Larval feeding ecology of the stag beetle *Lucanus cervus* (Coleoptera: Lucanidae)

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KEYWORDS
Fecal pellets, growth rate, processed wood, white rot fungi, wood consumption

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Relatively little is known about the feeding ecology of the European stag beetle (*Lucanus cervus*) during its larval period. In order to shed light on the feeding habits of its hidden larvae, 49 third instar larvae were reared to adults in four different feeding substrates in which larvae are found. These substrates consisted of wood from different tree species, decayed by white rot fungi to different hardnesses. Decayed wood chips were used as well. The results clearly showed that larval growth trajectories had a saturating pattern, whereby male larvae grew to a larger size than female larvae. Larvae reared on hard decayed wood showed less growth and produced the smallest amount of processed wood, caused by a lower accessibility of such wood. Easy processable material like soft decayed wood and decayed wood chips yielded larger larvae.

Introduction

Saproxylic beetles depend during part of their life cycle, on dead wood, wood-decaying fungi or other saproxylic organisms (Speight 1989). Removal of dead wood as part of forestry management resulting in habitat destruction and degradation, poses a major threat to the conservation of saproxylic beetles (Grove 2002). As a consequence, circa 22% of the assessed species in the European Union are threatened, and 13% are near threatened (Cálix *et al.* 2018).

The European stag beetle, *Lucanus cervus* (Linnaeus 1758), is protected internationally by the Habitat Directive (Council Directive 92/43/EEC). Its large size and its characteristic morphology, make it a charismatic species that can be used as an umbrella species for the conservation of other insects depending on dead wood in mature forests. In the last two decades, much work has been devoted to understanding the biology of the stag beetle, with conservation purposes (e.g, Bardiani *et al.* 2017, Harvey 2007, Harvey *et al.* 2011, Rink 2006, Sprecher-Uebersax 2001). In particular, progress was made in sampling methods for monitoring (Bardiani *et al.* 2017), habitat use (Rink & Sinsch 2006, Thomaes *et al.* 2008), phenology (Álvarez Laó & Álvarez Laó 1995, Breitenmosser 2013, Fremlin 2009, Scaccini & Anaclerio 2016, Sprecher-Uebersax & Durrer 1998a) or dispersal ability (Rink & Sinsch 2007, Sprecher-Uebersax & Durrer 2001).

Given that larval development takes several years (Radnay 1995, Rink & Sinsch 2008, Tochtermann 1992), knowledge about larval ecology is essential for appropriate management and conservation of this species. Recent advances include the study of the number of larval instars (Fremlin & Hendriks 2014, Rink & Sinsch 2008), the presence of a mycangium (Fremlin & Tanahashi 2015, Hawes 2013) or the description of the stridulating organ (Sprecher-Uebersax & Durrer 1998b).

A major gap in current knowledge about the stag beetle is the feeding ecology of immature stages. In other saproxylic species, substrate quality and quantity influences the final size of larvae and adults (Tanahashi *et al.* 2009) and in insects, larger individuals have more fecundity (Honék 1993). For the stag beetle, only scattered information is available about its feeding ecology. With regard to the quality aspect of feeding substrate, sugar content and C/N ratio in stumps colonized by stag beetle larvae was reported (Sprecher-Uebersax 2001). In addition, preliminary evidence suggests that tree species utilized do not influence the size of the resulting adults (Rink & Sinsch 2008). The quantitative aspect has been addressed by means of the amount of faecal pellets produced (Pawłowski 1961). Early studies indicate that a larva of 5 g consumes 22.5 cm^3 of wood per day (Mamaev 1960) and that last instar larvae need 250 cm^3 of substrate per month (Tochtermann 1987).

The main aim of this study was to explore qualitative and quantitative aspects of the feeding ecology of stag beetle larvae by conducting a rearing experiment. We offered feeding substrates of different hardness to different groups of larvae to answer the following questions: (1) does growth and survival of the larvae differ among different feeding substrates?, (2) do male and female larvae grow at different rates? (3) does adult size differ among different feeding substrates?, (4) how much wood is processed during larval development?, (5) does the amount of wood processed differ, depending on the hardness of the substrate?

Material and methods

Study species

Stag beetle larvae (figure 1) feed on wood that is decayed by white rot fungi. They can be found in such wood in several stages of decay in all kinds of deciduous tree species (Fremlin 2013, Hawes 2009). Larvae scrape and splinter the decayed

1. Stag beetle larva. Photo: Paul Hendriks
1. Larve van het vliegend hert.

2. Larva defecating amidst splintered white rot wood. Photo: Paul Hendriks
2. Larve ontlast te midden van versplinterd witrothout.

3. (a) Frass (splinters and fecal pellets) before sieving and (b) pellets after sieving. Photo: Paul Hendriks
3. (a) Frass (splinters en keutels) vóór het zeven en (b) keutels na het zeven.

wood with their mandibles as they move through the surface of the wood and feed on these splinters (Fremlin & Hendriks 2011). In this environment they defecate as well, hence larvae are eventually moving around in frass, i.e., a mix of splintered decayed wood and faecal pellets (figure 2). Stag beetles have three larval instars (Fremlin & Hendriks 2014). At least in the last larval instar, sex can be recognized (Fremlin & Hendriks 2014). After several years, larvae pupate in the soil near the underground decayed wood in summer and stay as imago's in their pupal cells until the following spring (De Ligondes 1959, Pawłowski 1961).

Larval rearing, sexing and distribution into groups

In August 2008, three female stag beetles were collected in Hoog Soeren and Elspeet (province of Gelderland, the Netherlands). These females were placed together in a glass terrarium (20 × 25 × 40 cm) to lay eggs. The terrarium was half filled with logs decayed by white rot fungi, placed on decayed wood chips and sandy soil. Females produced a total of 49 larvae. The L1 and L2 stages were considered too delicate to handle, so the rearing experiment was limited to L3 larvae. L1 and L2 larvae were kept together at 25 °C and this greatly accelerated the moulting to the following stages compared to average natural conditions. Young L2 larvae were moved to a shallow terrarium where their moulting could be easily monitored. As soon as they moulted to the L3 stage in December 2008-January 2009 they were split in four groups of 14 larvae, except one with seven larvae, and were housed per group. To avoid bias due to different larval size across groups, the head capsule width (hcw) was measured with an accuracy of 0.1 mm and larvae with 'small' and 'large' head capsules were equally allocated to each group. This way, the obtained hcw's per group were within the range of 8.0-11.3 mm and in accordance with the range of hcw's given by Klausnitzer (1995). For the larvae in the groups with 14 larvae each, it was possible to get a relatively equal distribution of hcw's. The seven larvae in the fourth group all had a relatively large hcw (> 10 mm). Larvae were sexed following Fremlin & Hendriks (2014). Females had smaller hcw's than males (females: 9.4 ± 0.3 mm, n = 21; males: 10.6 ± 0.5 mm, n = 25; $F_{1, 44} = 104$, $p < 0.001$).

