

# Life cycle length of the lesser stag beetle (Coleoptera: Lucanidae: *Dorcus parallelipedus*)

Paul Hendriks

## KEYWORDS

Egg stage, larval stage, pupal stage, temperature

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The life cycle of the lesser stag beetle *Dorcus parallelipedus* is generally considered to last two to three years. It is not clear how this length is determined, as hardly any information about this life cycle is available. Through an experiment set up under natural conditions, the length of this beetle's life cycle was studied. This experiment gave an insight into the life cycle of this beetle. It seems that variation in oviposition (early or late in the season) and the temperature at its habitat, is the most probable reason for either a two or three years life cycle.

## Introduction

As one of our saproxylic beetles, the lesser stag beetle *Dorcus parallelipedus* (Linnaeus, 1758) is found mostly within decaying white rotted wood of several broadleaved tree species. In the Netherlands, this 2 to 3 cm long black and broad headed beetle (figure 1) lives a secluded life. Unlike other saproxylic beetles, the adult lesser stag beetle can live several years (Fremlin & Hendriks 2011) and therefore beetles of various ages can be found at the same time. The eggs are oviposited in decayed wood during late spring and summer. The larvae feed on the wood and stay in this wood during the entire larval stage. They pupate in the wood in (late) summer. The young beetles overwinter in their pupal cell and become active in spring the following year (Klausnitzer 1995). In the literature, a life cycle of 2 to 3 years is given for this species (Ehnström & Axelsson 2002, Franciscolo 1997, Klausnitzer 1995, Lachat et al. 2012, Méndez 2005, Nikitsky et al. 1996). How the length of this life cycle is established and why it varies is not mentioned.

To study the length of the life cycle under natural conditions and explain the variation therein, a life cycle experiment was set up. Thereby the possible influence of temperature on the length of the life cycle was considered. The weight of larvae in relation to the length of the life cycle was studied as well.

## Material and methods

In this life cycle experiment, the length of the life cycle was defined as the period from ovipositing until the emergence of young beetles. As these beetles can live several years (Fremlin & Hendriks 2011), it is possible to find beetles from various ages in a certain habitat (for example a piece of dead wood). This makes it impossible to establish whether an adult beetle developed inside a specific habitat or developed elsewhere and in another period, unless it is still present in its pupal cell. For this reason, only the beetles and pupae collected in the autumn in their pupal cells in logs that were used in the experiment and in which females oviposited, were considered as originating from the experiment. As these would have emerged the following spring, the life cycle was considered to be extended to the following

year. For example, beetles and pupae originating from the oviposition in 2014 and collected from their pupal cells in autumn 2016, were considered to have a three years life cycle, as they would have emerged in the spring of 2017.

The study site was situated in a garden in Groningen, the Netherlands (53.202°N 6.440°E). Six white rotted beech logs in a comparable state of decay were dug in half, in a sun exposed plot in May 2014 (table 1). Each autumn after collecting all larvae, pupae and adult beetles from the old logs, new logs (all with white rot) were dug in the same way and at the same place as the year before. Partly burying these logs prevented them from drying out and ensured fungal activity through moisture in the surrounding soil (figure 2). The standardized use and placement of the logs was done to prevent an influence on the development of larvae due to differences between the logs. Oviposition by female beetles in these logs was stimulated by placing a log with sixteen beetles from earlier experiments next to the unpopulated logs. The oviposition in the unpopulated logs in the spring of 2014 was the starting point of the experiment. The parent beetles remained in the garden (were not taken from the experiment). The logs were monitored each year in the autumn by carefully opening them with a screwdriver (figure 3) whereby all eggs, larvae, pupae and beetles were collected. Monitoring at this time of year ensured that young beetles were still in their pupal cells. This was important as adult beetles can live several years (Fremlin & Hendriks 2011), and therefore it is impossible to distinguish between new beetles and the parent beetles once the beetles have emerged from their pupal chamber. Only the beetles and pupae collected in autumn in their pupal cells were considered to be originating from the 2014 oviposition.

