands	Rings	Window traps	Light 1997-2006**	Digging tree foot
Calodromius bifasciatus (Dejean)	1654	1219	3	64	2	0	0	0
Calodromius spilotus (Illiger)	378	219	2	86	2	0	0	1
Dromius quadrimaculatus (L.)	377	254	1	165	3	6	3	0
Dromius agilis (Fabricius)	41	32	0	2	0	0	0	0
Dromius angustus Brullé	0	0	0	0	0	0	6	0
Paradromius linearis (Olivier)	38	22	2	4	0	2	3	0
Phylorhizus melanocepalus Dejean	10	6	0	4	0	2	0	1
Total *Dromius* s.l.	2498	1752	8	325	7	10	12	2
Total other*	189 (16)	151 (12)	3427 (73)	48 (8)	0	970 (54)	>10.000 (76)	2 (1)
Total	2686	1903	3435	373	7	980	>10.000	4

* number of species between brackets. ** 370 observations in 10 years.
* aantal soorten tussen haakjes. ** 370 waarnemingen in 10 jaar.

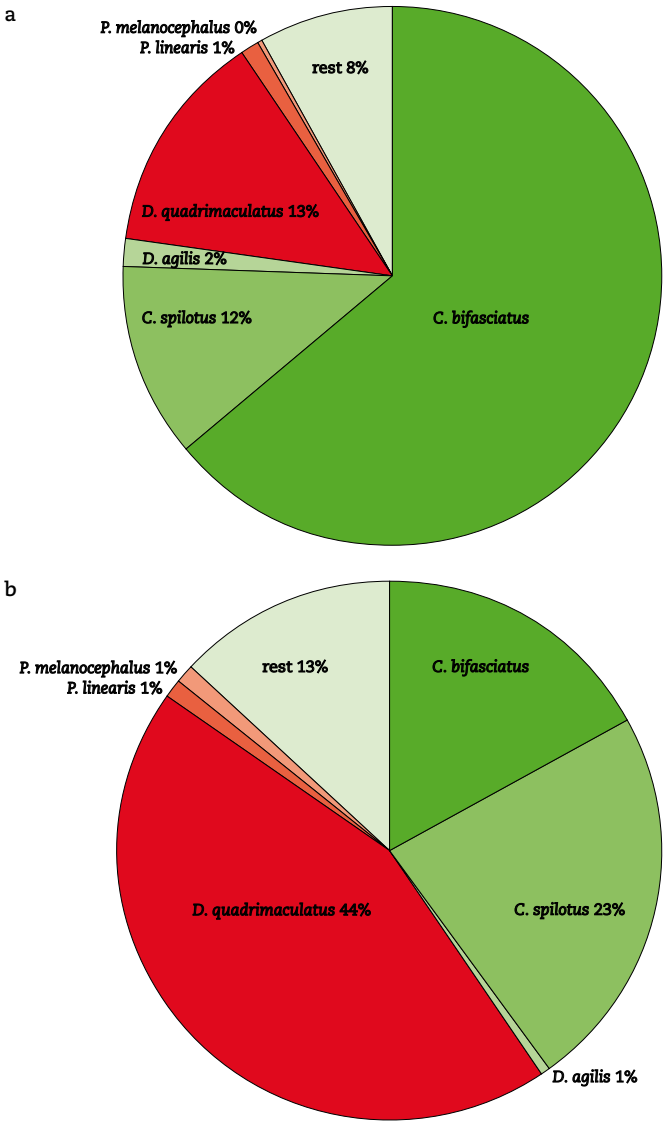
7. From left to right *Calodromius spilotus*, *C. bifasciatus* and *Dromius quadrimaculatus*. *Calodromius bifasciatus* measures 3.5 mm. Photo: Ron Felix.
7. Van links naar rechts *Calodromius spilotus*, *C. bifasciatus* en *Dromius quadrimaculatus*. *Calodromius bifasciatus* is 3,5 mm.

Presence of *Calodromius bifasciatus* on oak trees

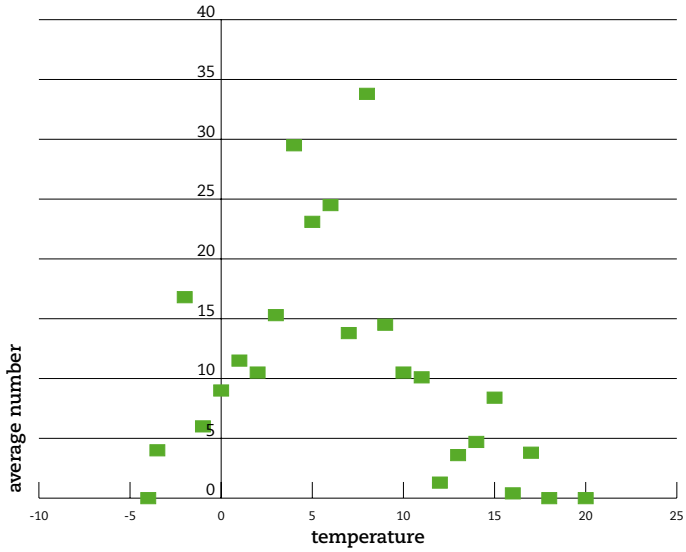
We observed 1654 *C. bifasciatus* (figure 7) on the 26 oaks during 144 nights. In the 104 weekly observations during more than 2 years (included in the 144 nights) 1219 specimens were counted. It is likely that we counted some specimens more than once during our investigations. The highest number of specimens during one night observation is 85, the lowest 0. The bands showed us only 64 *C. bifasciatus* in more than 4 years. Also here we probably counted several specimens more than once. In table 2 the results of all methods are listed.

Figure 8 shows the species composition of Carabidae on weekly observations at night (8a) and behind the bands (8b). More than 85% of the observed Carabidae are *Dromius* s.l. *Calodromius bifasciatus* accounts for 64% of the 1903 Carabidae observed at night, but for only 17% of the 373 found behind the bands. *Dromius quadrimaculatus* (figure 7) shows the opposite: 13 and 44%, respectively.