Table 1. Volume (cm³) of wood added to each container at each date. Tree and fungus species are also indicated. For Soft plus Hard, the soft and hard wood parts are separately reported. For Warm, the wood parts and chips volumes are separately reported. NA indicates that no wood was added at that date.
Tabel 1. Volume (cm³) van het toegevoegde hout in elke container en op elke afzonderlijke datum. De boom- en schimmelsoort zijn aangegeven waar dit bekend was. Voor Soft plus Hard zijn de harde en zachte houtblokken afzonderlijk vermeld. Voor Warm zijn de houtblokken en snipperhoeveelheden apart weergegeven. NA geeft aan dat er geen hout was toegevoegd op die datum.

Date	SOFT Tree	Fungus[1]	Volume	SOFT + HARD Tree: soft/hard	Fungus: soft/hard[1]	Volume	CHIPS Tree[2]	Fungus[1]	Volume	WARM Tree	Fungus[1]	Chips[2]	Volume: soft + chips
01/01/2009	Beech	F	4032	Beech/Beech	F/C	2589 + 1110	CM	?	7260	Beech	C	CM	502 + 3295
31/01/2009	Beech	F	3406	Beech/Beech	F, U/C	2697 + 576	CM	?	9672	Beech	F, U, C	CM	901 + 1424
28/02/2009	Beech	F, U	3120	Beech/Oak	F, U/?	764 + 800	CM	?	7595	Beech	F, C	CM	495 + 2261
29/03/2009	Beech, Oak	G, H	1667	Beech/Oak, Beech	H, C/?, R?	1981 + 1476	CM	?	7560	Beech	H, C	CM	320 + 2436
26/04/2009	Beech	G, H, C	594	Beech/Beech	F, C/H	1168 + 1992	CM	?	9828	Beech	H, C, F	CM	557 + 2920
24/05/2009	Beech	G, H, F	284	NA/Beech	NA/H, F	2840	CM	?	10584	Beech	H, F	CM	265 + 3042
20/06/2009	Oak, Birch	?, F	1300	NA/Birch, Beech	NA/G?, H	3320	CM	?	12400	Birch, Beech	G?, H	CM	520 + 3008
19/07/2009	Birch	F	1770	NA/Birch	NA/W(?)	3090	CM	?	11113	Birch	F, W(?)	CM	230 + 3628
14/08/2009	Willow	C	2130	NA/Willow	NA/C	2360	CM	?	9672	Willow	C	CM	300 + 3558
13/09/2009	Beech	F	1400	NA/Willow	NA/C	3680	CM	?	10206	Willow, Beech	C, F	CM	210 + 3098
10/10/2009	Poplar	H, C	1410	Oak, Poplar/NA	H/NA	1260	CM	?	9650	Poplar	C, H	CM	580 + 2727
07/11/2009	Oak	T	1220	NA/Oak, Beech	NA/T, H	880	CM	?	7130	NA	NA	CM	1302
08/12/2009	Beech	H	1400	NA/Beech	NA/H	1360	CM	?	9000	NA	NA	NA	NA
06/01/2010	Beech	G	1560	NA/Beech	NA/H	1520	CM	?	10600	NA	NA	NA	NA
31/01/2010	Beech	G	1043	NA/Beech	NA/H	1000	CM	?	11000	NA	NA	NA	NA
25/02/2010	NA	NA	NA	NA/Beech	NA/H	800	NA	NA	NA	NA	NA	NA	NA
21/03/2010	Oak	H	360	NA/Oak	NA/A	360	Oak	H	360	NA	NA	NA	NA

[1] A: *Armillaria mellea*, C: *Coriolus versicolor*, F: *Fomes fomentarius*, G: *Ganoderma applanatum*, H: *Hypholoma fasciculare*, R: *Rigidopurus ulmarius*, T: *Tricholoma sulphureum*, U: *Ustulina deusta*, W(?): unknown whiterot, ?: unknown.
[2] CM (Chip Mixture): *Salix alba*, *Cornus sanguinea*, *Prunus avium*, *Amelanchier lamarckii*, *Ilex aquifolium*, *Sambucus nigra*, *Fraxinus excelsior*, *Acer platanoides*.

The feeding substrates

Each group of larvae was transferred to one of the following feeding substrates and kept together as a group: (1) Soft, consisting of soft decayed wood; (2) Soft plus Hard, consisting of soft plus hard decayed wood; (3) Chips, consisting of decayed wood chips; (4) Warm, consisting of soft and hard decayed wood and wood chips, and was heated to a constant temperature of 24 ± 2 °C. Feeding substrates 1 and 2 represent the two main substrates in natural habitats of the stag beetle (Mamaev 1961, Tochtermann 1992). The used soft decayed wood had white to yellowish coloration, strong fungal smell, visible white patches of mycelia, and could easily be broken by hand. The hard type of decayed wood had similar characteristics but was harder and penetrable by a screwdriver to 0.5-1.0 cm. Hardly any mycelia were visible in this type of decayed wood. The decayed wood used in Soft, Soft plus Hard and Warm was from various tree species with various fungi and taken from branches and logs in a forest in Roden (Drenthe province, Netherlands) (table 1). It was not possible to get wood from a single tree species and with a single fungus species. This was not considered to be crucial, because it is the activity of white rot fungi in wood that is considered essential for larval growth (Hendriks 2007, Mamaev 1961, Rink 2006, Tochtermann 1992). Feeding substrate 3 and partly 4 consisted of decayed wood chips that originated from shredded twigs and small branches from a mixture of various tree species from the first author's garden (table 1). In the spring of 2007 this material was shredded to thin sliced chips with a length of 1 to 3 cm and consisted mainly of *Salix alba* (50%). The other wood species utilized as chips, are given in table 1. When used in this experiment, these wood chips were decayed, had a dark brown color and were broken down to a size of approximately 1 × 1 cm. Wood chips are utilized in some anthropogenic environments such as gardens or sawmills (Hawes 2009). Feeding substrate 4 was included to test for the effect of a constant, favorable temperature on the development of the larvae (Rink & Sinsch 2008).

The use of feeding substrates

In Soft, Soft plus Hard and Chips, plastic containers with a lid (length × width × height: 32 × 25 × 18 cm) were used. In Warm, a shallow terrarium with a glass lid (length × width × height: 35 × 31.5 × 3 cm) was used. Decayed wood was added and renewed on a monthly basis. In order not to disturb the fungal activity in the wood, no additional preparation of the used substrates was performed, such as boiling or drying and re-wetting. Inspection of the blocks was performed to remove invertebrates that could damage the larvae or influence the amount of food processed. In Soft plus Hard, the amount of soft decayed wood renewed was reduced and finally discontinued in subsequent monthly replacements, once it became clear that larvae were able to feed on the harder decayed wood blocks (table 1). The used decayed wood was sawed in blocks with an average size of 300 ml (min. 50 ml, max. 900 ml) to be able to divide the soft parts from harder parts and pack them efficiently in the containers and shallow terrarium in Soft, Soft plus Hard and Warm. Small blocks also made it easier to collect larvae that had dug in to them. The blocks were placed in the containers and shallow terrarium in amounts given in table 1. For Soft and Soft plus Hard, the blocks were covered with a layer of sandy soil, covering the blocks and filling the remaining spaces between the blocks to a height of approximately 10 cm. Thus larvae were able to move between the blocks, thereby mimicking their natural habitat. In Warm, the remaining space in the shallow terrarium between the blocks of soft and hard decayed wood was filled with wood chips up to 3 cm on which the glass lid was directly placed, making it possible to follow the behavior of the larvae in this

Table 2. Summary of growth conditions and remarkable events in larval development in each feeding substrate.
Tabel 2. Opsomming van de groeicondities en opmerkelijke gebeurtenissen voor de larvale groei in elk voedingssubstraat.