As the parent beetles were present in the garden during the whole experiment, new oviposition could therefore be expected in the logs used in this experiment. The additional eggs and larvae that were found at monitoring moments after 2014 were therefore taken from the experiment.

From the collected larvae the headcapsule width was measured and the larval stage was established according to Klausnitzer (1995). Length measurements of specimen were taken in millimetres with callipers of 0.5 mm accuracy. All larvae, pupae



1. Male *Dorcus parallelipedus*. Photo: Paul Hendriks  
1. Mannetje van *Dorcus parallelipedus*.



3. Opened log at the monitoring on 16.x.2016. Photo: Paul Hendriks  
3. Geopend stammetje tijdens de monitoring op 16.x.2016.



2. Formation of logs for the life cycle experiment for *D. parallelipedus* on 3.viii.2014. Photo: Paul Hendriks  
2. Opstelling van stammetjes voor het levenscyclusexperiment voor *D. parallelipedus* op 3.viii.2014.



4. Relocation of *D. parallelipedus* larvae. Photo: Paul Hendriks  
4. Herplaatsen van *D. parallelipedus*-larven.

Placement of logs	Log	Diameter (cm)	Length (cm)	Tree species
18.v.2014	1	14	32	beech
	2	13	32	beech
	3	15	30	beech
23.xi.2014	1	15	30	beech
	2	12	22	beech
	3	14	27	beech
22.x.2015	1	27	40	hornbeam

Table 1. Used logs in the life cycle experiment.

Tabel 1. Gebruikte stammetjes in het levenscyclusexperiment.

**Table 2.** Number of collected specimen at each monitoring.  
**Tabel 2.** De aantallen verzamelde individuen tijdens elke monitoring.

Monitoring	Wood log nr.	Diameter (cm)	Length (cm)	Tree species	Eggs	L1	L2	L3	Pupae	Beetles
23.xi.2014	1	14	32	beech			22	8		
	2	13	32	beech	2		13	2		
	3	15	30	beech			10			
Total specimens						2	45	10		
22.x.2015	1	15	30	beech				10	1	4
	2	12	22	beech				4		1
	3	14	27	beech				5		
Total specimens								19	1	5
16.x.2016	1	27	40	hornbeam						9
Total specimens										9

**Table 3.** The total length and weight of all collected beetles and the weight of a collected pupa.  
**Tabel 3.** De totale lengte en gewicht van alle verzamelde kevers en het gewicht van een verzamelde pop.

Monitoring	Male beetles		Female beetles		Pupa	Remarks
	Total length (mm)	Weight (g)	Total length (mm)	Weight (g)	Weight (g)	
22.x.2015	21.0	teneral	20.0	0.424	1.107	3 dead beetles
16.x.2016	22.4	0.489	22.8	0.597		
	22.7	0.490	24.0	0.642		
	23.5	0.548	24.8	0.712		
	24.6	0.607	22.2	0.546		
	23.9	0.604				



**5.** Young dead beetle surrounded by the fungus *Armillaria ostoyae*, found at the monitoring on 22.x.2015. Photo: Paul Hendriks  
**5.** Jonge kever omgeven door de schimmel *Armillaria ostoyae*, gevonden tijdens de monitoring op 22.x.2015.



**6.** Teneral beetle collected at the monitoring on 22.x.2015. Photo: Paul Hendriks  
**6.** Weke jonge kever verzameld tijdens de monitoring op 22.x.2015.



7. Teneral and dead beetles, pupa and part of the larvae, collected at the monitoring on 22.x.2015 (the arrows point out teneral and dead beetles). Photo: Paul Hendriks

7. Jonge en dode kevers, pop en een deel van de larven, verzameld tijdens de monitoring op 22.x.2015 (de pijlen wijzen de jonge en dode kevers aan).