Calodromius bifasciatus is present on the bark of oaks at an air temperature between –3.5 and 17°C, and the most are found at 4-8°C (figure 9). The maximum number of specimens noted on one evening was 85 at November 20 and December 27, 2003. The temperature was 8 and 6°C, the wind was southwest strength 4 and 3, respectively. On both evenings the humidity was high but the stems were not wet.



8. Relative abundace of Carabidae during weekly observation at night (a) and in the bands (b). (a) Of the 1903 Carabidae observed weekly at night, *Dromius* s.l. accounts for 92% and *Calodromius bifasciatus* for 64%. (b) Of the 373 Carabidae observed in the bands, *Dromius* s.l. accounts for 87% and *C. bifasciatus* for 17%.
8. Samenstelling van Carabidae bij wekelijkse waarneming 's nachts (a) en in de verbanden (b). (a) 92% van de 1903 Carabidae, die wekelijks 's nachts werden gezien, behoren tot *Dromius* s.l. en 64% is *C. bifasciatus*. (b) 87% van de Carabidae die in de verbanden werden aangetroffen behoort tot *Dromius* s.l. en 17% is *C. bifasciatus*.



9. Presence of *Calodromius bifasciatus* on the stems of the oaks related to temperature. The average number of *C. bifasciatus* reaches a maximum at 4-8°C.
9. Relatie tussen de aanwezigheid van *C. bifasciatus* op de eikenstammen en de temperatuur. Het gemiddeld aantal *C. bifasciatus* bereikt een maximum bij 4-8°C.

The total number of *C. bifasciatus* spotted on each tree in the 104 consecutive weekly observations at night varies from 20 (B12) to 169 (B19) (figure 10). The oaks have a different circumference and therefore a different area was investigated (considered as circumference × height of inspection, disregarding the surface structure), which goes from 2.2 (B7) up to 5.7 m^2. Taking this in consideration the numbers of individuals/m^2 varies from 4.7 (B10) to 34.5 (B19) (see also figure 10). The eight stems of row A accommodate on average 37 specimens/oak on 104 nights, whereas the 19 stems of row B yield 48.6 specimens/oak. If the investigated area is taken into consideration the number is almost equal for both rows: 11.0 versus 11.4 specimens/m^2 for row A and B, respectively.

The variability in presence on one oak between moments on one night varies considerably. We observed oak A1 at 1-hour intervals. On November 20, 2003 at 22:00 h, for instance, we noted seven *C. bifasciatus*, at 23:00 h only two were found, but at this time also a single *C. spilotus* (figure 7) and a single *D. quadrimaculatus*. The specimens were observed in completely different sites on the tree on these different moments.

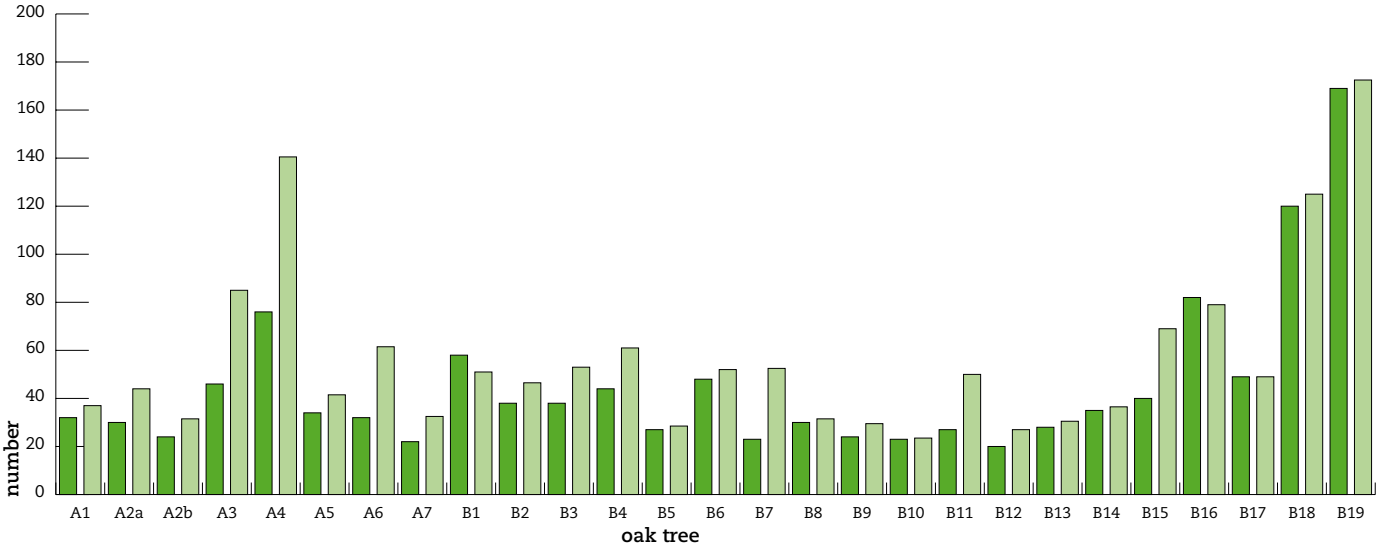
Calodromius bifasciatus, *C. spilotus* and *D. quadrimaculatus* were present in the bands on the stem of oak A5 and in the band of oak B6. The three species were even collected 6 m high at a branch, 4 m from the main stem (band A5-5). For details see table 3.

The weekly observations on the lower 2.5 m of the tree stems at night during more than 2 years provided enough data to construct phenology diagrams for *C. bifasciatus*. In figure 11 the relative monthly presence (number of specimens/number of observation nights) on the 26 oaks in 29 consecutive months is depicted and in figure 12 the relative average monthly presence. *Calodromius bifasciatus* is active in winter. Its presence is at a maximum in the winter: November 2003 to January 2004, December 2004 and February 2005, whereas there are no or very few specimens in June, July, August and September (figure 11 and 12). Of all *C. bifasciatus* we observed 97.5% were present from October until May.

