Drilus larvae in the Netherlands (Coleoptera: Elateridae: Drilini)

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Two *Drilus* species occur in the Netherlands: *D. concolor* and *D. flavescens*. *Drilus* larvae develop into an adult in about two years, passing different larval instars and types. This hypermetamorphosis is described in detail. Differences between the larvae of *D. concolor* and *D. flavescens* are described, mainly based on colour and colour pattern. The red, hairy *Drilus* larvae prey on various snail species. Before a *Drilus* can feed on a snail, it has to paralyze it, therefore the larva bites its prey several times. Our observations of their predation behaviour are described, supplemented with information on some of the snail species we found them in. The distribution of both species is mapped; *D. concolor* occurs mainly in the centre of the Netherlands and *D. flavescens* mainly in the south of Limburg.

Introduction

The larvae of *Drilus* beetles prey on snails and are therefore called ´snail eaters´. Two *Drilus* species occur in the Netherlands: *D. concolor* Ahrens (figure 1a) and *D. flavescens* (Geoffroy) (figure 1b). *Drilus concolor* is the black snail eater; it is mainly present in the centre of the Netherlands. *Drilus flavescens* is the common or red snail eater and occurs mainly in the south of the province of Limburg.

The genus *Drilus* contains 35 species and occurs mainly in the West-Palaearctic region (Wittmer 1944; Kundrata & Bocak 2011). *Drilus* beetles are most common in lowland or lower mountain forest habitats in Central-Europe, and in the Mediterranean region in coastal marshes and high-altitude habitats (Bocak *et al*. 2010). *Drilus concolor* and *D. flavescens* are the only known *Drilus* species north of the Alps (Bocak *et al*. 2010).

Larvae of the Dutch *Drilus* species prey on various snail species; we found them primarily in *Cepaea nemoralis* (Linnaeus) and *Cornu aspersum* (Muller). Numerous snails are eaten by a single *Drilus* larva during its lifetime. *Drilus* larvae catch snails by paralyzing them. After eating the soft tissue, they moult inside the shell. The presence of a larval skin makes it easy to decide whether a snail has died by predation of a *Drilus* larva or not.

Like *D. mauritanicus* Lucas (Faucheux & Agnas 2016) and several Greek *Drilus* species (Baalbergen *et al*. 2014, Kundrata *et al*. 2015), a *D. concolor* and *D. flavescens* larva hibernates by entering a resting stage; it becomes a ´pseudopupa´. A full-fed *Drilus* larva pupates in spring and develops into a winged male or a larviform female. The larviform female lives as the larvae on the soil surface, mostly hidden inside a shell (Bocak *et al*. 2010). Hence, most observations of *Drilus* beetles in general are of the adult males.

We provide the first complete illustrated description of the development of *Drilus* species in the Netherlands from egg to adult. Detailed descriptions of the larvae of both species make it possible to identify them without DNA or emerging adults. We have combined data from collection specimens and observations to provide a distribution map of both species in the Netherlands. Finally, we provide new insights into the predation behaviour of the larvae, illustrated with movies.

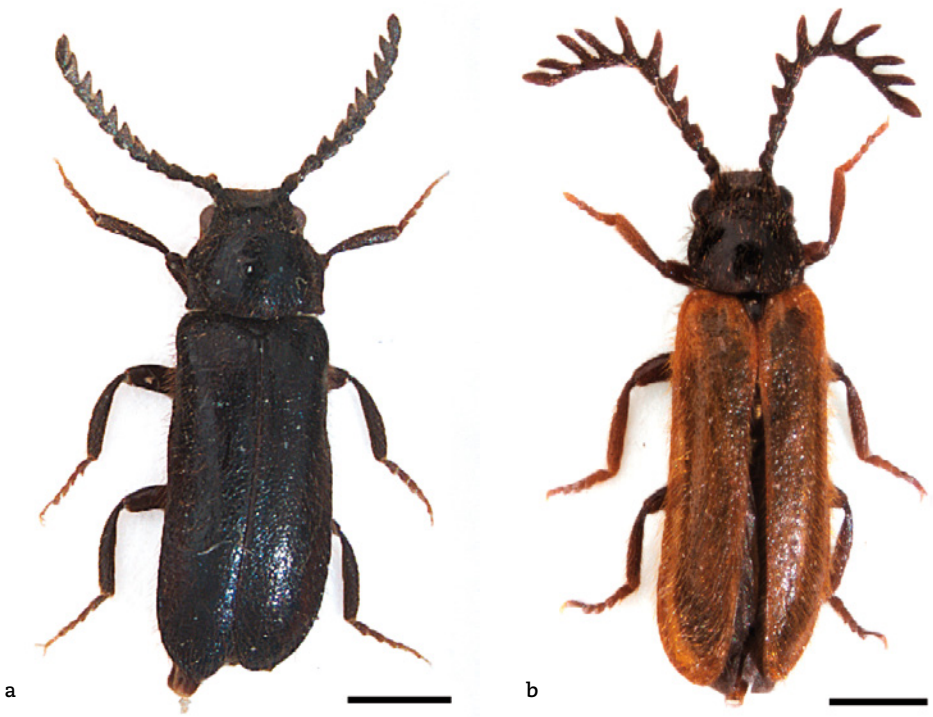
Morphology and development

During its lifespan, which lasts for two or three years, a *Drilus* passes through different larval stages (figure 2). Unlike most beetles with only 'normal' active larva, a *Drilus* larva develops into a resting stage during winter, the 'pseudopupa'. This is called hypermetamorphosis. The morphology of the different stages was studied. Unfortunately, the complete development of an individual from egg to adult could not be observed. During our study several larvae developed into a female and only one developed into a male. Therefore, a reliable comparison of the development of both sexes was only possible for the pupa, in which the sex difference is obvious. Different parts of the hypermetamorphosis were studied by breeding specimens (7 *D. concolor*, >30 *D. flavescens* (developing eggs not included)), collected from several places in the Netherlands. The specimens were kept under moist conditions on tissues at room temperature. These observations were supplemented with observations in their natural habitat. The morphology of larval skins found in snail shells gave additional information, resulting in an overview of all life stages from egg to adult.