8. Imagos of *D. parallelipipedus* found at the monitoring on 16.x.2016. Photo: Paul Hendriks

8. Imago's van *D. parallelipipedus* gevonden tijdens de monitoring op 16.x.2016.

and beetles were weighed to establish possible weight differences between life cycles of various length. Weights were taken with a Mettler PM100 weighing scale (Max. 110 g, d = 0.001 g). After weighing, all collected pupae and beetles were placed in wood (pupae) or released in the garden (beetles). Only larvae were placed back in new white rotted logs as they had not completed their life cycle. Relocation of larvae took place by drilling holes in new white rotted logs in which the larvae were placed (figure 4). These holes were sealed with the sawdust from the drilling. The logs were half buried in the same spot in the garden as where the earlier logs stood with the holes facing up. The experiment ended when no more larvae originating from the 2014 oviposition could be found. As the beetles and pupae were collected from the logs in autumn and would otherwise have emerged the following spring, the length of the life cycle is therefore the time between oviposition (spring and summer 2014) and collecting date of the pupae and beetles plus one winter.

During the life cycle experiment, temperatures were measured in and on the logs every Sunday around 16:00 hours. For the air temperature on the logs, a thermometer of unknown make with a range from -10 to 60 °C was used. With a meat probe and thermometer the temperature of the core of one of the logs was measured at the same time. The probe remained in the wood. When it wasn't possible to measure the temperature on Sunday afternoon, the readings were postponed a week. Both thermometers had no calibration report. Therefore the readings from both devices were compared. They didn't differ, even at low temperatures.

## Results

### Length of life cycle

Table 2 and 3 give an overview of the specimens found in the wood logs at the various monitoring dates. Based on this infor-

mation the length of the life cycle was established and is shown in table 5.

At the monitoring on November 23, 2014, two L1, 45 L2 and ten L3 larvae were collected, a total of 57 specimens. They were all were placed back in new white rotted logs. On October 22, 2015, nineteen L3 larvae were retrieved and placed back in a single white rotted log. On this date one pupae, one teneral beetle (not yet hardened) and one hardened beetle were found. Three dead beetles in a state of decay were retrieved as well and were surrounded by the fungus *Armillaria ostoyae* in their pupal cell (figure 5). Given their state of decay, these dead beetles were not weighed and measured, nor was it possible to see if these were teneral beetles. The teneral beetle was not weighed, as the abdomen was not fully retracted (figure 6) and further weight loss would have occurred in the process of hardening. Although it was not possible to measure the three dead beetles, their length was estimated to be the same as the living ones, being 20 to 21 mm. Figure 7 shows some of the collected (dead) beetles, pupa and larvae, retrieved on October 22, 2015. In 2015, eggs were laid in the logs. Five eggs and four L1 larvae were found therein on October 22, 2015 and removed from the experiment.

At the monitoring in 2016, nine fully hardened beetles were found (figure 8) originating from the L3 larvae collected at the monitoring in 2015. Like in 2015, eggs were laid in the log in 2016. At the monitoring on October 16, 2016, ten L1, six L2 larvae and one very young L3 larva were collected and removed from the experiment. As only beetles and no larvae were found that originated from the 2014 oviposition, the experiment ended that year. The time from the 2014 oviposition until the emergence of beetles was calculated and is shown in table 5. It clearly shows that a group of specimen went through their life cycle in two years, another group took three years to go through their life cycle.

**Table 4.** Average values and standard deviation for head capsule width (hcw) in mm and weight of collected larvae in grams in the life cycle experiment.

**Tabel 4.** Gemiddelde waarden en standaard afwijking voor de kopkapselbreedte (hcw) in mm en het gewicht in grammen van de verzamelde larven in het levenscyclus experiment.