Reproduction and other behaviour

During 144 nightly observations we noted 63 copulas amongst 1654 *C. bifasciatus* and in the 104 weekly observations there were 46 copulas amongst 1219, almost 8% of the specimens for both observation types (see figure 12). Copulas were seen from October (only one) until April, and at –1 to 17°C. On November 20, 2003 a maximum of nine copulas (21% of the specimen) was seen. That evening temperature was 8°C and humidity was high. There are no substantial differences in the number of copulas between rows A and B. Differences exist between individual trees but the numbers of copula/tree are very low (0-10 in 104 nights). *Calodromius bifasciatus* is thus not only active in winter, but it obviously also copulates during winter, even close to freezing point. Of the other *Dromius* s.l. only *C. spilotus* was seen in copula: five times amongst 378 specimens (almost 3%), also during winter.

Although we intensively searched for larvae of *Dromius* s.l., we never found one – neither on the stems at night, nor in the bands or rings or pitfalls we discovered larvae. However, on August 24, 2001 we found two *C. bifasciatus* with soft elytra and an incompletely developed colour pattern, indicating recent pupation at this location.

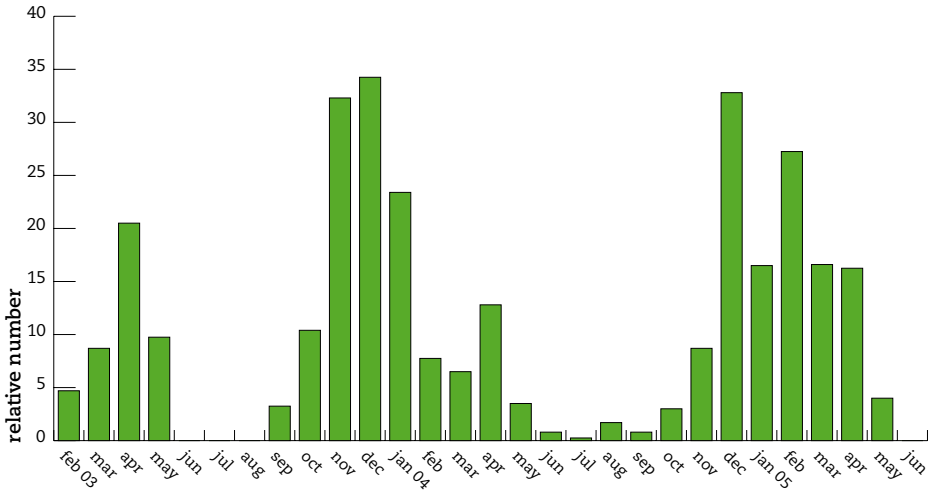


10. The presence of *Calodromius bifasciatus* on 26 individual oaks (27 stems: A2 splits up near the bottom). Dark green: absolute numbers, light green: numbers per m^2 (× 5). The numbers are based on 104 weekly observations.
10. De aanwezigheid van *C. bifasciatus* op 26 eiken (27 stammen: A2 splitst vlak boven de grond in twee stammen). Donkergroen: absolute aantallen, lichtgroen: aantal per m^2 (× 5). De aantallen zijn gebaseerd op 104 wekelijkse waarnemingen.

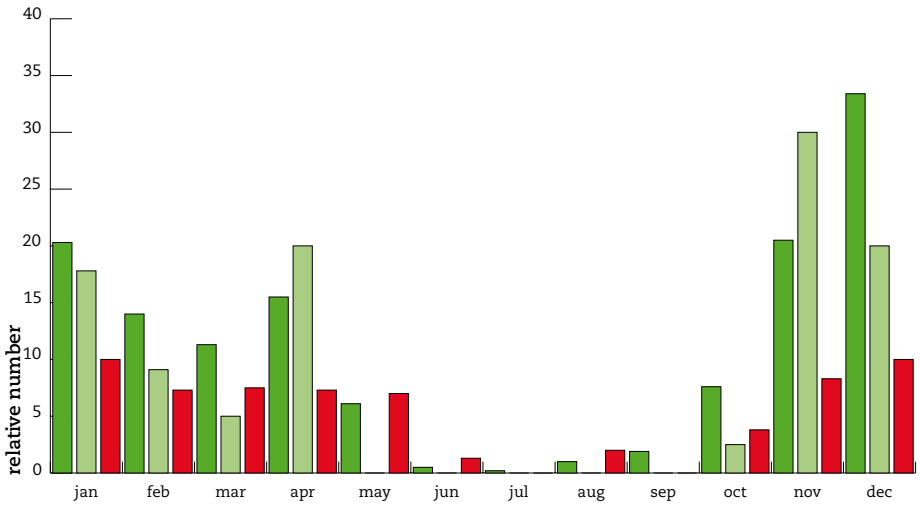
Table 3. *Dromius* s.l. in the tree bands.*
Tabel 3. *Dromius* s.l. in de verbanden om de bomen.*

	A5-1 (1.6 m)	A5-2 (4 m)	A5-3 (6 m)	A5-4 (7 m)	A-5 (6 m)	A5 total	B6 (1.6 m)	A5+B6
Calodromius bifasciatus	29	4	15	5	1	54	10	64
Calodromius spilotus	23	16	18	10	3	70	16	86
D. agilus	-	-	-	-	-	-	2	2
D. quadrimaculatus	40	29	49	23	6	147	18	165
D. melanocephalus	3	1	-	-	-	4	-	4
Paradromius linearis	3	1		-	-	4	-	4

*See table 1 for the characteristics of the tree at the site of the band and sampling time.
*Zie tabel 1 voor de eigenschappen van de boom op de plaats van het verband en de verzamelperiode.