Egg

The development of eggs was observed in May-June 2014 after mating of a couple *D. flavescens* collected in IJmuiden (figure 3a). By keeping the eggs under moist conditions more than 90% of the eggs hatched.

The day after copulation, the female laid approximately 250 eggs (figure 3b). By laying her eggs, the female shrinks considerably in size. The eggs are spherical, about one millimetre in diameter and stick together. Freshly laid eggs are white to pale yellow. While the larvae develop, the eggs become darker yellow to orange.



1. (a) *Drilus concolor* ♂ (collection Naturalis Biodiversity Center), (b) *Drilus flavescens* ♂ (collection Naturalis Biodiversity Center). Scale bar = 1 mm. Photos: Els Baalbergen
1. (a) *Drilus concolor* ♂ (collectie Naturalis Biodiversity Center), (b) *Drilus flavescens* ♂ (collectie Naturalis Biodiversity Center). Maatstreepje = 1 mm

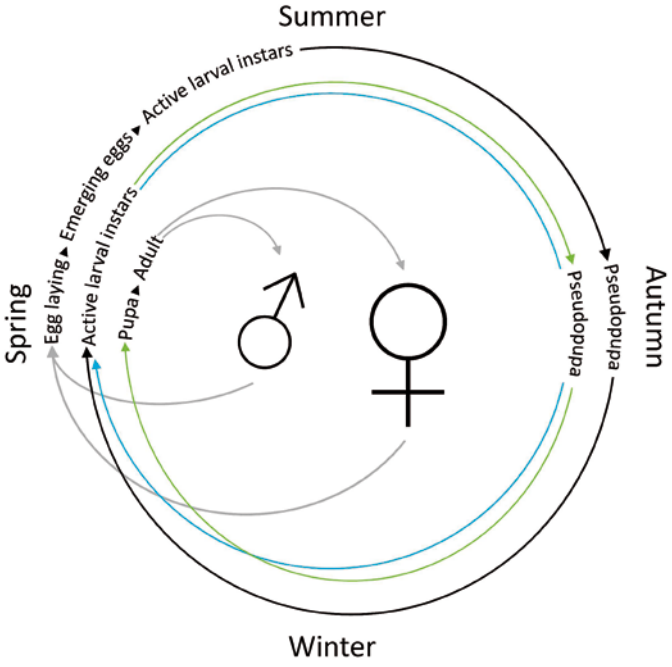
A week before they hatch, the larvae become visible within their shell, initially only the eyes (figure 3c), subsequently also the abdominal segments (figure 3d). The eggs hatch after thirty days. After breaking the egg-shell the pale yellow larva crawls out (figure 3e). Within a few hours the larva turns from pale yellow into a coloured first instar *Drilus* larva (figure 3f-3g). The first instar larva starts searching for its first snail victim within a day. Unfertilized females sometimes lay eggs too. These eggs are sterile and will not develop.

Active larva

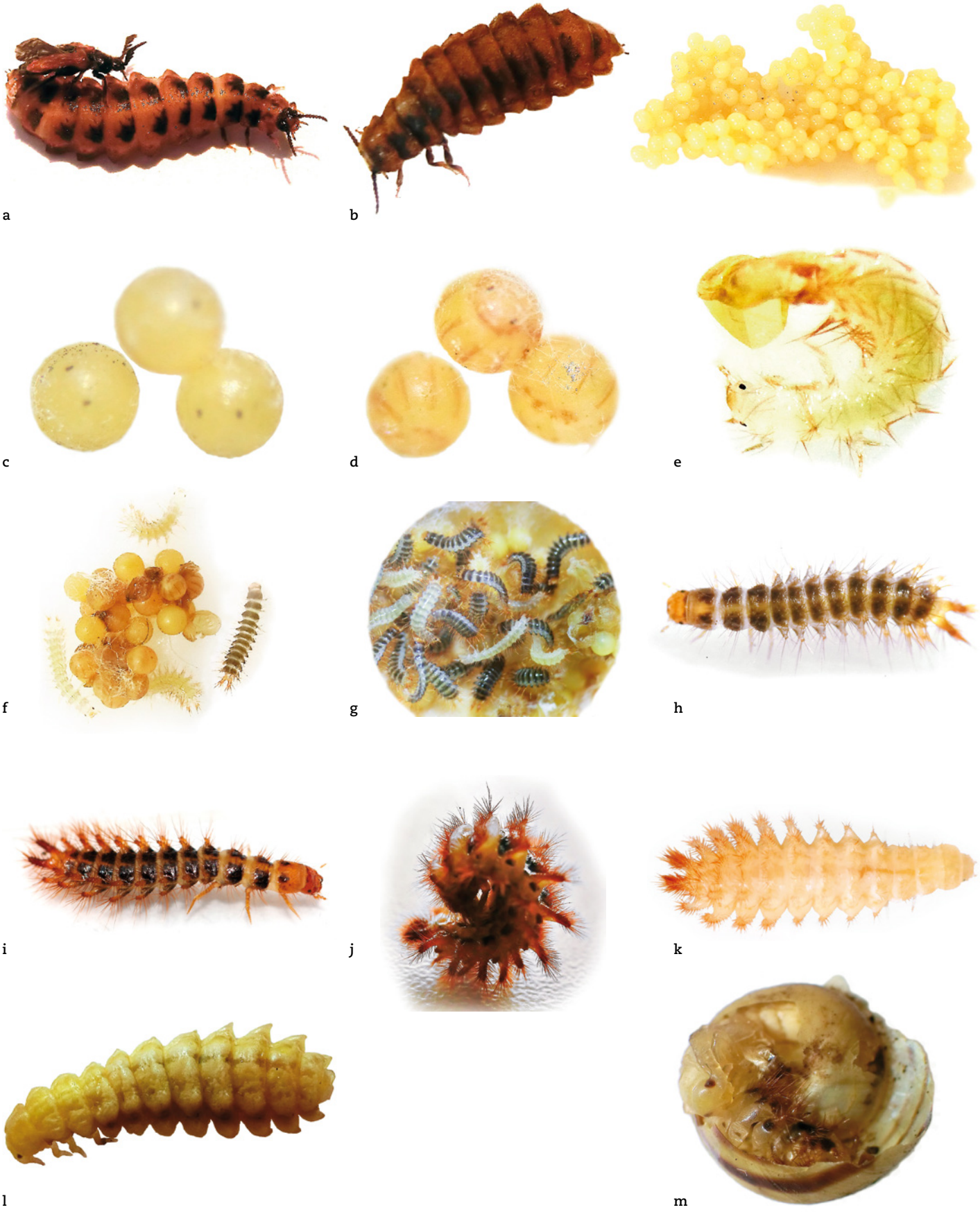
The active larva has a conspicuous vestiture of long hairs, especially on the dorsal surface of the abdomen (Bocak *et al.* 2010). The tergites are heavily sclerotized and pigmented (Bocak *et al.* 2010). The head is sclerotized, short and partly retracted into the prothorax (Bocak *et al.* 2010). The mandibles, widely separated at the base, are narrow and falcate and have a mandibular channel (Beutel 1995). This mandibular channel probably helps to inject a venomous fluid into their prey (Symondson 2004). The last abdominal segment bears a pair of stout, fixed urogomphi or cerci with numerous well-developed hairs (figure 4c, Lawrence *et al.* 2011). The tenth segment forms a sucker-like pygopod dorsally (figure 4d, Lawrence *et al.* 2011).

