

The life cycle of the European stag beetle *Lucanus cervus* is three years minimum in the field (Coleoptera: Lucanidae)

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TREFWOORDEN

Cetonia aurata, immature stage, rat predation, wood chips

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The European stag beetle *Lucanus cervus* has a reportedly long life cycle. Recent rearing trials simulating natural conditions indicate that it can be three to four years. In order to obtain spontaneous field data, two artificial habitats were set-up in 2010. In March a stump was buried on a bed of wood chips and, at the end of June, two piles of fresh wood chips were set up. The immature stage was monitored in the wood chips during the second year, 2012. In February many larvae were found at various stages of development strongly suggesting two generations. The first-generation larvae, 2010, pupated after overwintering twice, confirmed by the presence of teneral imagos in late September 2012. The larvae of the second generation, 2011, developed gradually; by the end of July 2012 the majority had reached the third instar. A few immature larvae found at the end of September, proved that there was a third oviposition. In 2013 the first emergence holes appeared near the stump. Thus, females responded promptly to both habitats and a minimum three-year life cycle was obtained twice. The importance of a dynamic habitat management for the conservation of this species is discussed.

Introduction

The European stag beetle *Lucanus cervus* Linnaeus, 1758 (Coleoptera: Lucanidae) has become an object of intensive study across its range since it has been included as a species of special concern in the Bern Convention (Appendix III) 1982. Recently a review has summarised what is known so far about this elusive species (Méndez & Thomaes 2020).

Some progress has been made regarding the knowledge of the duration of their life cycle, in particular the larval stage which is the significantly variable part of the cycle (Harvey *et al.* 2011a). *Lucanus cervus* larvae have three instars, the third one, L3, has the longer duration (Fremlin & Hendriks 2014, Thomaes *et al.* 2022). The length of their development in rearing trials in outdoor enclosures, seems to be from two to three years (Hendriks & Méndez 2018, Rink & Sinch 2008, Thomaes *et al.* 2022). However, data from spontaneous colonisation is lacking; but could be obtained by taking advantage of the fact that, in favoured areas, this species seems to colonise promptly habitats such as buried fence posts (Smit & Hendriks 2005), fresh stumps (Tini *et al.* 2017), chips from hardwood trees (Fremlin 2018a, Hendriks & Van der Ploeg 2006), logs (Fremlin 2013) or compost heaps (Pfaff 1989). In fact, there is already one clear-cut example when, purely by chance, I observed a female stag beetle going inside a crack in the stump of a freshly cut false-acacia *Robinia pseudoacacia*. The first imagos emerged three years later (Fremlin 2010, 2012).

Therefore, in order to obtain more data, I have decided to

tempt the females with a couple of artificially set habitats: one stump buried with wood chips, like a miniature ‘Hirschkäfer-wiege’ (stag beetle cradle, ‘broedstoof’) (Tochtermann 1987), and a pile of fresh hard wood chips. The results of these experiments are reported below.

Methods

Field site

I set-up two field experiments in an urban area, Colchester, Essex, UK, (51.88° N, 0.88° E, 30 - 35 m elevation). This area is a well-known stag beetle hotspot (Fremlin 2009). The soil is a quick-draining light loam underlain by sand and gravel and the gardens are well established, over 100 years old.

Apple stump – On 16 March 2010 a large stump (approx. 40 cm diameter and 56 cm long) from a recently cut apple tree *Malus sylvestris* was rescued from a nearby garden, prior to be taken to the dump. It was buried in a bed of wood chips with just a bit of the wood showing. The wood chips were sourced from oaks at Highwoods Country Park, Colchester. The location was approximately 1 m away from an old stag beetle breeding site: a small holly *Ilex aquifolium* stump whose decomposition time had been extended by the addition of an oak *Quercus robur* log. This habitat was left undisturbed.

Wood chips – On 28 June 2010, when a large Norway maple *Acer platanoides* in a private garden in my road was being



1. Wood chip containers just before the first monitoring, 24.ii.2012. Note the cherry tree stumps on the left. Photo: Maria Fremlin
1. Houtsnippercontainers net voor de eerste monitoring, 24.ii.2012. Let op de kersenboomstronken aan de linkerkant.

trimmed, at my request a large load of wood chips was delivered to my drive. On the same day they were moved to the composting area in my back garden. Two containers (90×60×70 cm³, about 370 l each) used in the past to make leaf mould, were filled to the top with wood chips and covered up with large plastic bags to conserve the moisture. Note that these containers are next to two cherry trees *Prunus* stumps which are active breeding grounds for stag beetles (figure 1); they are about 17 m away from the buried apple stump in the adjacent garden.