11. Phenology of *Calodromius bifasciatus*: relative presence in 29 consecutive months. Relative presence: the number of beetles per month divided by the number of nightly observations during that month (the number of nightly observations varied between 2 and 4 per month).
11. Fenologie van *C. bifasciatus*: de relatieve aanwezigheid in 29 opeenvolgende maanden. Relatieve aanwezigheid: het aantal waargenomen kevers per maand gedeeld door het aantal nachtelijke waarnemingen in de betreffende maand (het laatste getal varieert tussen 2 en 4).

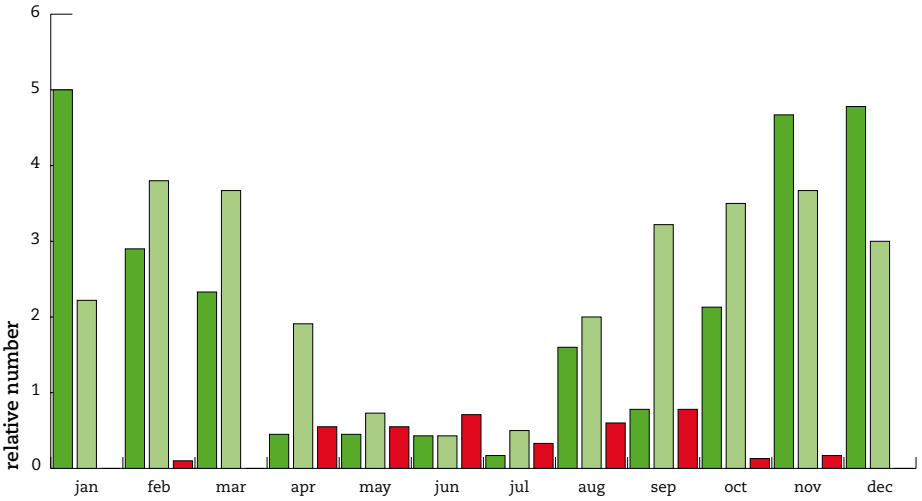


12. Phenology of *Calodromius bifasciatus* including copulas and spheres (as depicted in figures 14-16): relative average presence per month over more than 2 years. Relative presence: see figure 11 (the number of nightly observations varies between 5 and 12 per month). Dark green: *C. bifasciatus*, light green: copulating individuals (× 10), red: spheres (× 10).
12. Fenologie van *C. bifasciatus* inclusief copulas en 'bolletjes' (zie afbeeldingen in figuur 14-16): de gemiddelde relatieve aanwezigheid per maand berekend over meer dan 2 jaar. Relatieve aanwezigheid: zie onderschrift figuur 11 (het aantal nachtelijke waarnemingen per maand varieert tussen 5 en 12). Donkergroen: *C. bifasciatus*, lichtgroen: copulerende individuen (× 10), rood: bolletjes (× 10).

When *C. bifasciatus* specimens stroll around it looks like they are inspecting the bark. We sometimes observed specimens biting in algae or lichens on the bark, directing their abdomens upwards with their hind legs stretched. Sometimes they were observed biting the layer of algae or lichens, stepping forward and scratching the tip of their abdomen over the spot where they just had bitten. The posture is now reverse: the front legs stretched, the hind legs bent and the abdomen low to the trees surface. This behaviour was displayed on eleven evenings by female specimens with a sphere on their abdomen. The temperature ranged from 3-13°C. On one of those evenings it was dry, on eight it was humid or very humid and on two evenings we did not take a note on air humidity. In contrast, of the 104 weekly observations at night only 38 scored humid (37%). Our figures suggest that the described behaviour is displayed preferably when humidity is high.

During 144 nightly observations we noted 69 female *C. bifasciatus* with a sphere at the end of the abdomen; in the 104 weekly observations there were 60, about 4-5% of the specimens for both observation types. The presence has a broad maximum from November until May, but a single specimen was seen with a sphere in June and August 2004 (figure 12). There are no substantial differences in the number of spheres between rows A and B. Differences exist between individual trees but the numbers of spheres/tree are very low (0-7 in 104 nights).

Spheres were seen when temperature ranged from 3-15°C. On 9 February six and 30 March five spheres were noted, with 16 and 38% of the specimens, respectively. On those evenings it was 8 and 11°C and the humidity was high. Our figures show that spheres, like the mere presence of *C. bifasciatus*, have a maximum presence from 3-11°C (not shown) and suggest a preference for high humidity.



13. Phenology of *Calodromius spilotus*, *Dromius quadrimaculatus* and *D. agilis*: relative average presence per month. Relative presence: see figure 12. Dark green: *C. spilotus*, light green: *D. quadrimaculatus*, red: *D. agilis*.
13. Fenologie van *C. spilotus*, *D. quadrimaculatus* en *D. agilis*: relatieve gemiddelde aanwezigheid per maand. Relatieve aanwezigheid: zie onderschrift figuur 12. Donkergroen: *C. spilotus*, lichtgroen: *D. quadrimaculatus*, rood: *D. agilis*.

The spheres of *C. bifasciatus* (and other *Dromius* s.l.) can be very different in size, from about 0.3 until 1.0 mm (figures 14 and 15). The outside is granulate while the inside is very smooth (see figure 15 and 16). Possibly the granules on the outside are soredia of lichens, because they are fairly constant in size and shape. In De Kaaistoep these soredia could be of *Lecanora expallens* (A. Aptroot, personal communication). On a few occasions we noted a filament on the sphere and the abdomen (figure 17).

Our numbers of copulas and spheres on individual oaks are too small to reveal any relation between them.

At daytime *C. bifasciatus* and other *Dromius* s.l. are not seen on the bark of the oaks. They undoubtedly seek shelter deep in the clefts like they do at night when they are disturbed by the light of the torches. Their flat body allows hiding in narrow clefts. On disturbance *Dromius* s.l. can run very quickly.

The activity on the tree stems at night varies. A few times we noted high activity ('nervous behaviour'), whereas on other days they were quite slow. Once, on April 29, 2004, we noted that all 23 *C. bifasciatus* were strikingly active on the stems. That evening temperature was 15°C and it was very humid, although the stems were not wet. Low temperature seems not always associated with low activity. At two occasions we made a note of low activity, once at 7°C and once at -3°C. Based on our data, high activity seems to be associated with high air humidity. However, water on the stem obstructs their movements completely, and when it rains they hide in the clefts –not surprising for such a small and thin animal (3-3.5 × 0.6 mm).