Abdominal segments usually have well-developed lateral tergal and pleural processes (figure 4a-4b, Crawshay 1903). When an active larva was handled during this study, it often reacted by rolling itself into a ball, with its pleural and tergal processes and hairs directed outwards (figure 3j). These processes may have another function. A couple of days after they had attacked a snail, the larvae were observed moving back and forth inside the shell, leaving undigested brown snail remains in front of the aperture. The hairs and processes of the larva possibly help the larva to clean the inside of the shell of its prey (Crawshay 1903).

Most of the skins that were found in shells are from active larvae. In summer an active larva moults inside a shell into the next active larval stage. A few days after shedding its skin, it leaves the shell. Usually, a larva leaves its skin behind inside

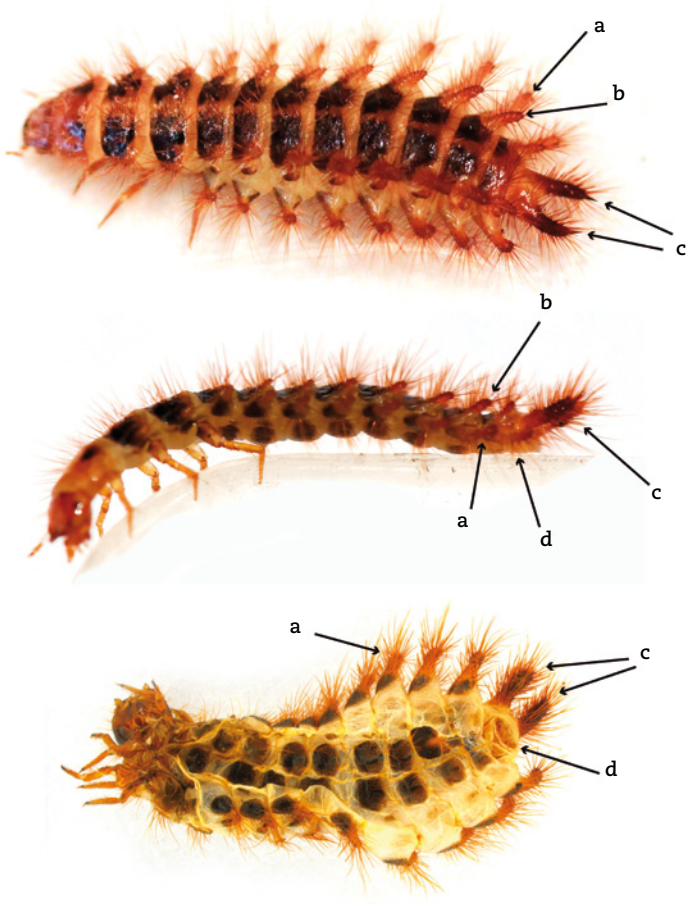


2. The hypermetamorphosis of a *Drilus* from egg to adult. Eggs laid in spring hatch in about a month. A larva eats a number of snails and moults once a month between May-September. In its first autumn it becomes a pseudopupa. The following spring, it turns again into an active larva and starts feeding on snails. At least twice in its lifespan a *Drilus*-larva becomes a pseudopupa, which means that it takes at least two years to develop into an adult (green line). It can also take a third year to become fully mature (blue line). In its last spring the fully matured pseudopupa transforms through a pupa into an adult.
2. De hypermetamorfose van een *Drilus* van ei tot volwassen kever. De eieren worden in de lente gelegd en komen na ongeveer een maand uit. Na het eten van een aantal slakken, en na ongeveer één vervelling per maand tussen mei-september, transformeert hij in zijn eerste herfst naar een pseudopop. In de volgende lente wordt hij opnieuw een actieve larve en eet hij nog een aantal slakken. Op zijn minst twee maal in zijn leven is een *Drilus* een pseudopop. Dat betekent dat het op zijn minst twee jaar duurt van ei tot volwassen kever (groene lijn). De larve kan ook een extra jaar nodig hebben om volwassen te worden (blauwe lijn). In zijn laatste lente ontwikkelt de larve zich dan via een pop tot een volwassen kever.



3. Life stages of *Drilus flavescens* (a-j, l-m) and *Drilus concolor* (k). (a) Winged male and larviform female, copulation. (b) A day after copulation, the female has laid her eggs and shrunk. (c) A week before the eggs hatch, the eyes of the larvae become visible. (d) A couple of days before the eggs hatch, the abdominal segments become visible. (e) A larva leaves its egg-shell. (f & g) A few hours after a larva has hatched from its egg, it darkens. (h) Second larval instar. (i) Third larval instar. (j) A larva rolled into a ball. (k) A pseudopupa. (l) A female pupa. (m) A male pupa in a snail shell together with its former larval skins. Photos: Els Baalbergen

3. Levensfases van *Drilus flavescens* (a-j, l-m) and *Drilus concolor* (k). (a) Gevleugeld mannetje en larviform vrouwtje, copulatie. (b) De dag na de copulatie heeft het vrouwtje eieren gelegd en is ze gekrompen. (c) Een week voordat de eieren uitkomen, worden de ogen zichtbaar. (d) Een paar dagen voordat de eieren uitkomen, worden de achterlijfssegmenten zichtbaar. (e) Een larve verlaat de eischaal. (f & g) Een paar uur na het uitkomen wordt de larve donkerder. (h) Tweede larvale stadium. (i) Derde larvale stadium. (j) Een opgerolde larve. (k) Een pseudopop. (l) Een vrouwtjes-pop. (m) Een mannetjespop samen met zijn eerdere larvenhuidjes in een slakkenhuisje.