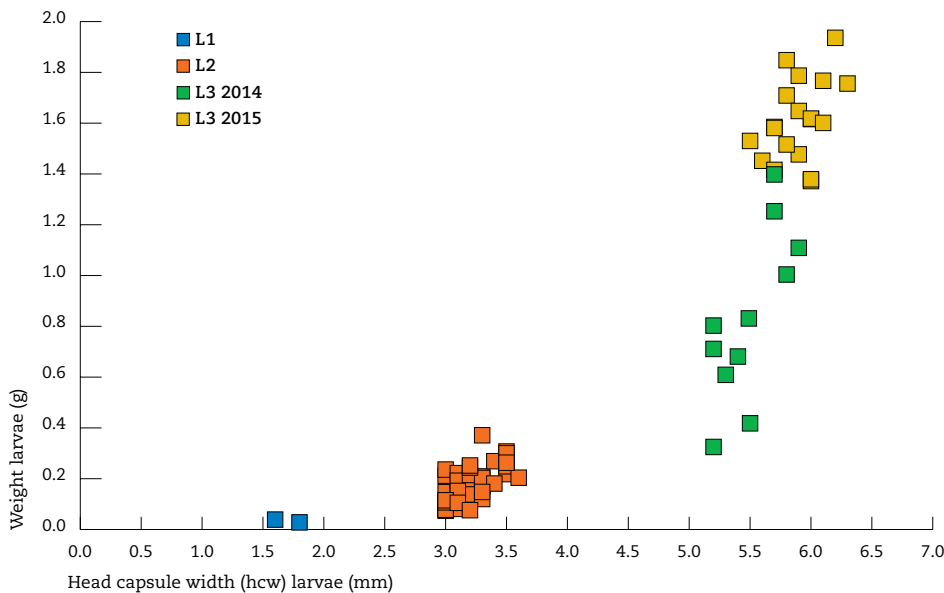
		average	st. dev.
L1	hcw	1.7	0.10
	weight	0.034	0.006
	n	2	
L2	hcw	3.2	0.17
	weight	0.183	0.069
	n	45	
L3 2015	hcw	5.5	0.25
	weight	0.831	0.335
	n	10	
L3 2016	hcw	5.9	0.20
	weight	1.610	0.155
	n	19	

## Difference in larval and beetle size

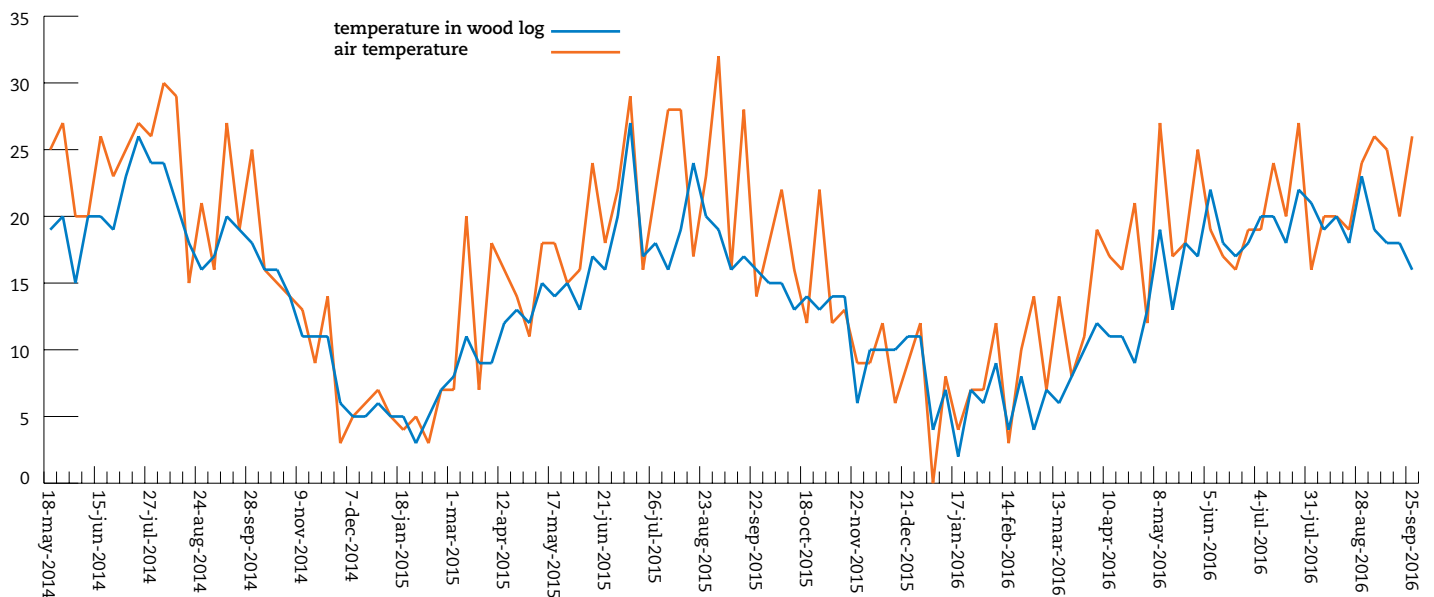
Table 4 and figure 9 show a clear distinction between the width of the headcapsules and weight for the L3 larvae collected at the 2014 monitoring and the 2015 monitoring. The L3 larvae collected in the 2015 monitoring were considerably heavier than the ones from 2014. This is also the case for the collected beetles. All three beetles from the 2015 monitoring measured 20 to 21 mm. The collected dead beetles were of the same size. The collected beetles in 2016 measured 22 to 25 mm, clearly being larger than the ones from 2015.