Although we observed about 2500 *Dromius* s.l. during our studies, we noticed only three times a possible prey. A *Paradromius linearis* that had a colembole between its mandibulae, a *C. spilotus* with a mite or small spider and a *D. agilis* with an unidentified prey.

Discussion

Perhaps the hidden way of life of *C. bifasciatus* is the cause of our fragmentary knowledge of this species. Like many other arboricol *Dromius* s.l. species it is only accidentally found underneath bark of dead trees. Many species turn out to be far more abundant on the stems of live trees during the night, which also matches better with their reproduction behaviour (Will 1998). Moreover, *C. bifasciatus* is seen more during the cold period than during the warmer months, at least in The Netherlands, Belgium and Germany. Few entomologists search for beetles at night on live trees, let alone on cold nights in wintertime.

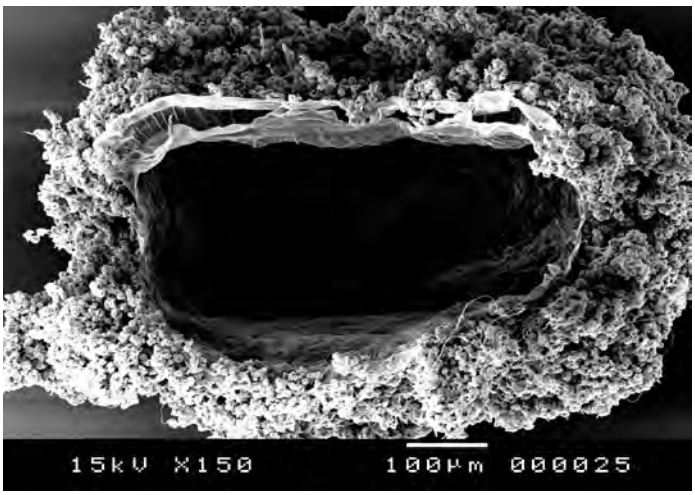
Dispersal and migration

Because of the appearance of *C. bifasciatus* in De Kaaistoep and its peculiar distribution pattern, we became interested in its dispersal capacities. Pitfall-trapping during more than a year in two series of 12 pitfalls yielded only three *C. bifasciatus*. This suggests that activity on the ground is low in *C. bifasciatus*. Three window traps intercepted flying insects during more than 2 years. Not a single specimen of *C. bifasciatus* was collected in these traps, not even in the window trap between two oaks, notwithstanding the capture of numerous carabids. We conclude that *C. bifasciatus* does not fly at heights between 1.25 and 2.50 m. Surprisingly, six *D. quadrimaculatus* were collected in the window traps, all of them during summer in the screen between the two oaks. *Dromius quadrimaculatus* is present on the lower parts of the trees in summer (figure 13) and flies between tree stems at lower heights.

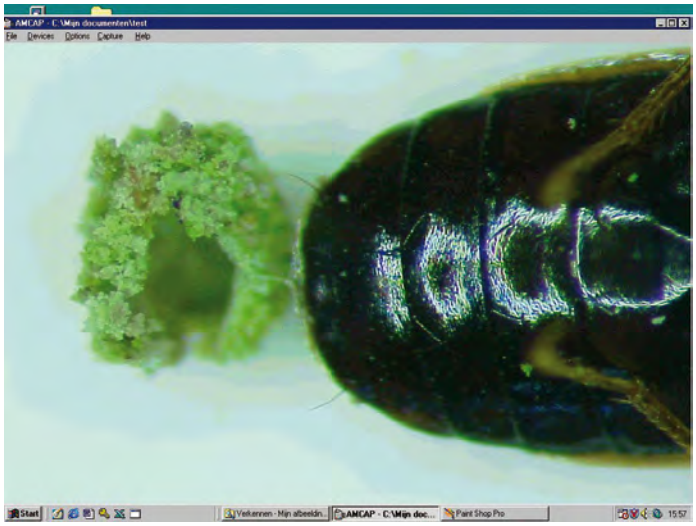
From our data (table 2) it became evident that despite a few specimens of *D. angustus*, *D. quadrimaculatus* and *P. linearis*, *Dromius* s.l. is only rarely attracted by light. The three specimens of *D. quadrimaculatus* noted in 10 years on light were also seen in summer. However, other species of *Dromius* s.l. are attracted by light, like *Dromius vagepictus* (Fairmaire) and *Calodromius mayeti* (Bedel) in the United Arab Emirates (Tony van Harten, personal communication). Casale *et al.* (1996) attracted *Dromius meridionalis* (Dejean) with black light during summer and autumn. Our data from window traps and light showed low flying activity which is in line with Simon (2001) who stated: 'die Flugaktivität von *Dromius*-Individuen in Wäldern ist sehr gering'. Further investigations on flying capacity and activity periods are in need. We recommend other methods, for example flight interception devices high up in the trees and other light sources.