The wood chips heated up promptly; occasionally some were removed from the left container for other experiments during the first year. Apart from that, they were left undisturbed until 24 February 2012, when they were monitored for the first time. Monitoring consisted of gradually removing the contents of each container on to a large plastic sheet, while setting aside the larvae, which were identified, and recorded for instar, head capsule and weight. At this stage I took the opportunity to study the development of the L2 *L. cervus* larvae. I set aside a cohort of L2 larvae in a 14 litre bucket filled with the mould, covered up with a large plastic bag, and placed it in the adjacent container, now empty; this sub-set experiment was monitored about monthly from March until September 2012. Initially thirteen larvae were set aside, average weight, 1.3 ± 0.3 g; but as at the next month monitoring two had vanished, eight more were sourced from the main container in case greater losses should be incurred. Setting aside these L2 larvae was a very fortunate move because from the end of May rats *Rattus* were very active in the adjacent container; this lasted several months despite setting up rat traps and poison. The bucket escaped their predation. In late September 2012, I monitored the main container for the second time, as described above, with addition that the layer of soil at the bottom was dug up to a spade depth to check for imagoes. At the end, the mould was put back in just one container, together with the all the larvae found.

The head capsule width was measured with digital callipers

to 0.01 mm accuracy; their weight was first recorded on a Salter electronic diet scale, model 1250, to 0.1 g, then with a Scalix CB-310 electronic scale, to 0.01 g accuracy.

Results - wood chips

First monitoring

On 24 February 2012, twenty months after the start of the experiment, the wood chips had decayed rather fast and were mostly a very dark mould; their volume had decreased by about 50% (figure 1). In total, I found 252 larvae, approx. 1 larva per 0.7 l of mould (table 1). The majority were *L. cervus* larvae, 191: L2 stage, 35; L3 stage, 156; 8 larvae were fatally injured in the process in spite of taking great care while handling the mould. Also present were 61 L3 *Cetonia aurata* larvae. These larvae are very distinctive; they have a very small head, short legs and a tendency to crawl on their backs when disturbed.

The weight of the *L. cervus* larvae had a very wide range: L2, from 0.6 to 2.4 g, average 1.4 ± 0.5 g (n=34); L3, from 2.0 to 13.3 g, average 7.1 ± 2.3 g (n=150) (figure 2); most of the L3 larvae with weights over 8.5 g had a rather yellow coloured flesh (n=45). This is an indication of maturity; they were certainly further developed than the lighter weight L3 larvae (figure 3).

L. cervus L2 development

The weight of the L2 larvae increased steadily and reached 2.3 ± 0.6 g (n=19) in early June, just before they started moulting (figures 4-5). By the end of July all the larvae had moulted; average head capsule changed from 5.2 to 9.7 mm, three died. In late September their average weight was 6.8 ± 1.2 g (n=16).