## Temperature

Figure 10 shows that the air temperature in the summer season is higher than the temperature in the wood. In winter this difference is less. The minimum and maximum temperature in the logs varied during the rearing experiment from 2 °C in winter to 27 °C in summer. In the egg oviposition period from May to September, the temperature differed as well and dropped to approximately 15 °C at the end of September.



**9.** The weight, headcapsule width and instar of all collected larvae, based on table 4.  
**9.** Het gewicht, kopkapselbreedte en larvenstadium van alle verzamelde larven, gebaseerd op tabel 4.



**10.** Air temperature and temperature in the wood logs of the life cycle experiment.

**10.** Luchttemperatuur en temperatuur in de stammetjes uit het levenscyclusexperiment.

**Table 5.** Established length of the life cycle of *D. parallelipedus*.  
**Tabel 5.** Vastgestelde lengte van de levenscyclus van *D. parallelipedus*.

Period	Cumulative time periods (months)	Number of pupae/ beetles	Cumulative time until expected emergence beetles in May (months)	Length of life cycle (years)
18.v.2014-23.xi.2014	6	none	inapplicable	inapplicable
23.xi.2014-22.x.2015	6 + 11 = 17	6	17 + 7 = 24	2
22.x.2015-16.x.2016	17 + 12 = 29	9	29 + 7 = 36	3



**11.** Larvae of *D. parallelipedus*, probably with antifreeze fluids in their gut on 26.ii.2012. Photo: Paul Hendriks  
**11.** Larven van *D. parallelipedus*, vermoedelijk met antivriesvloeistof in de darm op 26.ii.2012.