We observed specimens of *C. bifasciatus* and to a lesser extend also *C. spilotus* at night on the lower parts of the trees, from the foot up until about 2.5 m, almost exclusively in winter (figures 12 and 13). We did not see them in summer. The common opinion seems to be that *Dromius* s.l. is not seen on the lower parts of the trees in summer because they are high up in the crown (Reddersen & Jensen 1991, Scheffler 1997, Irmler 1998, Simon 2001, Hannig *et al.* 2006). They argue that micro-environmental conditions are better in the crown in summer. In winter *C. bifasciatus* and other *Dromius* s.l. are frequent on the lower parts of the tree. At night they wander much higher as we found them in and behind higher bands. Maybe they go high up in the crown as far as they can go in search for prey. Irmler (1998) used window traps at different heights (1.5-27 m). He found *D. agilis* and *D. quadrimaculatus* more in higher window traps than in lower ones in spring, summer and autumn. The presence in

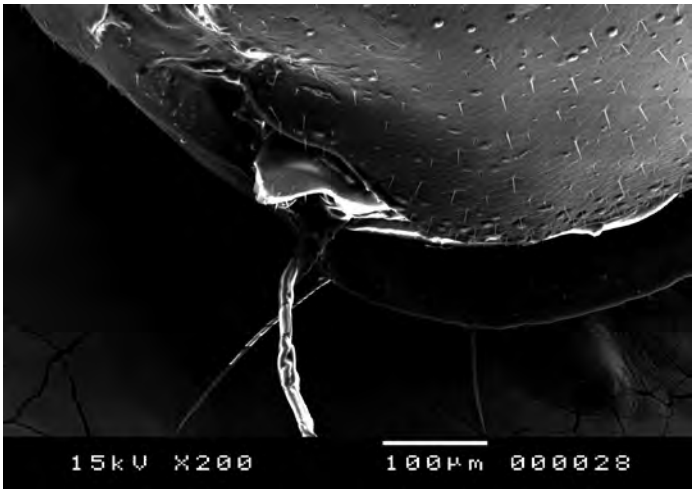
14. The abdomen with tergites of *Calodromius bifasciatus* with a small sphere attached to it. Photo: Ron Felix.
14. Het abdomen met tergieten van *C. bifasciatus* met een klein bolletje er aan vast.



16. A sphere of *Calodromius bifasciatus*. Photo taken with scanning electronmicroscopy. Note the smooth cavity and the granulate outside. Photo: Dr. Cris Hesse, Nationaal Herbarium Nederland/Leiden University.
16. Een bolletje van *C. bifasciatus* gefotografeerd met de scanning elektronen microscoop. Let op de gladde binnenkant en de korrelige buitenkant.



15. Abdomen with sternits of *Calodromius bifasciatus* with a sphere. Note the smooth cavity and the granulate outside of the sphere. Photo: Ron Felix.
15. Abdomen met sternieten van *C. bifasciatus* met een bolletje. Let op de gladde binnenkant en de korrelige buitenkant van het bolletje.



17. The end of the abdomen of *Calodromius bifasciatus* with a filament. Photo taken with scanning electronmicroscopy, by Dr. Cris Hesse, Nationaal Herbarium Nederland/Leiden University.
17. Het eind van het abdomen van *C. bifasciatus* met een draad gefotografeerd met de scanning elektronen microscoop.

higher window traps could mean that these *Dromius* climb high up into the trees to fly away. But it does not necessarily mean that they stay this high during summer. We found these *Dromius* species also on the lower parts of the trees in summer. Simon (2001) investigated coniferous trees and because he hardly found *Dromius* s.l. lower on the stems, he suggested that when temperatures are increasing they migrate to the crown of the trees, possibly also influenced by the availability of food and by humidity, as the crowns are cooler and more humid during summer (Simon 2001).

However, we call for caution until direct evidence is available for the actual presence of *C. bifasciatus* or other *Dromius* s.l. high up in the tree crown in summer. Hannig *et al.* (2006), for instance, found it likely that *C. bifasciatus* migrates to the higher tree strata at temperatures higher than 12°C, only because they could not find them on the lower parts. Although window traps proved that *Dromius* s.l. must have been there during nightly migration, prove of staying there for a longer period is still lacking. Our bands around the stems provided no indication for migration upward to the tree crown in summer. We hypothesize that adults of *C. bifasciatus* die before summer, apart from a few specimens that had an exceptionally long life span.

When threatened or disturbed by light, *C. bifasciatus* immediately seeks shelter into the clefts of the stem. This behaviour is difficult or even impossible higher up in the tree where stem and branches hardly have clefts. *Calodromius bifasciatus* and other *Dromius* s.l. are very thin, but relatively broad, and are built to seek hiding in very narrow places. Hiding during daytime is essential in avoiding predation, e.g. by birds. Probably it dwells all over the trees when it is dark and during daytime it stays in the lower regions, where hiding is easier. Moreover, our impression is that oaks with (at least partially) a structure of many fine and narrow clefts (in the lower parts of the stem) are more appreciated by *C. bifasciatus* and other tree-living *Dromius* s.l. then stems with deep, but open and wide clefts (figure 18a,b).

Finally, we doubt whether the crown of our oaks is cooler and more humid in summer than deep clefts in the stem at lower parts on the shady north sides of the trees.

18. The structure of the bark of oaks in De Kaaistoep differs substantially. Photo's taken at equal distance and magnification. a. bark of B12. b. bark of B19. Photos: Ron Felix.
18. De structuur van de schors van de eiken in de Kaaistoep kan zeer verschillend zijn. Foto's gemaakt op gelijke afstand en vergroting. a. schors van B12; b. schors van B19.

Calodromius bifasciatus probably avoids contact with the ground. We hardly found them in the pitfalls (sometimes they fell down while loosening the paper bands high up in the tree) and not at all in the ground around trees after digging at the foot (see table 2). We observed them during a very cold, freezing night, clustering at the very bottom of the tree, even 1 cm beneath the surface, but always on the bark and in crevices and never in contact with the soil. Migration from one tree to another by walking on the ground is not common for *C. bifasciatus* (or *C. spilotus*, or *D. quadrimaculatus*). On the other hand, Van Malderen (2007) mentions that *C. bifasciatus* can be found by sifting leaves and dead wood underneath oaks and poplars.

Simon (2001) discusses migration on trees of other *Dromius* s.l. He mentions Trautner (1984) and Scheffler (1997) who stated that many arbicolous insects hibernate at the foot of the tree. Animals were found exclusively on the lower parts of the trees and mostly in winter and early spring. Our experience is the same, although *C bifasciatus*, *C. spilotus* and *D. quadrimaculatus* do not hibernate there, but stay there immobile while temperature is far below freezing point. According to Simon (2001), also referring to others, *C. spilotus* was collected at all heights (1.5, 5, 10 and 13 m) in equal numbers and *D. agilis* preferred the lower regions. This contrasts with some other investigators who found *D. agilis* and *C. spilotus* mainly high up in the trees (Irmler 1998, Reddersen & Jensen 1991).