4. Morphology of an active larva. From top to bottom: dorsal (*D. flavescens* larva), lateral (*D. flavescens* larva) and ventral view (*D. concolor* larval skin). (a) Pleural process. (b) Tergal process. (c) Urogomphi or cerci. (d) Sucker-like pygopod. Photos: Els Baalbergen
4. Morfologie van de actieve larve. Van boven naar beneden: dorsaal (*D. flavescens* larve), lateraal (*D. flavescens* larve) en ventraal aanzicht (larvenhuidje van *D. concolor*). (a) Pleurale uitstulping. (b) Tergale uitstulping. (c) Urogomphi of cerci. (d) Zuignapachtige pygopode.

the shell in the same position as it has entered it: with its head pointing towards the apex.

A first instar larva and a fully mature larva not only differ in size but also in shape. The first instar *Drilus* larva is characterized by a simple colour pattern on the dorsal surface, undeveloped lateral and tergal processes, only a few hairs on each segment and very thin, almost transparent cerci (figure 3f-3g). After each moulting the number of hairs increase, the lateral tergal and pleural processes become stronger, the colour pattern on the head and dorsal surface of the segments becomes more conspicuous and the shape of the cerci becomes more species-specific (second instar larva: figure 3f, third instar larva: figure 3g). The number of active larval instars is uncertain, but likely five per year: they moult approximately once every month, probably from May to September.

Pseudopupa

Usually towards the winter, a *Drilus* larva develops into a resting stage. This is called a ´pseudopupa´ (figure 3k), in accordance with Fabre (1857), who used the same term for meloid beetles. The pseudopupa has reduced legs, mouth parts and cerci, which gives it the appearance of a pupa. The colour is pale yellow, with orange hairs especially present on the back and towards the cerci. It never leaves a shell in this stage. However, it appears to have certain special characteristics. Crawshay (1903) showed that a pseudopupa can survive in solutions of alcohol and glycerine. Probably, it possesses unique physiological characteristics to survive highly stressful situations.

A *Drilus* larva turns at least twice its lifetime into a pseudopupa (figure 2). To turn into a pseudopupa it has to moult the active larval skin. Usually, a *Drilus* larva remains a pseudopupa during winter. Towards spring, if it is not yet fully matured, it moults again and leaves the shell as an active larva. If it is fully matured, it first turns around so that its head is pointing toward the aperture, and only then it develops into a real pupa.

There is a morphological difference between a pseudopupa that develops again into an active larva, and one that is fully matured and ready to become an adult (Crawshay 1903). The fully matured pseudopupa is larger and has more strongly reduced mouthparts, legs and cerci.

Some of the studied larvae seemed to require an intermediate step in order to become a pseudopupa. They moulted twice within the same shell, the reduction of mouth parts, legs and cerci increasing with each step (figure 5). This was irregularly observed for both pseudopupae that developed into an active larva afterwards and fully matured pseudopupae. This intermediate stage might be similar to the 'secondary larva' described by Faucheux & Agnas (2016) for *D. mauritanicus* and *Malacogaster passerinii* Bassi. Although there are some differences: their 'secondary larva' shows much more sclerotization and it is described as a regular stage in the development, whereas it was only observed sporadically during our study.

Faucheux & Agnas (2016) found that a pseudopupa (or 'tertiary larva') normally develops into a pupa and that development of a pseudopupa into an active larva is an anomaly and possibly a consequence of breeding in captivity. There might be differences in development between Drilini species. We observed an effect of breeding in captivity on the development of *D. flavescens* and *D. concolor*. Larvae which live in captivity for more than a year can develop abnormalities. Some of these larvae remained in a pseudopupal stage for more than a year and developed into an active larva or adult in the middle of winter, some active larvae had malformed legs and some emerging adults had malformed antennae. However, since development of a pseudopupa into an active larva was regularly observed, even in recently caught specimens, we consider this part of the normal development of *D. concolor* and *D. flavescens*.

Pupa

A fully matured *Drilus* pseudopupa is ready to become a pupa. This pale yellow pupa is situated between the pseudopupal skin and the active larval skin. The pupal skin stays in this place after the adult has emerged. Like adult *Drilus* beetles, the pupa shows sexual dimorphism. Both male and female pupae share characteristics with the pseudopupa, such as short hairs and a pale yellow body. Actually, the female pupa is basically a pseudopupa with some visible characteristics of the female, such as short antennae (figure 3l). The difference between the male pseudopupa and pupa is more prominent: in the pupa the wings and long antennae are visible (figure 3m).

Adults

The adults of *Drilus* show a strong sexual dimorphism. Only males are able to fly. The males are moderately sclerotized beetles, have long antennae (reaching one third of elytral length) and prominent compound eyes (figure 1a-1b, Bocak *et al.* 2010). In contrast, females are weakly to moderately sclerotized, have short antennae (as long as the width of the head) and small compound eyes (figure 6g-6h, Bocak *et al.* 2010). All known

5. Sometimes a *Drilus* larva moults twice in a row in order to become a pseudopupa, the first pseudopupa appears to be an intermediate one. From left to right: Active larval skin, 'intermediate' pseudopupal skin and pseudopupa of *D. concolor*, all from a single snail shell. Photos: Els Baalbergen
5. Soms vervelt een *Drilus*-larve tweemaal achter elkaar om een pseudopop te worden, de eerste pseudopop lijkt een tussenvorm te zijn. Van links naar rechts: huidje van actieve larve, huidje van pseudopop in 'tussenvorm' en pseudopop van *D. concolor*, allemaal uit één slakkenhuisje.

species of *Drilus* females have a larviform morphology of the thorax and abdomen (Bocak *et al.* 2010). A dissected female showed most of her body to be filled with eggs. As in most *Drilus* species, the adult female is larger than the adult male. A female larva grows larger and can be found in shells of larger snails than a male larva (Crawshay 1903).