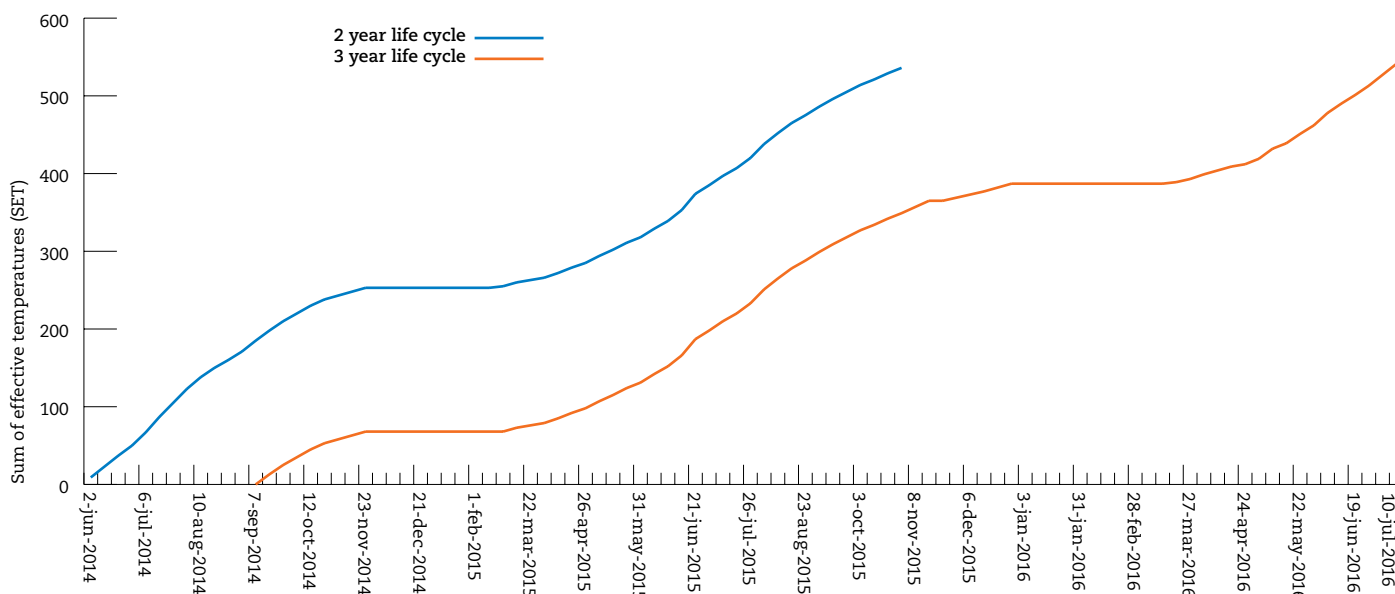
## Discussion

### Length of life cycle

The results of the life cycle experiment confirm two to three year life cycle for *D. parallelipedus* (table 5). Due to their relatively long oviposition stage, all larval stages can be found at the end of the summer in which oviposition took place. The larval stage in this period largely determines if pupation happens the first year after ovipositing or the second year, thus leading to a two or three year life cycle. In the discussion, this is further explained.

### Reaching the L3 stage

The eggs found at the monitoring in 2015 (table 2) show that female beetles can lay eggs until late in the summer season or even in the beginning of autumn. Larvae from eggs oviposited early in the summer will develop faster due to higher summer temperatures (figure 10). These larvae can reach the L3 stage in the year of oviposition (table 2). The development of larvae from eggs oviposited later in the summer season is slowed down by declining temperatures in September. In earlier rearing experiments with larvae of *D. parallelipedus* (Hendriks unpublished), it was observed that in winter periods with temperatures of approximately 6 °C or below, larvae stopped eating and their gut was filled with a yellowish translucent liquid (figure 11). This was also observed by Fremlin (2016). No other information of this phenomenon was found in literature for *D. parallelipedus*, but is described for another stag beetle that develops in wood



**12.** Sum of effective temperature (SET) for eggs and larvae of *D. parallelipedus* with a two and three years life cycle, based on weekly measured temperatures.

**12.** Som van effectieve temperaturen (SET) voor eieren en larven van *D. parallelipedus* met een twee- en driejarige levenscyclus, gebaseerd op wekelijks gemeten temperaturen.



**13.** *Dorcus parallelipedus* inhabiting a large pin oak *Quercus palustris*. Photo: Paul Hendriks

**13.** *Dorcus parallelipedus* bewoont een grote moeraseik *Quercus palustris*.

above the ground (Neven *et al.* 1986) and other beetles (Lee & Denlinger 1991, Nickell *et al.* 2013). This liquid might contain antifreeze, in which compounds like glycerol could prevent larvae from freezing. Larvae in such conditions do not feed. In milder winter conditions, larvae feed little, but do not moult to the L2 and L3 stage until the temperature rises in the following spring (personal observation). First and second instar larvae that go through the winter, will therefore reach the third stage in spring and summer the following year.