If *C. bifasciatus* avoids contact with the ground and do not fly regularly, this could explain that there is little exchange between neighbouring trees. This matches our observation that B16 and B18 contained relatively high numbers of specimens, while B17 had much fewer (figure 10).

Phenology – presence in relation to biotic and abiotic factors

Adults of *C. bifasciatus* are active in winter and nearly absent during late spring and summer (figure 11). Hannig *et al.* (2006) came to the same conclusion. As long as temperatures are above freezing point they are active on the lower part of the tree stem in contrast to many other beetle species we noticed. This phenomenon is quite unexpected for a species supposed to have a southern European and northern African distribution (Felix & Van Wielink 2000). The same remarkable activity pattern holds for copulas, which are present from October until April, and for females with spheres, which were seen mostly during winter (figure 12).

Our results indicate a relation between the presence of *C. bifasciatus* and temperature. *Calodromius bifasciatus* is active between –3.5 and 17°C and most are found between 4 and 8°C (figure 9). These data are in agreement with those of Hannig *et al.* (2006) who found *C. bifasciatus* between –3 and 12°C during daily observations from half November until the first of June. About 8% of our *C. bifasciatus* were observed outside this period and about 12% above 12°C. We believe that Hannig *et al.*'s conclusion that *C. bifasciatus* is hardly present on the lower part of the tree stem after the middle of March and not present at all at temperatures above 12°C is based on too little data.

We found no correlation between *C. bifasciatus* numbers on individual trees with factors like tree circumference, competition with other *Dromius* s.l., or presence of sow-bugs, ants or other fauna elements. We have no indication that a higher or lower abundance of algae, lichens or mosses is a discriminating factor, nor the exposure to wind, sun and rain. Maybe the structure of the bark of an individual oak is important. *Calodromius bifasciatus* and other *Dromius* s.l. need small clefts (0.5-0.8 mm) to survive. The number, width and depth of these clefts on individual trees are undoubtedly highly variable and independent of the circumference of the oaks we investigated (figure 18).

Scheffler (1997) found that *C. spilotus* prefers places in which it experiences pressure: aggregation experiments showed that more specimens crawl underneath flat filter paper on the bottom of Petri dishes, than under folded paper. Maybe *C. bifasciatus* finds enough hiding places (and pressure) in the clefts, and the bands (and especially the used rings) do not provide much more shelter. *Dromius quadrimaculatus*, which is much bigger, probably experiences more profit from the extra shelter provided by the bands.

We also obtained data about the phenology of three other *Dromius* s.l. species (figure 13). The pattern of *C. spilotus* looks very much like that of *C. bifasciatus*. Simon (2001) found that *C. spilotus* was present all year, but hardly in December and January, and most frequently in spring until the end of April and in late summer and autumn. Our experience is rather different: *C. spilotus* – like *C. bifasciatus* – is hardly found from April until August, most frequent in November, December and January. *Dromius quadrimaculatus* is different in having a maximum in early spring and late autumn (figure 13). *Dromius agilus* is exceptional: this species is most abundant in summer and in the lower region of the stem. We did not see it in December, January and March (figure 13). These data of *D. agilis* harmonize with those of Simon (2001). *Dromius agilis* is also exceptional because we only observed it on row B and not on row A.

Like *C. bifasciatus* we observed *C. spilotus* and *D. quadrimaculatus* at low temperature active on the bark of the oaks. Activity in winter at low temperature is therefore not a unique quality of *C. bifasciatus*. Our data do not allow to estimate the density of *C. bifasciatus*, neither per tree nor per row.

Reproduction

In de Kaaistoep we observed copulas from October to April. Although the data on presence of copulating specimens and weather conditions are limited, our observations suggest that copulating, like the mere presence of *C. bifasciatus*, has an optimum between 2 and 9°C (80% of all copulas) and at high humidity.

The phenomenon of sphere making was not recorded before in Europe. Hannig *et al.* (2006) studied *C. bifasciatus* in detail but did not mention the presence of spheres. However, spheres are mentioned by Will (1998) in his extensive description of the behaviour prior to oviposition of *Dromius piceus* (Dejean) in Ithaca (NY, USA). He distinguishes four stages:

- 'searching': apparently random movements on the stem, sometimes with pauses of 1-5 s.
- 'scraping': loosening algae and bark with their mandibles by rapid movements, frequently paused.
- 'bolus formation': the beetles walk over the scraped particles, until the end of the abdomen is above the particles, then the abdomen is lowered and with short swift movements to and fro the material is picked up. Step 2 and 3 are repeated until the sphere ('bolus') is ready.
- 'oviposition': the beetle searched an area of about 1 m^2, lowered the abdomen and remained motionless during 1-2 minutes, then deposited the sphere with a rapid movement and with the same sticky substance as was used for its manufacturing.

Casale *et al.* (1996) mention 'egg cases' for *D. meridionalis* and *D. quadrimaculatus*. This phenomenon is not only seen with *Dromius* s.l. but also with other Carabidae (King 1919, Thiele 1977). It is suggested that eggs are covered with soil or algae particles, apparently implying the presence of eggs before the spheres are completed. However, we never found eggs in the spheres of *C. bifasciatus* (nor in those of *C. spilotus* and *D. quadrimaculatus*): all were empty. Perhaps the egg (eggs?) is inserted into the sphere just before it is dropped, as is in line with Will's (1998) description of oviposition. In this respect the sphere could be named 'pre-oötheca'.

We noticed pre-oötheca almost every month but predominantly in winter. Depending on developmental time of the embryo and possible dormancy of the young larva, larvae could be active from early winter onwards. Subsequently adults may appear from August or late summer onwards. This is in line with the discovery of two fresh (teneral) adults in August. Although we never found larvae, we assume larvae to live on trees and not on the ground. Casale *et al.* (1996) observed larvae of *D. meridionalis* on a large-leaved lime (*Tilia platyphyllos*) in a busy street where the floor seemed not suitable as an environment for carabid larvae (no vegetation and pavement around the foot of the tree).