Females expose themselves at daytime, probably to attract a male, but prefer a sheltered position overnight. After a male is attracted, they mate, which can take hours. Several pictures can be found on the internet of *Drilus* females mating with more than one male at once (http://sxbrc.org.uk/news/jabba-the-grub and www.entomart.be/INS-2640.html). In accordance with Crawshay (1903), a *Drilus* male can fertilize several females. After mating, the female goes into shelter again. After laying eggs, the female dies.

Differences between species

It is easy to separate the adult male of *D. concolor* and *D. flavescens*: the former has brown-black elytra and serrate antennae, while the latter has brown-orange elytra and comb-shaped antennae (figure 1a-1b, Geisthardt 1979). Adult females are less easily separated, but there is a difference in the colour (see below) and antennae (usually 10 antennomeres for *D. flavescens* females and 12 for *D. concolor* females, Geisthardt 1979, Kobieluszova & Kundrata 2015). For more details about the differences between the adults, we refer to Geisthardt (1979). Here we focus on the larvae, which are most difficult to distinguish.

At first glance active larvae of *D. concolor* and *D. flavescens* seem identical; both are red and hairy. Korschefsky (1951) used the shape of the abdominal appendages and the curvature of the cerci for identification. However, the cerci were found to be very flexible and sometimes (in dead specimens) fixed in an unnatural position. Identification of the larvae by the curving of the cerci is therefore unreliable. In this study the colour pattern of the larva was found to be the best character to tell the species apart.

Specimens from Cadier en Keer (*D. flavescens*, leg. E. Baalbergen, 11.v.2015), Millingen aan de Rijn (*D. concolor*, leg. E. Baalbergen, 10.vi.2012), IJmuiden (*D. flavescens*, leg. E. Baalbergen *et al.*, 21.vii.2012) and Wageningen (*D. concolor*, leg. E. Baalbergen, 19.vi.2012) were studied. Species identification was confirmed by DNA (for sequences see Kundrata *et al.* 2015) or by rearing the larvae into adults.

Fresh specimens and larval skins of both species were photographed; these show some of the variation in colour intensity and colour pattern of both species (figure 6a-6f). Identification is most difficult for young instars. It is impossible to identify first instar larvae (figure 6f-6g) and it is difficult for the second instar (figure 6h). In these instars, the colour pattern has not yet fully developed.

Colour pattern and colour intensity of the larvae are the most obvious differences. However, there may be individual variation, so it is important to check all characters. A relatively safe identification is possible by using the following four characters. (i) The most reliable character is the shape of the colour markings on the dorsal surface of the thoracic and abdominal segments. Larvae of *D. concolor* have more or less trapezoidal markings, while those of *D. flavescens* have markings that are deeply indented. (ii) There is a difference in the colour markings on the dorsal surface of the first thoracic segment. In *D. flavescens*, these markings are small or absent. In *D. concolor* they usually have the same size as the markings on the other segments and are never absent. (iii) Another character is the colour pattern on the base of the head. Larvae of *D. concolor* usually have two large spots that can even form a dark band along the base of the head (figure 6c). In larvae of *D. flavescens* these markings are almost lacking. (iv) The last character is the body colour. Larvae of *D. flavescens* are intensely orange, those of *D. concolor* are rather orange-brown, but the difference is subtle. Fresh specimens should be used to evaluate this character (figure 6a-6d).

Although the larva of *D. concolor* is usually the darkest, colour intensity varies. In both species very dark specimens occur, which makes it difficult to see the pattern. In such specimens, a *D. flavescens* larva is likely to be identified as *D. concolor*. The reverse is less likely, because the shape of the markings on the dorsal surface of *D. concolor* are never deeply indented.

Differences between the larvae of *D. concolor* and *D. flavescens* are probably related to the differences between the adults. A male *D. concolor* has dark elytra and a male *D. flavescens* has red elytra, which corresponds with *D. concolor* larvae usually being darker than *D. flavescens* larvae. Like the larvae, the females of *D. concolor* (figure 6g) are darker, and the colour marking on the dorsal surface of the first thoracic segment of females of *D. flavescens* is usually smaller or absent.

6. (a) *Drilus concolor*, living active larva. (b) *Drilus flavescens*, living active larva. (c) *Drilus concolor*, fresh active larval skin. (d) *Drilus flavescens*, fresh active larval skin. (e) *Drilus concolor*, active larval skin embedded in Euparal. (f) *Drilus flavescens*, active larval skin embedded in Euparal. (g) *Drilus concolor* ♀, alive. (h) *Drilus flavescens* ♀, alive. Scale bar = 2 mm. Photos: Els Baalbergen
6. (a) *Drilus concolor*, levende actieve larve. (b) *Drilus flavescens*, levende actieve larve. (c) *Drilus concolor*, vers huidje van actieve larve. (d) *Drilus flavescens*, vers huidje van actieve larve. (e) *Drilus concolor*, huidje van actieve larve ingesloten in Euparal. (f) *Drilus flavescens*, huidje van actieve larve ingesloten in Euparal. (g) *Drilus concolor* ♀, levend. (h) *Drilus flavescens* ♀, levend. Maatstreepje = 2 mm.