#### Pupation in the first year after oviposition

The results of the life cycle experiment showed that the larvae reaching the L3 stage in 2014, were not able to pupate that same year. The larvae had not been able to fully develop, which was reflected in a relatively low average weight of 0.83 g

(table 4) at the monitoring in 2014. These larvae further developed to older larvae in 2015 of which six pupated. The remaining L3 larvae in that year grew to an average weight of 1.61 g ( $n = 19$ ).

The pupa and five beetles that were found at the monitoring on October 22, 2015 had gone through the larval stage in little less than a year and a half, including a winter period with less growth. Nineteen L3 larvae remained. Only six out of 25 L3 larvae were able to pupate in 2015. Pupation took place relatively late in the season given the fact that one pupa and one general beetle was found at the monitoring. It shows that only six out of 25 L3 larvae were mature enough to enter pupation before winter.

#### Pupation in the second year after oviposition

At the monitoring in 2016, no mature L3 larvae were found. Only relatively large beetles compared to the ones found in 2015 (Hendriks 2013) were present in their pupal cells. In 2015 the L3 larvae were already large and well developed, given their average weight. They were able to further gain weight from October 2015 until pupation in 2016. Pupation clearly had taken place earlier than in 2015, given the earlier monitoring date on October 16, 2016 and the fully hardened beetles that were found. Their larval stage lasted from the summer of 2014 until the summer of 2016, a period of two years that held two winter periods. Such a period is considerably longer than the developing period of the larvae that pupated in 2015. It shows that if larvae are not able to pupate before winter, pupation is prolonged to the following summer. This automatically leads to an approximately ten months longer L3 stage (autumn year 1 to summer year 2) in which larvae might be fully matured, but will not pupate until the temperature is sufficient. Such a lengthened L3 stage in which the larvae might keep feeding, depending on the winter conditions, may yield larger larvae and therefore larger adults (Hendriks 2007).

A prolonged larval stage due to lower temperatures can be made visible by calculating the sum of effective temperatures (SET) (Honék 1996, Szujeci 1987). Given the prolongation of the larval stage with nearly one year in colder conditions, it was interesting to see if the SET differs between a two and three year life cycle. In this SET calculation, day temperatures that are lower than the temperature at which the development of the considered immature stage ceases, must be removed (Honék 1996). Given the absence of feeding substrate in the gut of larvae (figure 11) at temperatures of approximately 6 °C and below, a development threshold (LDT) of 6 °C was used for calculating SET. This was done for the weekly measured temperatures in a log during the experiment (figure 10). As it was not possible to calculate the required average daily temperature above LDT, the value of SET for this specific temperature data only indicates the differences between a two and three year life cycle and cannot be used as a reliable SET value. Figure 12 shows the course of the cumulated temperatures for the egg and larval stage of a two and three year life cycle. The final SET values for both life cycle lengths is nearly equal when the three year cycle ends in the beginning of July 2016. This indicates that the larvae with a three year life cycle might have pupated early in summer of that year. It also shows the great difference in the SET value before the beginning of winter in 2014 for early and late oviposited eggs. For larvae from a three years cycle, such a value was first reached in the middle of August 2015, leaving not enough time to fully develop and pupate before the winter of that year.



14. *Dorcus parallelipedus* inhabiting the stump of a small ash *Fraxinus excelsior*. Photo: Paul Hendriks

14. *Dorcus parallelipedus* bewoont de stobbe van een kleine es *Fraxinus excelsior*.