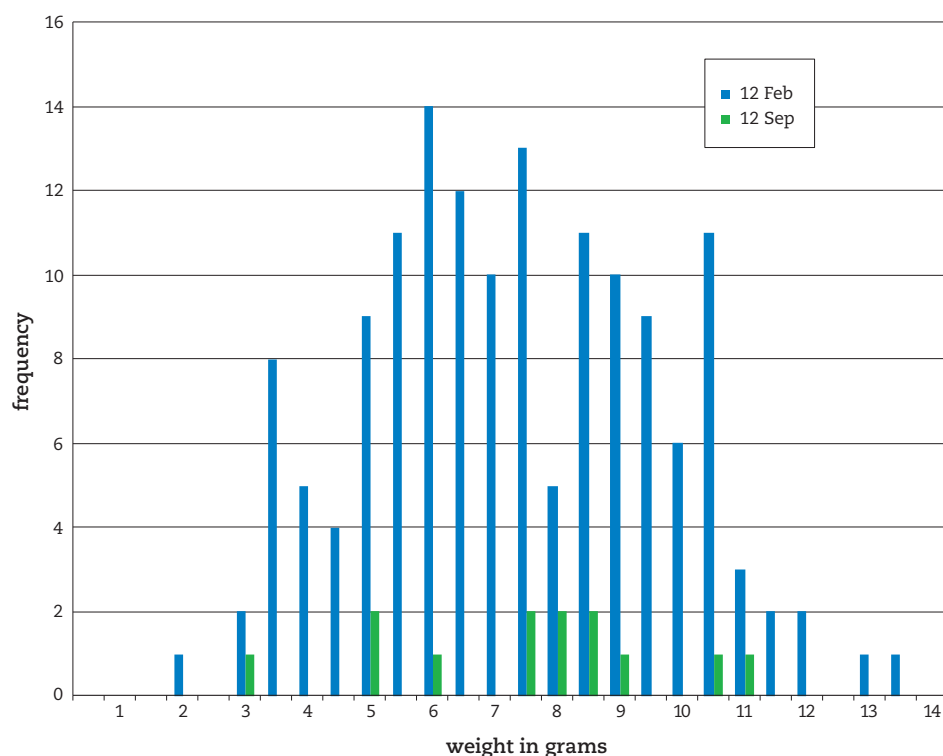
Second monitoring

By the end of September, the wood chips in the main container had decomposed even further and were now a homogeneous

Date	Species	L1	L2	L3	pupa	teneral imagos	Total
24.ii.2012	<i>L. cervus</i>		35	156			191
	<i>C. aurata</i>			61			61
28.ix.2012	<i>L. cervus</i>		1	13	1	9	24
	<i>C. aurata</i>		6	84		3	93

Table 1. Number of individuals of *Lucanus cervus* and *Cetonia aurata* found in the wood chips experiment set-up on 28 June 2010 and monitored on 24 February 2012 and 28 September 2012.

Tabel 1. Aantal individuen van *Lucanus cervus* en *Cetonia aurata* gevonden in het houtsnippersexperiment op 28 juni 2010 en gevolgd op 24 februari 2012 en 28 september 2012.



2. Weight distribution of *Lucanus cervus* third instar larvae monitored during 24 February (n=150) and 28 September 2012 (n=13).

2. Gewichtsverdeling van de larven van het derde stadium van *Lucanus cervus*, gevolgd op 24 februari (n=150) en 28 september 2012 (n=13).

dark mould. There was an abrupt decline of *L. cervus* larvae, mostly due to the predation by rats, only fourteen: 1 L2 stage, 0.20 g, and 13 L3 stage (table 1). The weight of the L3 larvae ranged from 2.60 to 10.90 g, average 7.27 ± 2.28 g (n=13) (figure 2). They were vastly outnumbered by *C. aurata* larvae: 90; all in the L3 stage, except 6 in the L2 stage and three teneral imagos (table 1). These larvae were far smaller when the rats appeared at end of May.

In the lower 10 cm of soil at the bottom of the container I found one dead pupa and nine teneral imagos of *L. cervus*: five males and four females (table 1 and figure 6). They apparently managed to evade the rats as L3 larvae perhaps because they had already moved down to the soil to pupate.

All individuals were put back in the container together with the remaining mould. This habitat was monitored for a few more years during which *L. cervus* larvae were always vastly outnumbered by *C. aurata* larvae, but it became extremely difficult to track their generations with a much smaller population.

Results - apple stump

In April 2011 the stump was dug up by a large animal at one end, no sign of larvae in the disturbed area. At that stage, the surface of the stump above the ground had lots of turkey tail *Trametes versicolor* fruiting bodies. Three emergence holes, typical of *L. cervus*, appeared in June 2013 (figure 7). After that the stump was no longer monitored because it became covered with vegetation.