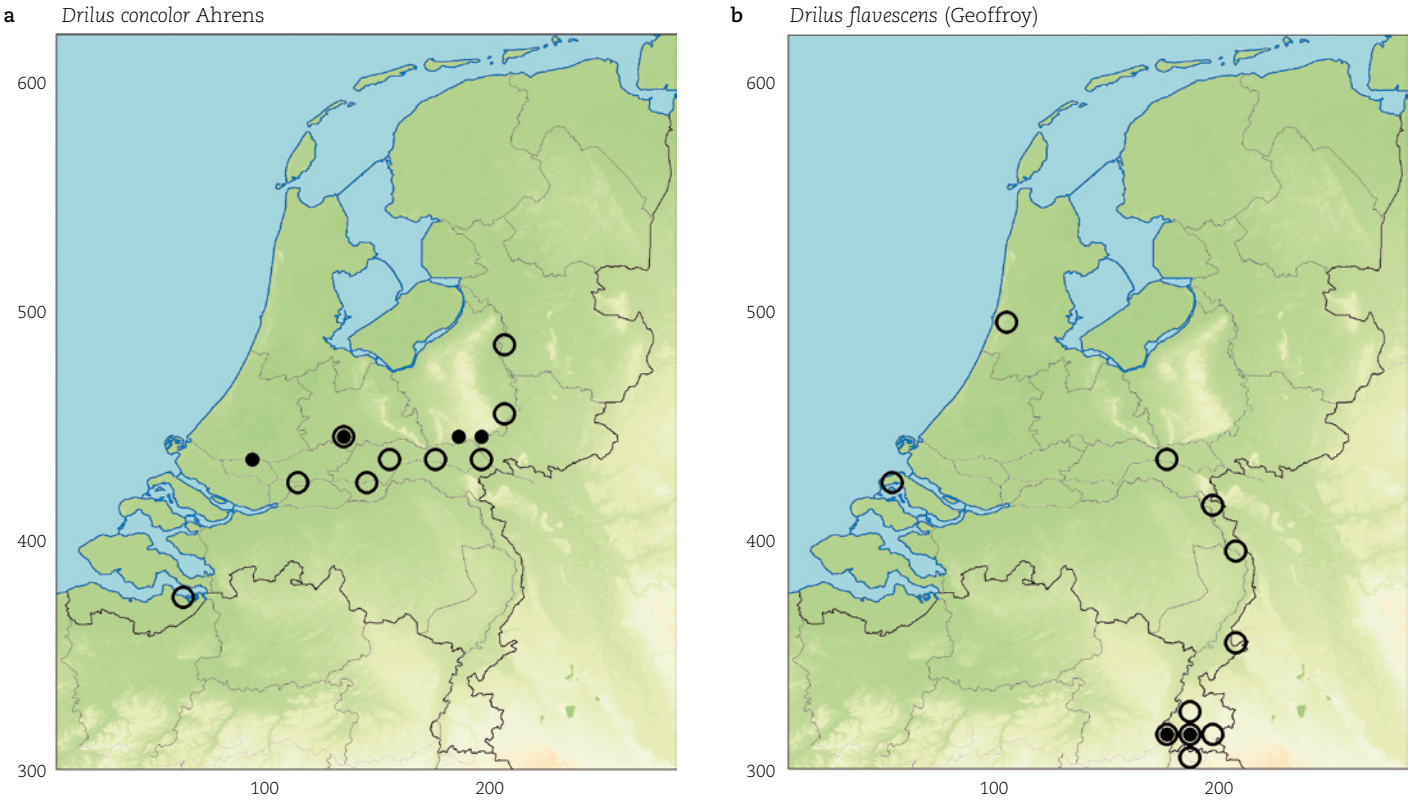
Differences between species in the pseudopupa were not noted; both are pale yellow. No differences between species in the female pupa were observed either. For the male pupa, there is a difference in the shape of the antennae, which is similar to that in adults. Since the active larval skin is also present in the shell, identification of most pupae and pseudopupae is possible.

Distribution

Drilus concolor and *D. flavescens* show different distribution patterns in the Netherlands. As stated in literature, *D. concolor* occurs in the provinces of Gelderland, Overijssel and Zuid-Holland and *D. flavescens* occurs in Utrecht and Limburg (Teunissen 2010). For this study historical data (Naturalis Biodiversity Center) were combined with recent observations (own observations supplemented with those of several entomologists; see acknowledgements) to create a more detailed distribution map for both species.

Drilus concolor occurs primarily in the area around the large rivers in the centre of the Netherlands (figure 7a). *Drilus flavescens* is common in the south of Limburg, but populations of *D. flavescens* occur in some other localities in the Netherlands (figure 7b). Nature reserve Blauwe Kamer, in Gelderland, is the only known site where both species co-occur.

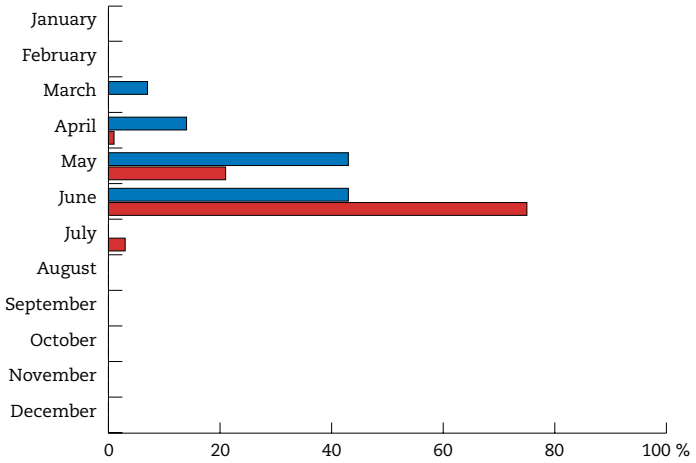
Drilus females are larviform and flightless, therefore they are hardly capable of active dispersal over a larger distance. The distribution of *Drilus* species can probably mainly be attributed to external factors. It is striking that many populations are located



7. (a) Distribution of *Drilus concolor* in the Netherlands. (b) Distribution of *Drilus flavescens* in the Netherlands. Note: 150 of the 168 *D. flavescens* observations are from the south of Limburg. ●=before 1950 ○=after 1950.
7. (a) Verspreiding van *Drilus concolor* in Nederland. (b) Verspreiding van *Drilus flavescens* in Nederland. Opmerking: 150 van de 168 *D. flavescens* waarnemingen zijn uit Zuid-Limburg. ●=voor 1950 ○=na 1950.

near the major rivers Rhine, Meuse, Waal as well as smaller streams. Their dispersal in the Netherlands might be determined by water displacement, *i.e.* through means of human activity (ships) or during high water levels, when floating shells containing *Drilus* larvae or larviform females will be carried for some distance along the riverbank.