Date	Soft	Soft+ hard	Chips	Warm
31/01/2009	No peculiarities	No peculiarities	No peculiarities	No peculiarities
28/02/2009	Bad growth due to dry substrate; larvae are soft and lost their shine	Larvae are seen returning in to already splintered substrate	No peculiarities	Larvae return in white rot that has been splintered earlier
29/03/2009	No peculiarities	No peculiarities	Bad growth due to wet substrate. 1 larva died	Larvae are seen eating decayed wood chips and white rot simultaneously
26/04/2009	No peculiarities	Added only hard white rot, no discernable effect on growth	No peculiarities	1 larva is seen eating its own pellet, directly after excreting it.
24/05/2009	Good growth on used beech with *Hypholoma fasciculare*	No peculiarities	No peculiarities	1 deceased larva. Weight loss larvae due to high temperatures. Larvae were placed in a colder area
20/06/2009	Good growth and a considerable number of produced pellets	No peculiarities	Partly anaerobic substrate; less growth	Good growth, notwithstanding the earlier hot period
19/07/2009	No peculiarities	Increased white rot in beech with *Coriolus versicolor*	No peculiarities	No peculiarities
14/08/2009	Bad growth due to high temperatures. Larvae become more yellow	Bad growth due to high temperatures. Larvae become more yellow	Bad growth due to high temperatures. Larvae become more yellow	No peculiarities
13/09/2009	Continuing growth of the largest (male) larvae.	No peculiarities	No peculiarities	1 larva stayed 4 weeks in one part of white rot
04/10/2009	No peculiarities	bad growth: substrate was relatively dry	No peculiarities	Larvae are ripe and are yellow. They hardly move.
05/11/2009	No peculiarities	Larvae only on soft white rot to let them recover. This substrate was totally eaten by the larvae; very good growth	No peculiarities	Hardly any movement and no feeding. 1 larva is sick.
08/12/2009	No peculiarities	No peculiarities	No peculiarities	Larvae seem to be building cocoons
06/01/2010	No peculiarities	No peculiarities	No peculiarities	The sick larva died
31/01/2010	1 larva got sick and died	No peculiarities	No peculiarities	No changes, no feeding. Larvae hardly move
24/02/2010	Larvae inactive due to low temperatures. Larvae have shrunk and became increasingly yellow. Every single larva was put in a plastic cup for pupation. This cup contained 50 cm^3 white rot and soil	Larvae inactive due to low temperatures. Larvae have shrunk and became increasingly yellow. Every single larva was put in a plastic cup for pupation. This cup contained 50 cm^3 white rot and soil	Larvae inactive due to low temperatures. Larvae have shrunk and became increasingly yellow. Every single larva was put in a plastic cup for pupation. This cup contained 50 cm^3 white rot and soil	No changes, no feeding. Larvae hardly move
05/06/2010	Because the larvae didn't pupate in cups, they were placed back in their former containers with only soil. White rot was eaten; additional growth of larvae	Because the larvae didn't pupate in cups, they were placed back in their former containers with only soil. White rot was eaten; additional growth of larvae	Because the larvae didn't pupate in cups, they were placed back in their former containers with only soil. White rot was eaten; additional growth of larvae	No changes, no feeding and weight of the larvae is stable
July to October 2010	Cocoon building startedin July. The last beetle emerged at the end of September	Cocoon building started in July. The last beetle emerged at the end of September	Cocoon building started in July. The last beetle emerged at the end of September	Cocoon building started in the middle of July. The last beetle emerged in November

Date	Hcw	Feeding substrate	W	C	S	S+H
Initial	< 0.0001	0.869	a	a	a	a
31/01/2009	< 0.001	0.002	ab	a	ab	b
28/02/2009	< 0.0001	< 0.001	a	b	b	b
29/03/2009	< 0.0001	0.001	a	ab	b	b
26/04/2009	< 0.0001	< 0.0001	a	a	b	b
24/05/2009	< 0.0001	< 0.001	a	a	ab	b
20/06/2009	< 0.0001	< 0.001	a	a	a	b
19/07/2009	< 0.0001	< 0.001	a	a	a	b
14/08/2009	< 0.0001	< 0.0001	a	b	b	c
13/09/2009	< 0.0001	< 0.0001	a	a	ab	b
04/10/2009	< 0.0001	< 0.0001	a	a	a	b
05/11/2009	< 0.0001	0.048	a	a	ab	b
08/12/2009	< 0.0001	0.012	a	a	a	b
31/01/2010	< 0.0001	0.004	a	a	ab	b
05/06/2010	< 0.0001	0.004	a	a	ab	b

Table 3. P-values of the ANCOVA testing differences in L3 weight of stag beetle larvae among feeding substrates, for each date. Head width capsule (hcw) was included as a covariate. In the last four columns, feeding substrates sharing the same letter were not significantly different in larval weight according to the Tukey HSD post-hoc test. W: Warm; C: Chips; S: Soft; S+H: Soft plus Hard.
Tabel 3. P-waarden van de ANCOVA geteste verschillen in de gewichten van L3-larven van het vliegend hert in de verschillende voedingssubstraten voor elke datum. De kopkapselbreedte (hcw) was inbegrepen als een covariant. In de laatste vier kolommen zijn de voedingssubstraten met eenzelfde letter niet significant verschillend als het gaat om de gewichten van de larven volgens de Tukey HSD post-hoc test. W: Warm; C: Chips; S: Soft; S+H: Soft plus Hard.

substrate. In Chips, a layer of approximately 10 cm of decayed wood chips was placed. As larvae moved freely through this material and are found in wood chip piles in the wild without soil coverage, no layer of soil was added on top of this substrate.