15. Female *D. parallelipedus* feeding on a larva of the same species. Photo: Paul Hendriks

15. Vrouwetje van *D. parallelipedus* voedt zich met een larf van dezelfde soort.

### Influences on the length of the life cycle

Larvae of *D. parallelipedus* are found in standing trees and trunks up to 8 m high (figure 13), as well as in (small) logs, lying on the ground. Even root stocks of tree stumps are inhabited (figure 14). These habitats can either be sun exposed or in the shade. As larvae develop in wood decaying by white rot, direct influence from sun exposure will not occur. But a sun exposed, relatively small branch can get much warmer than an underground rootstock in a shady place. It is to be expected that the amount of sun exposure in relation to the temperature buffering of the wood or surrounding soil, will have an influence on the growth of the larvae. Larvae hatched from eggs oviposited late in the season in relatively cold (underground) habitats possibly take longer to develop than the ones in warm conditions, especially when originating from eggs oviposited early in the season. In colder, temperature buffered habitats, most or all larvae might not reach the L3 stage in the year of oviposition and need an extra year to fully develop and pupate, resulting in a three year life cycle. On a larger scale this might occur as well through the western European distribution of *D. parallelipedus*. Larvae seem to be well adapted to cold winter conditions when looking at its eastern distribution well into Russia and Scandinavia and the possible antifreeze compounds in their gut. In the west European countries with a much milder maritime climate, the border of its distribution does not spread far north. A possible explanation can be found in the relatively low summer temperatures that might keep L3 larvae from pupation. Possibly, a four year life cycle might occur at the border of the north western distribution of *D. parallelipedus*. This is not to be expected for the mainland of the Netherlands as Groningen is the most northerly situated province with a coastal region. The life cycle experiment showed that both a two and three year life cycle is possible for an area that is only 20 km south of the coast. Whether this is influenced by recent change in temperatures, caused by climate change, is not further studied but could be possible.

### Cannibalism?

Out of 57 larvae collected at the monitoring of 2014, fifteen beetles eventually developed (26%, table 2). This relatively low percentage of surviving adults could not be explained from possible mortality of larvae that were relocated on 2014 and 2015 as no remains of larvae or parasites thereon were found. In earlier rearing trials, where larvae were reared in to adults, the handling, weighing and measuring of larvae did not affect larvae, nor did it lead to mortality. The collected larvae at the three monitoring dates looked healthy. It is possible that cannibalism within the logs played an important role in the demise of larvae. In observing larvae and beetles in earlier rearing trials, it was noticed several times that female beetles predated on their larvae (figure 15). Predation amongst larvae also occurs (Dodds et al. 2001), between larvae of successive instars when food is scarce or space is limited (personal observation). Predation among *Dorcinae* have been noticed by others (Lai & Hsin-ping 2008, Tanahashi & Togashi 2009). Predation of larvae by adults as well as preparing feeding substrate by adults is described by Mori & Chiba (2009) for the Lucanid *Figulus binodulus*. In *Dorcinae*, cannibalism might provide the relatively long living females with protein and possibly enables them to oviposit for several years.

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## Samenvatting

**Levenscycluslengte van het klein vliegend hert (Coleoptera: Lucanidae: *Dorcus parallelipedus*)**

De literatuur geeft voor het klein vliegend hert *Dorcus parallelipedus* doorgaans een levenscyclus van twee tot drie jaar (van ei tot imago). Hoe de lengte van deze cyclus is bepaald, wordt niet duidelijk. Aan de hand van een levenscyclusexperiment kon de lengte worden bepaald, waarbij een twee- tot driejarige cyclus werd bevestigd. De resultaten van het experiment zijn vergeleken met eerder uitgevoerde kweekproeven bij verschillende temperaturen. Doordat in natuurlijke omstandigheden de larven aan het einde van de zomer een koude periode ingaan, wordt het larvenstadium verlengd. Larven die het eerste jaar in het derde larvenstadium de herfst ingaan, kunnen dan aan het einde van de zomer het jaar erop verpoppen en als imago in mei het daaropvolgende jaar actief worden. Dit betekent een levenscyclus van twee jaar. De larven die uit later in het zomerseizoen gelegde eieren in het eerste of tweede larvenstadium de herfst ingaan, hebben een jaar langer nodig om het larvale stadium te doorlopen en verpoppen twee jaar later in de zomer. De larven leven in zowel liggend, staand en soms ook ondergronds dood hout. Niet alleen het klimaat beïnvloedt de lengte van de levenscyclus, ook de beschaduwing of de locatie waar het dode hout zich bevindt (boven- of ondergronds), heeft hier invloed op door verschillen in temperatuur.

Paul Hendriks

Oostwold (Leek)

hendriksmast@home.nl