In Europe, *D. concolor* mainly occurs in countries east of the Netherlands, while *D. flavescens* mainly occurs in countries south of it (Bocak 2013). *Drilus concolor* appears to have mainly colonized our country via Germany via the Rhine and subsequently the Waal, Lek and IJssel. *Drilus flavescens* appears to have colonized the Netherlands from Belgium via the Meuse. This may explain the distribution of the two species in the Netherlands.



8. Phenology of adult *Drilus* (observations in percentage per month). Blue: *D. concolor* (n=14) Red: *D. flavescens* (n=146)
8. Fenologie van volwassen *Drilus* (percentage waarnemingen per maand). Blauw: *Drilus concolor* (n=14) Rood: *Drilus flavescens* (n=146)

It is likely that both species are present at more localities, but have not been found yet because of their inconspicuous lifestyle. We found fresh *Drilus* specimens especially along the slope of overpasses, on the outskirts of cities and in areas with unattended vegetation, often with nettles and hawthorn, where snails were abundant. The larvae were mostly found inside a shell near the trunk of a bush, sometimes together with several other shells that contained larvae.

The larvae hide inside a shell, and are not visible from the outside once they have eaten most of the soft part of the snail. So without opening a shell, many of the *Drilus* larvae will be overlooked.

Larvae can be found year-round. During autumn and winter they are inactive and hibernate as pseudopupae. Adult females and males are mostly found in May-June. During this study we found *D. concolor* adults earlier in the season than *D. flavescens* adults (figure 8, Chi-square test, P-value = 0.0002). Females can be found with the larvae on the soil surface near or in shells. Males can be found flying around or near females.

Predation behaviour

During fieldwork in 2012-2015 in the Netherlands several larvae and larval skins of *D. concolor* and *D. flavescens* were collected in shells of *Cepaea nemoralis*, *Cornu aspersum*, *Arianta arbustorum* (Linnaeus), *Alinda biplicata* (Montagu), *Monacha* sp. Fitzinger and *Oxychilus* sp. Fitzinger.

Two active larvae of *D. concolor* were observed while attacking *C. nemoralis*. Multiple active larvae (>15) of *D. flavescens* have been seen preying on either *C. nemoralis* or *C. aspersum*.

In this study, the larvae were fed mainly with *C. nemoralis*

9. (a) *Drilus flavescens* preying on *Cepaea nemoralis*. The larva first inspects the snail. (b) *Drilus flavescens* preying on *Cornu aspersum*. The larva bites the snail in the tissue close to the shell. (c) *Drilus flavescens* preying on *Cepaea nemoralis*. The larva has bitten the snail several times and enters the shell through the aperture to bite the snail a few more times, in order to paralyze it. (d) *Drilus flavescens* preying on *Cepaea nemoralis*. The larva has paralyzed the snail and pulls/manipulates it into the shadow. (e) *Drilus flavescens* preying on *Cepaea nemoralis*, the larva has just paralyzed the snail and has entered the shell with its dorsal side pointing towards the columella. Photos: Els Baalbergen
9. (a) *Drilus flavescens* die *Cepaea nemoralis* aanvalt. De larve inspecteert eerst de slak. (b) *Drilus flavescens* die *Cornu aspersum* aanvalt. De larve bijt de slak in het weefsel dicht bij het slakkenhuis. (c) *Drilus flavescens* die *Cepaea nemoralis* aanvalt. De larve heeft de slak een paar keer gebeten en gaat het slakkenhuisje binnen om nog een aantal keer te bijten en de slak te verlammen. (d) *Drilus flavescens* die *Cepaea nemoralis* aanvalt. De larve heeft de slak verlamd en verplaatst hem naar de schaduw. (e) Na het verlammen van de slak (*Cepaea nemoralis*) gaat de larve (*Drilus flavescens*) het huisje binnen met zijn dorsale zijde naar de columella gericht.

and sometimes *C. aspersum*. The smaller larvae were offered juvenile *C. nemoralis* and *C. aspersum* and various small snail species, like *Discus rotundatus* (Muller), *Oxychilus draparnaudi* (Beck) and *Cochlicopa* sp. Ferussac. There seems to be no clear preference for any of these species. However, when confronted with a slug, none of the *Drilus* larvae showed any interest.

Some *Drilus* species are known to enter or exit snails by boring holes through the shell wall (Baalbergen *et al.* 2014). We never observed this behaviour in *D. concolor* and *D. flavescens*, probably because most of the snail species they prey upon in the Netherlands are relatively easy to enter through the aperture.

A colour morph preference for *C. nemoralis* has been reported for other predators (O'Donald 1963). Field observations were done to examine whether *Drilus* larvae have a preference for a particular colour morph. A *D. flavescens* population in IJmuiden was used (fieldwork: 12-vii-2013), because most of them preyed on *C. nemoralis*. The results show that there are no significant differences between the number of *C. nemoralis* colour morphs predated (n=109) and not predated (n=1267) by *D. flavescens* (Chi-square test, p-value>0.1).

Usually the first days after a *Drilus* larva leaves its last prey, it does not search for another snail. A *Drilus* larva is active in the daytime, but seldom attacks a snail when it encounters one during daylight. A *Drilus* larva attacks snails both in rest (figure 9a, 9c) or crawling around (figure 9b). The larva walks around the snail for a couple of minutes or walks over the shell. At some point, the larva starts to bite the snail. If the snail is crawling around, the larva tries to bite the snail in the tissue close to the shell, between the head and the edge of the mantle (figure 9b). After one or more bites, the snail retracts into its shell. The snail is at least partly paralysed by the bite of the larva: after it has retracted, it tries to crawl away, but is not able to fully project its foot and tentacles out of its shell. After the attack the larva enters the shell and bites the snail again a number of times. Then it starts to eat the soft body of the snail while the snail is still alive. The snail usually reacts by moving its tail-end out of the shell. The larva always enters the snail with its dorsal side pointing towards the columella (figure 9e). A few hours after the first bite, the snail dies and the soft tissue is entirely eaten by the *Drilus* larva. Sometimes, after the larva has paralysed the snail, it starts to roll the shell to a different place (figure 9d), usually a more sheltered place. It uses its pygopod (figure 4d) to attach to the shell, after which it walks a few centimetres making the shell tumble a little bit further. This can be repeated numerous times and may take several hours.