Measurements on temperature and larvae

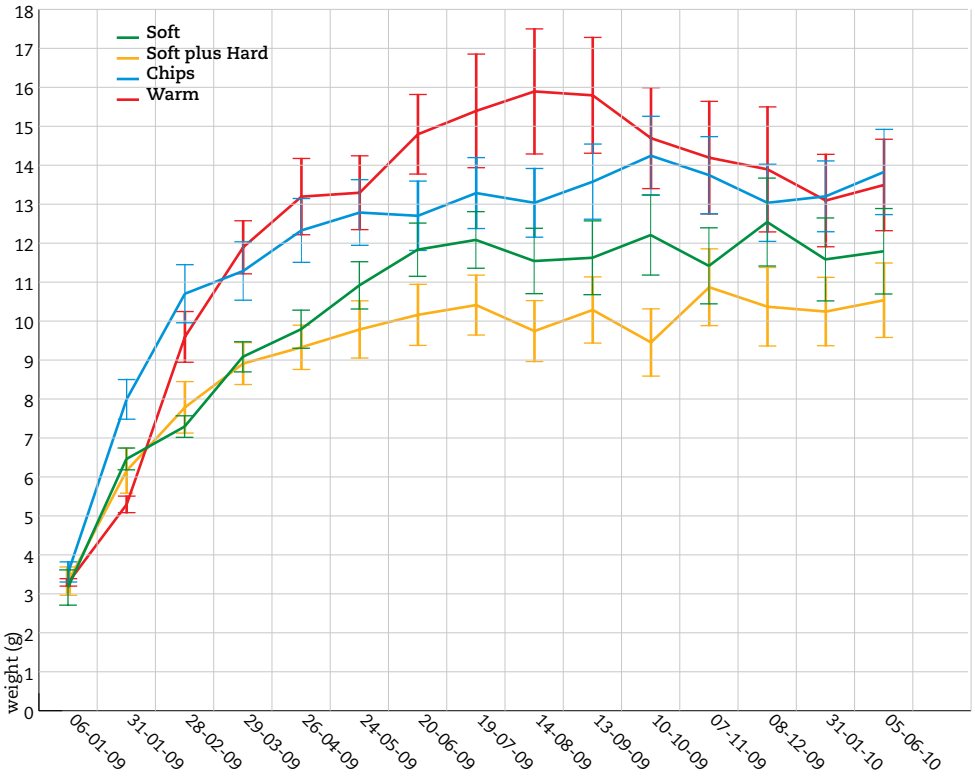
Feeding substrates 1-3 were kept at room temperature, ranging 17.5-24 °C. In the winter of 2010-2011, temperature was lowered to a minimum of 3 °C and during the spring of 2011 it was gradually raised again to 17 °C. These temperatures are in the range of soil temperatures near decaying wood inhabited by stag beetle larvae (Rink 2006).

Each month, the hcw of every larva was measured and its weight taken to the next 0.5 g in a scale, and checked for health status and survival. A summary of growth conditions and remarkable events is presented in table 2. After pupation, sex and total length in mm of the emerging imagoes was noted.

Measurements of feeding

Substrate from the containers and the shallow terrarium was divided into three fractions: fecal pellets, wood splinters and unused woody parts. The wood splinters and pellets (frass) were separated by sieving with a 0.5 × 0.5 cm sieve (figure 3). The volume of pellets produced indicates the actual amount of wood consumed. However, this has to be considered as a minimum value, because pellets can be reingested or crushed by larvae (P. Hendriks personal observations). The sum of fecal pellets and wood splinters is the amount of wood processed during the feeding activity of the larvae.

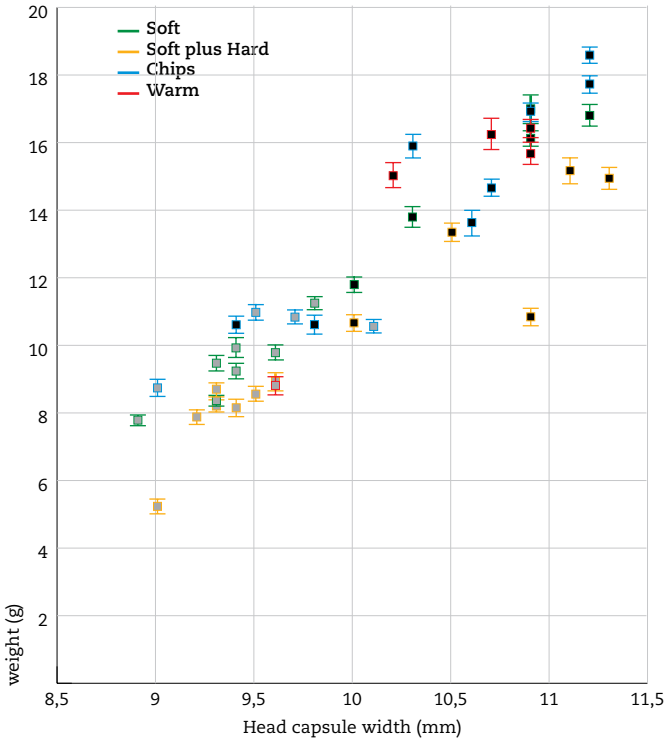
At the beginning of the rearing experiment and each time the wood in the containers was renewed, the volume of the wood



4. Weight of L3 stag beetle larvae for their larval stage in four different feeding substrates. Error bars indicate standard error. n = 12 in all cases, except Warm (n = 5).
4. Gewicht van L3-larven van het vliegend hert voor het gehele larvenstadium in de vier verschillende voedingssubstraten. De foutenbalkjes laten de standaardfout zien. n = 12 in alle gevallen, behalve Warm (n = 5).

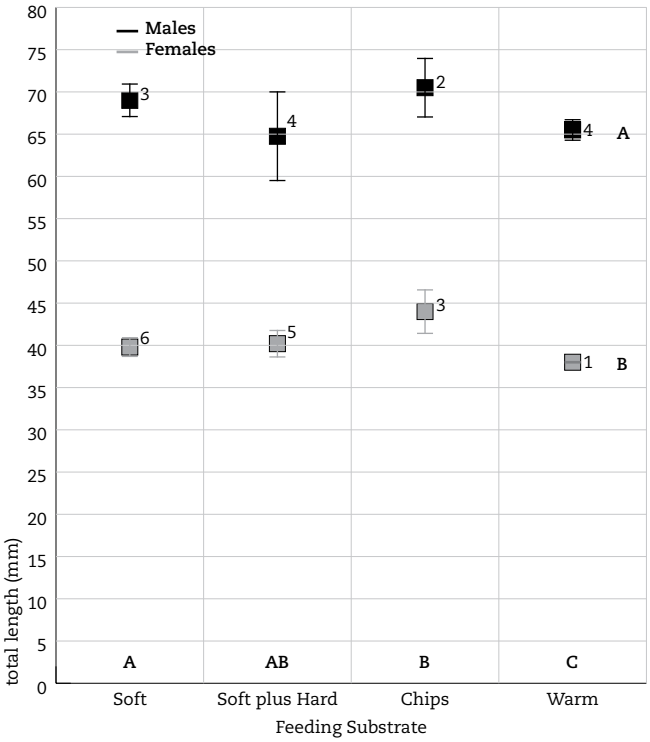
Variable	SS	DF	F	p
Head capsule width	405.3	1	389.833	< 0.0001
Feeding substrate (FS)	33.8	3	10.828	< 0.0001
Sex (S)	2.9	1	2.801	0.104
FS × S	7.5	3	2.393	0.087
Residuals	33.3	32		

Table 4. Results of the ANCOVA testing for differences in L3 plateau weight of stag beetle larvae as a function of feeding substrate and sex. Head capsule width was included as a covariate. Sums of squares (SS), degrees of freedom (DF), F value (F) and p value (p) are shown for these two factors.
Tabel 4. Resultaten van de ANCOVA waarbij is getest voor de verschillen in het stabiele gewicht van vliegende hertenlarven als een functie van het voedingssubstraat en sekse. De kwadraatsommen (SS), vrijheidsgraden (DF), F-waarde (F) en de p-waarde (p) zijn te zien voor deze twee factoren.