Conclusions

- *Calodromius bifasciatus* is active during winter at night on the lower 2.5 m of oak trees and it even copulates at freezing-point.
- It is most abundant at 4-8°C and at high air humidity.
- Pre-oötheca at the abdomen of females are smooth inside and covered with granulate particles. Egg-filled pre-oötheca were not found.
- Larvae were not found on the bark of the oaks.
- No evidence was obtained for the suggested seasonal migration (high in trees in summer, low in winter) and, instead, we suggest that *C. bifasciatus* is nearly absent in summer.
- Pitfalls, window traps in the field, light traps and rings are not suitable to detect *C. bifasciatus* and other *Dromius* s.l. (*C. spilotus*, *D. quadrimaculatus*, *D. agilis*).
- Inspecting trees at night is very rewarding, especially during, winter.

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Henk Spijkers participated at the start of our studies and stimulated our research with creative suggestions. The investigation with light and flight interception traps was supported by a grant of the Uyttenbogaart-Eliasen Foundation. TWM Gronden BV (formerly Tilburgsche Waterleiding-Maatschappij) gave us access to their properties and provided facilities. Jaap van Kemenade (conductor/manager) showed much interest and stimulated our research. Natuurmuseum Brabant facilitated the study and stored a part of the collected material, which is accessible for research. Frank van Oosterhout (Onderwaterpark De Rauwbraken) was a partner in the discussion. The Bryological and lichenological study group of the Royal Dutch Natural History Society (KNNV) carefully inspected the 26 oaks. André Oude-Vrielink made video recordings. Cris Hesse made some EM-photo's of *C. bifasciatus* and its spheres. Jan van Tol (Naturalis, Leiden) allowed us to use the equipment of the museum to make photographs of the three *Dromius* s.l.

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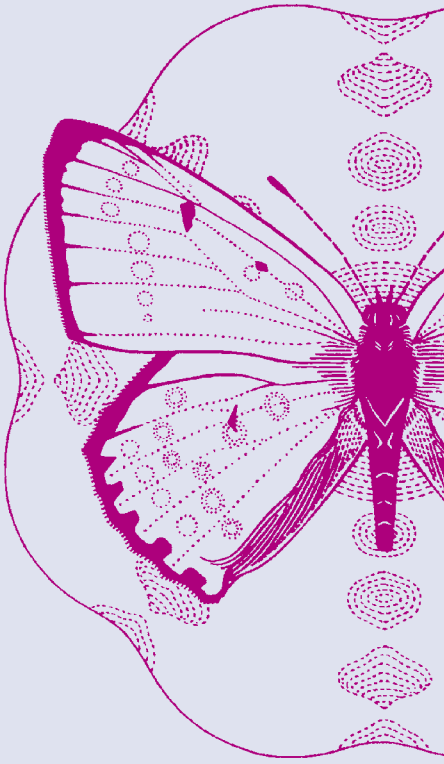
Samenvatting

Over de biologie van *Calodromius bifasciatus* en verwante soorten in 'De Kaaistoep' (Coleoptera: Carabidae)

Calodromius bifasciatus (Dejean), een kleine schorsloopkever, werd voor het eerst in Nederland ontdekt in De Kaaistoep (een terrein van de N.V. Tilburgsche Waterleiding-Maatschappij) in januari 1999. Er bleek een populatie aanwezig op twee rijen met in totaal 26 zomereiken. De Kaaistoep is alleen toegankelijk met vergunning en het terrein biedt allerlei faciliteiten, zoals voor het opbergen van materialen. Dit maakt het uitstekend geschikt voor het doen van (breed entomologisch) onderzoek, bijvoorbeeld naar het antwoord op enkele ecologische vragen omtrent de schorsloopkevers. Verscheidene vangmethoden, zoals potvallen, raamvallen en verbanden en ringen om de boomstammen en takken, werden toegepast om meer te weten te komen over de dispersie en migratie van *C. bifasciatus*. Gedurende meer dan twee jaar werden bijna wekelijks 's nachts de stammen van de eiken geïnspecteerd om meer van het gedrag van de kevers te leren. Ook werden 's nachts de onderzoeksbomen geïnspecteerd op overige fauna. Daarnaast werden gegevens verzameld over copuleren, voedsel zoeken, de aanwezigheid van een pre-oötheca aan het achterlijf, de plaats op de stam en de overige fauna, ook in relatie met de weersomstandigheden.
De fenologie van *C. bifasciatus* en een aantal andere *Dromius*-soorten geeft aan dat *C. bifasciatus* in de winter actief is en grotendeels ontbreekt gedurende de zomer. *Dromius agilis* daarentegen is niet aanwezig in de winter. *Calodromius bifasciatus* werd copulerend aangetroffen bij temperaturen tegen het vriespunt. De afwezigheid in de zomer wordt niet verklaard uit migratie naar hoger gelegen delen van de boom, vooral niet omdat *C. bifasciatus* gebonden lijkt aan stamdelen met veel nauwe spleten, zoals vooral de onderste meters. Wij veronderstellen dat *C. bifasciatus* in de zomer (vrijwel) niet aanwezig is.
Wij vonden grote variatie in de aanwezigheid van *C. bifasciatus* tussen individuele bomen, maar kunnen deze verschillen niet verklaren uit begroeiing, blootstelling aan wind, regen en zon, en ook niet uit concurrentie met andere *Dromius* s.l. of andere insecten. De enige onderscheidende factor lijkt de structuur van de schors.
Veel vragen zijn niet opgelost. Zo konden we geen larvale stadia ontdekken en weten we nog weinig over de dispersie. In dit artikel worden onze resultaten besproken en vergeleken met die van een recent verschenen Duits onderzoek over hetzelfde onderwerp.



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