The first few days after the larva has attacked the snail, it is visible in the aperture (figure 9e). Once it has eaten most of the soft tissue it moves further inward, becoming invisible from the outside unless the shell is (somewhat) transparent. After a *D. concolor* or a *D. flavescens* larva has eaten all the tissue of the snail and if the feeding period (May-September) is not over, the larva remains inside the shell for about thirty days. Then, after shedding its skin, it leaves the shell and starts to search for its next victim. For movies that illustrate this behaviour see: www.youtube.com/channel/UCpLEArDgu2tN8kscpSMeY9g

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References

Baalbergen E, Helwerda R, Schelfhorst R, Castillo Cajas RF, Van Moorsel CHM, Kundrata R, Welter-Schultes FW, Giokas S & Schilthuizen M 2014. Predator-prey interactions between shell-boring beetle larvae and rock-dwelling land snails. PLoS ONE 9(6): e100366. doi:10.1371/journal.pone.0100366

Beutel RG 1995. Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. Journal of Zoological Systematics and Evolutionary Research 33: 145-171.

Bocak L, Branham MA & Kundrata R 2010. 4.9. Family Drilidae Blanchard, 1845. In: Handbook of Zoology, Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim.) (Lawrence JF & Leschen RAB volume eds): 104-110. Walter de Gruyter GmbH & Co. KG.

Bocak L 2013. Fauna Europaea: Drilidae. In: Alonso-Zarazaga MA 2013. Fauna Europaea: Coleoptera (part). Fauna Europaea version 2.6.2. In: De Jong Y, Verbeek M, Michelsen V, De Place Bjørn P, Los W, Steeman F, Bailly N, Basire C, Chylarecki P, Stloukal E, Hagedorn G, Wetzel FT, Glöckler F, Kroupa A, Korb G, Hoffmann A, Häuser C, Kohlbecker A, Müller A, Güntsch A, Stoev P & Penev L 2014 Fauna Europaea - all European animal species on the web. Biodiversity Data Journal 2: e4034. doi: 10.3897/BDJ.2.e4034. Available on: http://www.fauna-eu.org/. [Consulted on 30 januari 2016]

Crawshay LR 1903. On the Life History of *Drilus flavescens*, Rossi. Transactions of the Entomological Society of London 51: 39-51.

Fabre JH 1857. Memoire sur l'hypermetamorphose et les moeurs des Meloides. Annales des Sciences Naturelles Zoologie Series 47: 299-365.

Faucheux MJ & Agnas M 2016. Les hypermétamorphoses de deux Drilini (Coleoptera : Elateridae), *Drilus mauritanicus* Lucas 1849 et *Malacogaster passerinii* Bassi 1833. Notion de larves primaire, secondaire et tertiaire. Bull. Soc. Sc. Nat. Ouest de la France, nouvelle série, tome 38 (hors-série 1) 2016 : 59 99.

Geisthardt M 1979. 28. Familie: Drilidae. In: Die Käfer Mitteleuropas. Band 6. Diversicornia (Freude H, Harde KW & Lohse GA eds): 51-53. Goecke & Evers.

Kobieluszova L & Kundrata R 2015. Taxonomic review of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) from Asia Minor, with descriptions of seven new species and comments on the female antennal morphology in Drilini. Zootaxa 4012 (1): 078-096.

Korschefsky R 1951. Bestimmungstabelle der bekanntesten deutschen Lyciden-, Lampyriden- und Drilidenlarven (Coleoptera). Beiträge zur Entomologie 1: 60-65.

Kundrata R, Baalbergen E, Bocak L & Schilthuizen M 2015. The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. Systematics and Biodiversity 13: 52-75.

Kundrata R & Bocak L 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zoologica Scripta 40: 364-378.

Lawrence JF, Ślipiński A, Seago AE, Thayer MK, Newton AF & Marvaldi AE 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici (Warszawa) 61: 1-217.

O'Donald 1963. Natural Selection by glow-worms in a population of *Cepaea nemoralis*. Nature 217: 194.

Symondson WOC 2004. Coleoptera (Carabidae, Drilidae, Lampyridae and Staphylinidae) as predators of terrestrial gastropods. In: Natural Enemies of Terrestrial Molluscs (Barker GM ed): 37-84. CAB International.

Teunissen APJA 2010. Drilidae. In: Catalogus van de Nederlandse kevers (Coleoptera) (Vorst O ed). Monografieën van de Nederlandse Entomologische Vereniging 11: 112.

Wittmer W 1944. Catalogue des Drilidae E. Oliv. (Coleoptera – Malacodermata). Revista de la Sociedad Entomológica Argentina 12: 203–221.

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Samenvatting

***Drilus*-larven in Nederland (Coleoptera: Elateridae: Drilini)**

In Nederland komen twee *Drilus*-soorten voor: *D. concolor* en *D. flavescens*. De rode, harige larven van deze 'slakkenvreters' jagen op huisjesslakken. In de lente en de zomer is de larve van een *Drilus* actief. In de herfst wordt de larve een pseudopop, die overwintert. Dit proces wordt hypermetamorfose genoemd. Na ongeveer twee jaar wordt een larve volwassen. Het mannetje van beide soorten is een actieve, gevleugelde kever, maar de vrouwtjes zijn larviform en leven evenals de larven op de bodem. De hypermetamorfose wordt in detail beschreven. De verschillen tussen de larve van *D. concolor* en *D. flavescens* worden beschreven, voornamelijk gebaseerd op kleur en kleurpatroon. De verspreiding van beide soorten is in kaart gebracht; *D. concolor* komt voornamelijk voor in Midden-Nederland, *D. flavescens* voornamelijk in Zuid-Limburg. Beide soorten worden overwegend gevonden in *Cepaea nemoralis* en *Cornu aspersum*. De larve bijt de slak, waardoor de slak wordt verlamd en de larve hem op kan eten. Vervolgens doet de larve er een maand over om te vervellen naar een nieuw larve-stadium en op zoek te gaan naar een nieuwe prooi.

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