5. Relationship between head capsule width and plateau weight of male (black) and female (grey) stag beetle larvae in each feeding substrate. Bars indicate the standard error of eleven weight measurements per larva.
5. Relatie tussen de kopkapselbreedte en het gemiddelde stabiele gewicht van mannelijke larven (zwart) en vrouwelijke larven (grijs) van het vliegend hert in de voedingssubstraten. De balkjes laten de standaardfout zien voor elf wegingen per larf.

6. Beetles from feeding substrate Soft, with smaller females and larger males. Photo: Paul Hendriks
6. Kevers van het voedingssubstraat Soft, met kleinere vrouwtjes en grotere mannetjes.

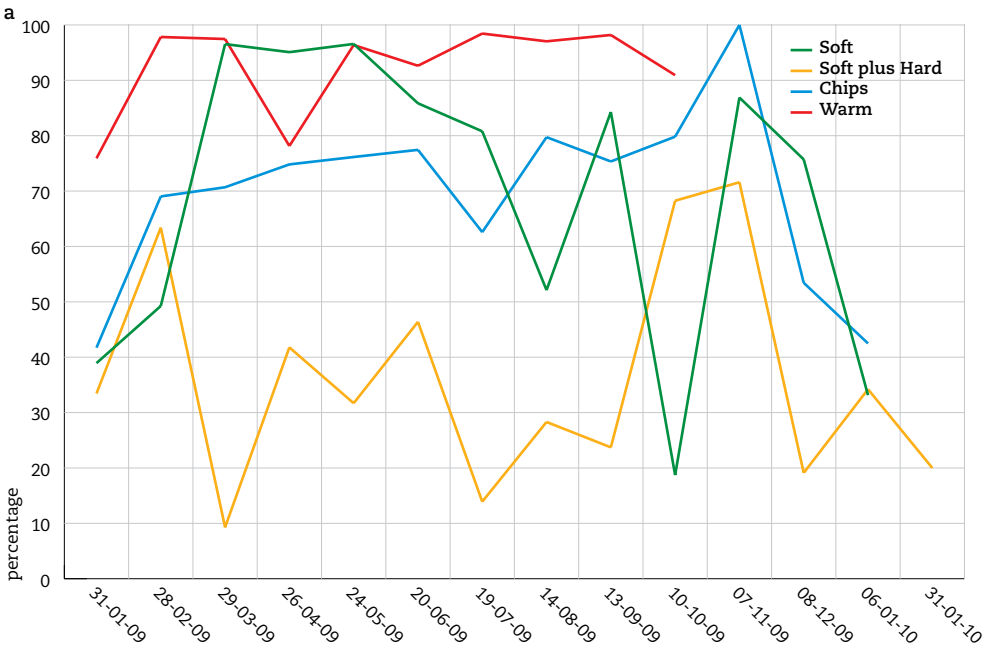


7. Total length of male beetles (filled circles) and female beetles (open circles) in each feeding substrate. Bars indicate the standard deviation. Factor levels (feeding substrate or sex) sharing a letter (see letters A, B and C) were not significantly different according to a Tukey HSD post-hoc test. Post-hoc comparisons between sexes (see letters) are shown in the right side of the figure, and post-hoc comparisons among feeding substrates close to the × axis.
7. Totale lengte van mannelijke kevers (ingekleurde symbolen) en vrouwelijke kevers (niet ingekleurde symbolen) in elk voedingssubstraat. De balkjes laten de standaard afwijking zien. 'Factor levels' (voedingssubstraat of geslacht) die eenzelfde letter hebben (zie A, B en C), waren niet significant verschillend op basis van de 'Tukey HSD post-hoc test'. 'Post-hoc'-vergelijkingen (zie letters) tussen de geslachten zijn te zien aan de rechterzijde van het figuur en 'post-hoc'-vergelijkingen van de voedingssubstraten staan bij de x-as.

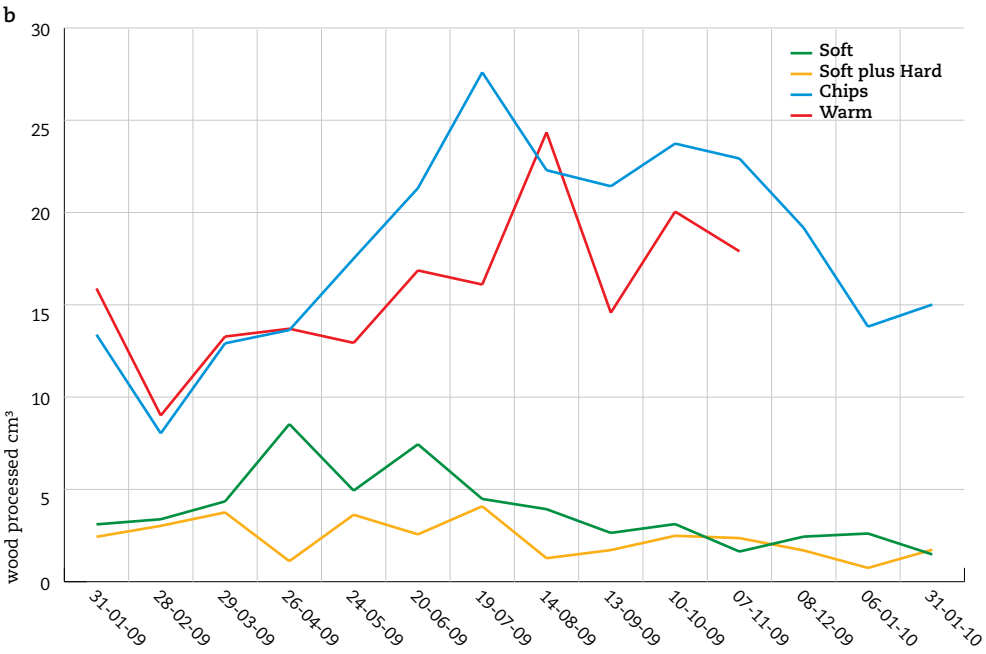
blocks added and of the remaining blocks was estimated by pressing them under water in a 2 l measuring cup, with a precision of 20 ml. The volume of fecal pellets and wood splinters was obtained by pressing this material in the same measuring cup until no more reduction of volume occurred. The amount of wood processed during each time period was estimated as the difference between the volume of wood added in time t-1 minus the volume of wood remaining in time t. This volume was divided by the number of larvae in each feeding substrate to obtain an average of the wood processed per larva every month.

Statistical analysis

To describe growth, average weight data of the L3 stage were



8. (a) Percentage of substrate processed and (b) substrate volume processed per larva per day in each feeding substrate.
8. (a) Percentage van het omgezette voedingssubstraat en (b) het omgezette volume per larf per dag in elk voedingssubstraat.

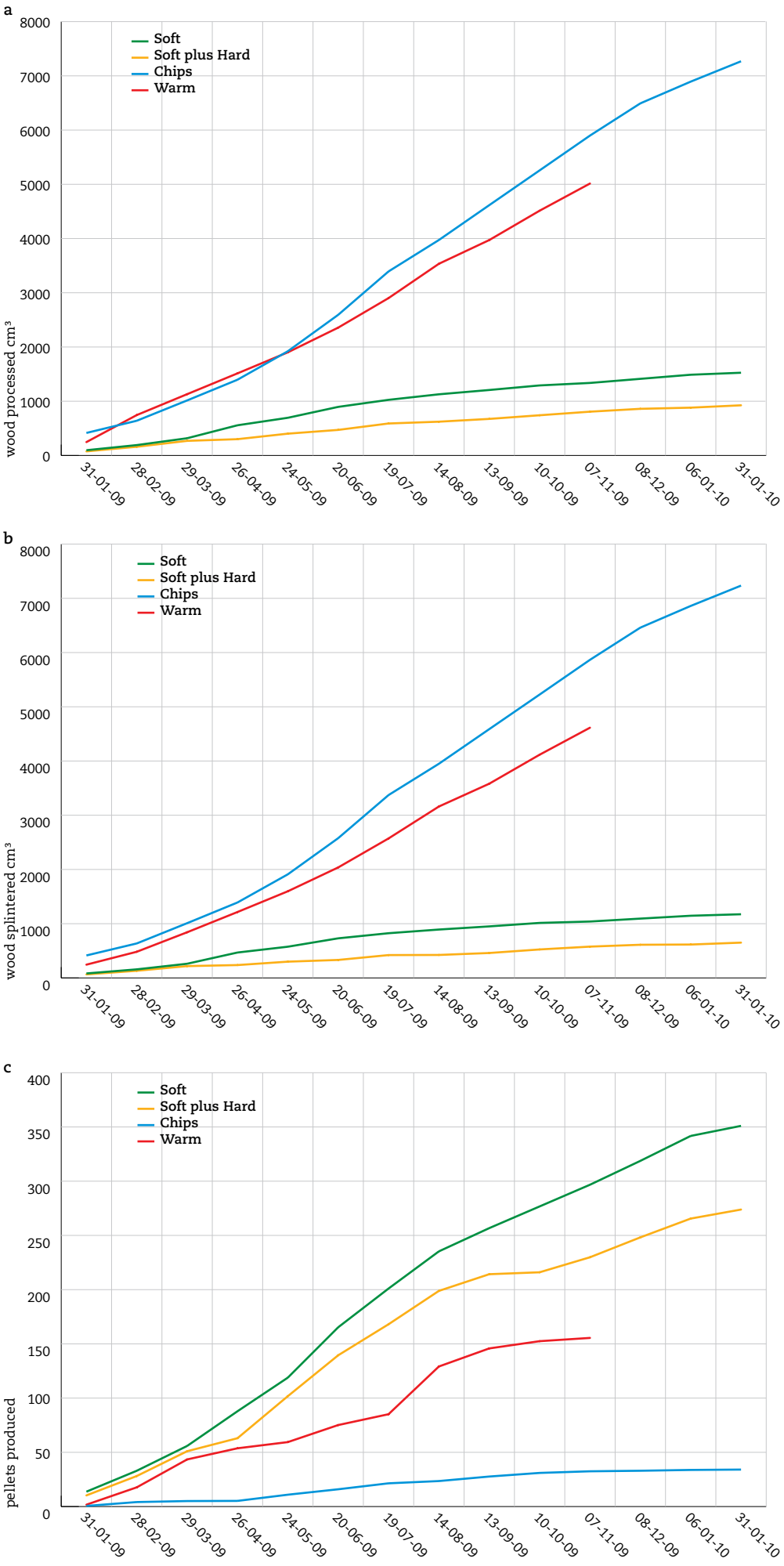


8. (a) Percentage of substrate processed and (b) substrate volume processed per larva per day in each feeding substrate.
8. (a) Percentage van het omgezette voedingssubstraat en (b) het omgezette volume per larf per dag in elk voedingssubstraat.

plotted by date for each feeding substrate. The dates of initial weight measurements of the L3 stage differed among larvae within and between feeding substrates by circa 30 days (December 18th 2008 to January 17th 2009) due to differences among larvae in moulting time. An ANCOVA to test for differences in initial L3 weight across moulting dates, using hcw as a covariate, did not find any significant differences among dates ($F_{6, 33} = 1.756$, $p = 0.139$). Nevertheless, we incorporated the initial weight of each group of larvae for completeness (figure 4). An ANCOVA was used to test for differences in larval weight across the four feeding substrates for each sampling date to proof random allocation. The hcw was used as a covariate. Sex was not considered in this analysis, because only one female was present in the Warm treatment (n = 7 larvae). Nevertheless, the significant differences in hcw between sexes allowed to get an indirect idea of the effect of sex by checking the significance of hcw. When ANCOVA indicated significant differences among treatments, the Tukey HSD was performed to identify the average values that significantly differed from each other.

In addition, we calculated the average weight of each larva after it reached its plateau weight in June 2009 (plateau weight, hereafter). Differences in the plateau weight among feeding substrates and sex were tested using an ANCOVA, with the hcw as a covariate. When ANCOVA indicated significant differences among treatments, the Tukey HSD was performed to identify the average values that significantly differed from each other.

A two-way ANOVA tested for the effect of the feeding substrates and sex on the total length of the imagoes. QQ plots of each sex indicated no strong departures from normality and a Barttlet test indicated homoscedasticity. A Tukey HSD was performed to identify the average values that significantly differed from each other.



9. Accumulated processed (a) feeding substrate per larva, (b) splintered and (c) pellets produced. Notice that Y axis on plot c has a different scale.
9. Cumulatieve volumes (a) omgezet voedingssubstraat per larf, (b) versplinterd en (c) geproduceerde keutels. Let op: de Y-as in grafiek c heeft een afwijkende schaal.

10. Smaller female larva and bigger male larva from feeding substrate Soft plus Hard. Photo: Paul Hendriks
10. Kleinere vrouwelijke larf en grotere mannelijke larf uit het voedingssubstraat Soft plus Hard.

Results

Within each feeding substrate, larvae increased in average weight from circa 3 g in December 2008-January 2009 to 10-14 g in May 2010 (figure 4). Pupation occurred in July 2010. Eight larvae died during the rearing experiment, two per feeding substrate. An additional 13 individuals died during the pupal stage, three in Soft, three in Soft plus Hard and seven in Chips. Most of the growth occurred in the first 100 days of the L3 stage, up to May 2009 (figure 4).

Larvae in the Hard plus Soft feeding substrate were smallest at all dates (figure 4, table 3). Larvae in the Warm and Chips feeding substrates were biggest at almost all dates, while those in the Soft feeding substrate were, in general, intermediate in weight (figure 4, table 3).

Larvae with wider head capsules had a significantly higher plateau weight (figure 5, tables 3 and 4). After removing the influence of head capsule on plateau weight, an effect of feeding substrates was still detected (table 4). Compared to the remaining feeding substrates, larvae in the Soft plus Hard substrate had significantly lower weights, according to a Tukey HSD post hoc test. Sex did not influence the plateau weight, once the effect of head capsule was taken into account (table 4).

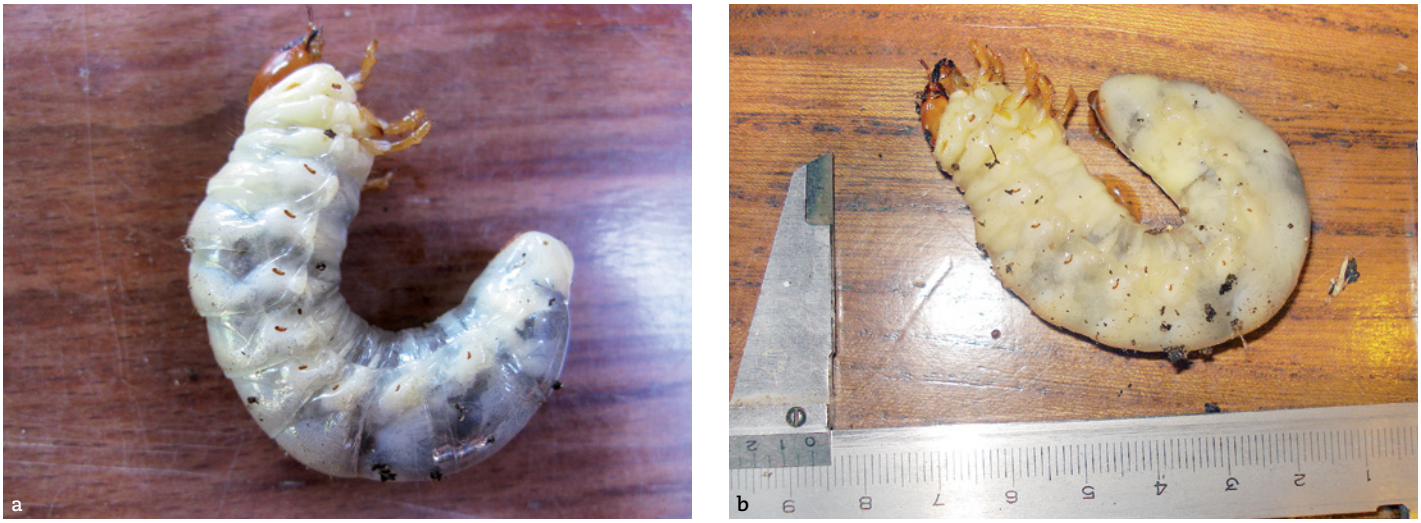
Total length of individuals reaching the adult state differed significantly among the feeding substrates ($F_{3,\ 20} = 18.597$, $p < 0.0001$) and among sexes ($F_{3,\ 20} = 629.458$, $p > 0.0001$) but there was no interaction between feeding substrate and sex ($F_{3,\ 20} = 1.078$, $p = 0.381$). According to a Tukey HSD post hoc test, males were larger than females (figures 6, 7) and individuals in Chips were the largest, while individuals in Warm were the shortest ones (figure 7).

The percentage of the substrate processed differed considerably and ranged from 19 to 97% in Soft, from 9 to 71% in Soft plus Hard, from 42 to 100% in Chips and from 75 to 98% in Warm (figure 8a). Only in Warm the percentage of substrate processed was usually over 90% (figure. 8a). This suggests that we worked in conditions of ad libitum food supply.

The average volume of wood processed per larva per day was 3.8 ± 2.02 cm^3 for Soft, 2.3 ± 1.02 cm^3 for Soft plus Hard, 18.0 ± 5.43 cm^3 for Chips and 15.9 ± 4.04 cm^3 for Warm. The volume of wood processed varied with time (figure 8b), particularly in Chips and Warm. The accumulated wood processed ranged from 925 cm^3 in Soft plus Hard to 7268 cm^3 per larva in Chips (figure 9a). In the latter, most of the wood chips were splintered (figure 9b). The accumulated amount of pellets produced followed a different pattern and ranged from 34 cm^3 in Chips to 351 cm^3 in Soft (figure 9c).

Discussion

Based on our experiment we can conclude the following regarding the larval feeding ecology of the European stag beetle: (1) the growth trajectory in third instar larvae followed a saturating pattern, with most of the growth occurring in the 100 initial days, (2) male larvae grew to a larger size than female larvae (figure 10), coinciding by sexual differences in head capsule width, (3) growth of larvae was higher in softer feeding



11. Larva from feeding substrate Soft. (a) Photo on 24.v.2009. (b) Same larva (a) on 6.i.2010 after fattening (notice the built up of tissue and yellowish coloration in the larva on the right). Photo: Paul Hendriks
11. Larve uit het voedingssubstraat Soft. (a) Foto van 24.v.2009. (b) Dezelfde larf op 6.i.2010 na groei (let op de opbouw van weefsel en de gelige kleur van de larf rechts).

12. Size of stag beetle larvae within the three larval stages. Photo: Maria Fremlin
12. Formaat van larven van het vliegend hert binnen de drie larvenstadia.

substrates, i.e. easier to process and/or more nutritious, (4) adult size increased in softer substrates for larvae and (5) in our feeding experiment with ad libitum food, the amount of substrate processed per larva ranged from 925 to 7268 cm^3 and was higher when the substrate was softer. In the following, we discuss the implications of these results.

Previous studies on the growth of stag beetle larvae have mainly focused on early larval instars (Sprecher-Uebersax 2001) or were limited to a description of growth based only on a few larvae (Rink & Sinsch 2008). In our study we followed the growth of 49 larvae divided over four different feeding substrates in order to determine some of the limiting factors to their growth. Growth trajectories of larval insects have been suggested to be exponential, based on hypothesized metabolism (Von Bertalanffy 1957). Actual rates range from exponential (Brindley 1930, Mackey 1978) to linear (Reynolds *et al.* 1985), sigmoid (Margraf *et al.* 2003, Phoofolo *et al.* 2009) or saturating (Gotthard 2004). In our study, growth of the larvae was saturating, not linear, during their third instar. Growth trajectories of L3 larvae in another horned beetle *Onthophagus taurus* were roughly linear, with a short period of stasis previous to the prepupal stage (Emlen & Nijhout 1999). The main difference with previous studies is perhaps the long period of plateau weight for the stag beetle larvae. According to Sebens (1987) species are able to adjust the duration of larval development or at least a particular instar to the resources available. In our experiment, the long plateau period was present in all feeding substrates, suggesting that its meaning is not related to optimization of the duration of larval development. This suggests that most of the time spent in the third instar is not devoted to increase weight but probably to other physiological processes such as fattening (Hendriks 2007, figure 11). This is especially true for the older L3 larvae. Events that occur earlier in this instar are more likely to influence weight. Future studies should address how this long plateau period in the larval development of stag beetle fits a life history perspective.

Weight was higher in larvae with larger head capsules. This reveals an influence of sexual dimorphism on weight. Once head capsule width was taken into account, no additional differences in weight were detected between sexes. In insects, sexual dimorphism in size appears in early instars and it gradually accumulates (Tammaru *et al.* 2010). Apparently, the weight gain was similar in both sexes of stag beetle larvae, but initial size was already slightly lower in female, compared to male larvae. Future experiments should isolate males from females to ascertain whether the initial higher weight is due to a higher substrate processing by males or to higher assimilation.

Different substrates led to differential weights of the larvae. How food quality influences the growth of stag beetle larvae has been a major source of speculation (e.g. Colas 1962). The results of our experiment showed that an important aspect to consider is food hardness, likely explained by processing ease. Hard wood was clearly leading to less growth, while soft wood and chips yielded larger larvae. Although Warm had a lower sample size, milder climatic conditions combined with easily processed wood, also yielded large larvae. The effect of temperature is not surprising, because cellulose fermentation can only occur at temperatures of 13 °C or higher (Pawłowski 1961). Regarding conservation measurements it therefore may be considered to use wood chips in certain situations, like gardens and urban environments with a lack of decayed wood, as this substrate yields large larvae. In some countries, stag beetles have been found using wood chips in anthropogenic environments (Fremlin 2013, Hawes 2009). This kind of substrate can enhance larval growth and positively influence stag beetle populations, compared to other management options such as pyramids, where wood is harder. Our results clearly showed that larval food influenced the size of the resulting adults. In beetle species with dimorphism in male horns, it is known that adult size and horn development are dependent on both genetic as well as environmental factors, including food quality (Emlen 1994, Hunt & Simmons 2000, Moczek 1998). Our rearing experiment suggests that ease of food processing, which influenced larval growth, is therefore also relevant for adult size. There

was a relatively good match between the effects of feeding substrates on weight and on adult size, except for Warm. Here growth was initially fastest (figure 4) but larvae stopped feeding in October 2009 and did not regain feeding activity by contrast with larvae in the remaining substrates, which continued feeding until the spring of 2010. Perhaps this prolonged inactive period eventually led to smaller adults. Our results have important conservation implications, because in insects, larger individuals have more fecundity (Honék 1993). In addition, higher quality of food could influence size distribution of males and indirectly male dispersal (Thomaes & Camps 2016). Thus, potential management with the aim of directly benefitting populations of stag beetles by using supplementary food, should consider the hardness of wood provided. A mixture of tree species will guarantee the availability of a wider range in various types of decayed wood, consisting of fast rotting soft wood tree species and slow rotting hard wood tree species.

In the experiment, the amount of wood provided exceeded, in general, the amount of wood processed, indicating that food was no limiting factor for growth. Warm was closest to full processing of wood, but this apparently was no limit to growth of the larvae. In fact, growth trajectories in the different substrates were rather similar, compared to the high variation in the percentage of wood processing.

The amount of wood processed was higher in Chips and Warm, compared to the other two feeding substrates. Differences in the amount of produced pellets and splintered wood, were likely caused by the differences in wood hardness among the feeding substrates. We occasionally observed the re-ingestion of pellets consisting of chips by larvae within Warm. This could explain the lower amount of pellets in both Warm and Chips.

Harder wood clearly decreased the amount of wood processed and pellets produced. This provides an easy mechanistic explanation for the lowest weight of larvae in Soft plus Hard. In addition, fungal mycelia were more accessible in the other feeding substrates. This is important because mycelia contain protein that increases larval growth (Tanahashi *et al.* 2009) and other Lucanidae benefit from this mycelium (Mishima & Araya 2016). Comparison with Mamaev (1960) has to be done with caution, assuming that his study can be compared with our Soft and Soft plus Hard substrates. Volume of wood processed was an order of magnitude lower than in Mamaev (1960), but the maximum amounts matched the quantity given by Tochtermann (1987). Differences in wood hardness, temperature of rearing or measuring methodology, among others, could account for these differences and underlay the need of agreeing on protocols for estimating wood processing by saproxylic larvae.

Our study provides useful insights into the larval feeding ecology of the European stag beetle. Nevertheless, future research should address the following issues in order to provide an even better understanding of the autecology of the stag beetle: (1) The amount of feeding by L1 and L2 larvae was considered neglectable because of their small size compared to L3 larvae (figure 12), but should be proven in following studies. (2) The differences in growth rate between males and females should be established. (3) A more detailed study on the quality of the wood and the growth rate is useful.

When conducting future rearing experiments it is advised to use duplicates per substrate in order to have a better statistical basis for the conclusions. Furthermore we advise to use solid wood in future experiments for it is far easier to establish the amount of splintered wood and fecal pellets in solid wood than in wood chips. A proper management of humidity is crucial. Faecal pellets remain intact better when the feeding substrate is relatively dry.

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Samenvatting

Voedselopname door larven van het vliegend hert *Lucanus cervus* (Coleoptera: Lucanidae)

Vijfentwintig procent van de xylophage kevers in de Europese unie staat er slecht voor of wordt direct bedreigd. Het beschermde en imposante vliegend hert is één van deze soorten. Ondanks dat er recent veel studie is verricht aan het vliegend hert ten behoeve van bescherming, is er nog maar weinig bekend over de groei en voedselopname van de larven. Door middel van een kweekexperiment is hierin meer inzicht verkregen. Larven van het vliegend hert voeden zich met door witrotschimmels aangetast dood hout, ook in de vorm van houtsnippers. Zij versplinteren dit hout, voeden zich hiermee en onlasten er in. Voor dit kweekexperiment zijn 49 L3-larven ingezet. Van deze larven zijn de kopkapselbreedte en het geslacht bepaald. 42 van deze larven zijn qua kopkapselbreedte gelijkelijk ondergebracht in drie containers op kamertemperatuur. Hierbij is in container 1 zacht witrot hout als voedingssubstraat toegepast. In container 2 is aanvankelijk zacht en hard witrot hout gebruikt, maar later alleen hard materiaal. In container 3 zijn vermolmde houtsnippers gebruikt. Een vierde groep van zeven larven is in een ondiep terrarium geplaatst met een mengeling van houtsnippers en witrot hout met een constante, hogere temperatuur van 24 graden Celsius. Het gebruikte voedingssubstraat bestond steeds uit materiaal afkomstig van verschillende boomsoorten en met verschillende schimmelsoorten. Maandelijks werden de L3-larven gewogen en werd het voedingssubstraat gescheiden in overblijvend hout/houtsnippers, splinters en keutels, waarvan het gewicht en volume werden bepaald. Uit de kweekresultaten blijkt dat in het L3-stadium eerst een sterke groei optreedt en vervolgens stagneert. Mannelijke larven lieten een sterkere groei zien dan vrouwelijke larven. Het verloop van de groei werd niet beïnvloed door het geslacht van de larven. Het aandeel omgezet hout (versplinterd met keutels) verschilde aanzienlijk tussen de voedingssubstraten, maar was tijdens de kweek nooit limiterend. In zacht witrothout werd per larf gemiddeld 3,8 ± 2,02 cm^3/d omgezet, in hard witrothout 2,3 ± 1,02 cm^3/d, in houtsnippers 18,0 ± 5,43 cm^3/d en voor de mix van substraten 15,9 ± 4,04 cm^3/d. Voor het gehele larvenstadium varieerde de omzetting van witrothout en houtsnippers van 925 cm^3 tot 7268 cm^3. De groei van larven in het harde witrothout was significant geringer dan in de andere voedingssubstraten, doordat dit materiaal moeilijk te versplinteren was voor de larven. Dit leidde dan ook tot een geringere omzetting van dit hout. De goede groei van larven in zacht witrothout en houtsnippers laat zien dat dit materiaal zinvol ingezet kan worden voor beschermingsdoeleinden. De kweekresultaten geven geen aanleiding te veronderstellen dat boomsoorten en witrotschimmelsoorten een aantoonbaar effect hebben op de groei van de larven van het vliegend hert.

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