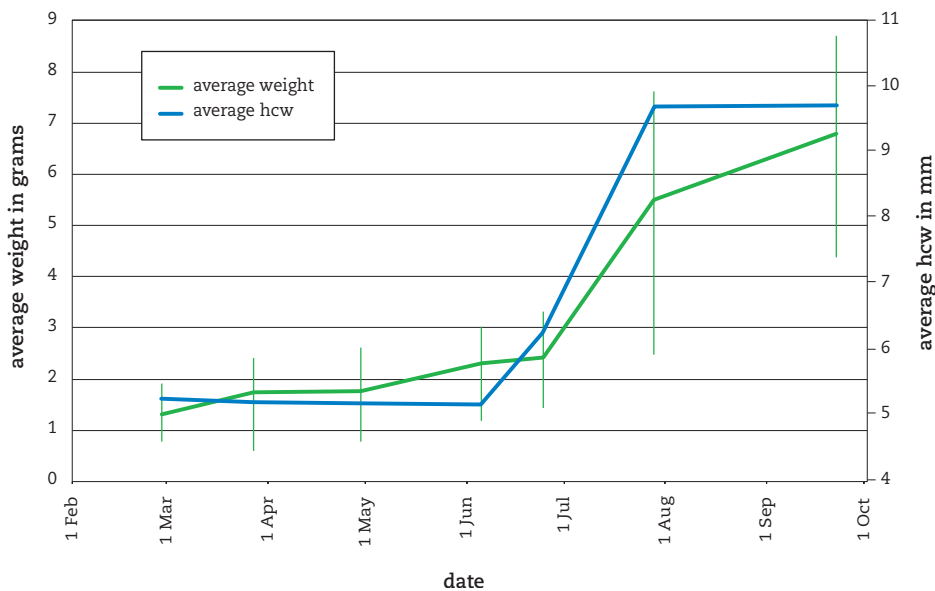
Discussion

Female stag beetles were tempted by both habitats, apple stump and wood chips, promptly as they were with the false-acacia stump (Fremlin 2012). In the wood chip habitat the first teneral *L. cervus* imagos appeared by the end of September, two years later; they would reproduce after overwintering in a quiescent state (Rink & Sinsch 2008) – leading to a minimum three-year life cycle from generation to generation. The first *L. cervus* emer-



3. *Lucanus cervus* larvae at a gradual stage of maturity (28.ii.2012); top row, second instar, L2; bottom row, third instar, L3. Note that their dark gut is the same colour as the mould, and the fat accumulation in the body of the larva in the bottom right. Photo: Maria Fremlin

3. *Lucanus cervus*-larven in oplopende stadia (28.ii.2012); bovenste rij, tweede stadiumlarve, L2; onderste rij, derde stadiumlarve, L3. Merk op dat hun donkere darm dezelfde kleur heeft als de schimmel en de vetophoping in het lichaam van de larve rechtsonder.



4. Average weight (green) and average head capsule width (blue) of a cohort of second instar *Lucanus cervus* larvae monitored about monthly from February until September 2012; moulting lasted from early June to the end of July 2012. The vertical lines indicate maximum and minimum weights.

4. Gemiddeld gewicht (rood) en gemiddelde kopcapsulebreedte (blauw) van een cohort van *Lucanus cervus*-larven in het tweede stadium die van februari tot september 2012 ongeveer maandelijks worden gevolgd; de vervelling duurde van begin juni tot eind juli 2012. De verticale lijnen geven maximale en minimale gewichten aan.

gence holes near the stump appeared on the third season – also implying oviposition in 2010 and confirming the minimum three-year duration.

The wood chip experiment was colonised by another species: *C. aurata*. This was to be expected because its range overlaps with *L. cervus* in Colchester and this species is more often tempted with wood chip piles (Davidson *et al.* 2020, Fremlin 2018b).

What attracts stag beetle females in favoured areas to such habitats? This question was first asked by Hawes (1998) but remains unanswered. Since then, it is known that the Lucanidae are partly fungivorous (Mishima & Araya 2016, Tanahashi *et al.* 2009) and have a mycangium (Tanahashi *et al.* 2010). The mycangium is a storage organ for symbiotic yeasts, which are vertically transmitted from the larva to the females soon after eclosion (Fremlin & Tanahashi 2015, Tanahashi & Fukatsu 2015). Later the yeasts are passed on during oviposition by the females by swabbing the area around each egg with their mycangium. As the larvae develop, the yeasts become free-living, and probably form an important component of their breeding sites mycobiome. Therefore, at this stage one can only conjecture that the combined volatiles of the fungi at the forefront of wood decomposition and the free-living mycangium symbiotic yeasts are the cues that the females follow.

At the same time, additional information was gathered about the *L. cervus* immature stage, discussed below.

First monitoring

The results of the February 2012 monitoring were totally unexpected: 191 *L. cervus* larvae. The question was: When did their oviposition/s occur?

Lucanus cervus females have twelve ovarioles per ovary, the ovarioles have a chain of eggs at a gradual state of development (Meyer 2016, Ritcher & Baker 1974). The eggs near the distal end of each ovariole develop first in one ovary, then after they are laid, the cycle is repeated with the other ovary. Subsequently, the process is repeated if circumstances allow. Therefore it seems to be no coincidence that an average of 24 eggs has been reported in the literature (Harvey *et al.* 2011a). In a rearing trial a female produced 20 eggs (unpublished), professional breeders report 30-50 eggs (Lai & Ko 2008), others even more (A. Thomaes personal communication). The presence of several L2 larvae, 35, and a significant number of immature L3 larvae, around 100, indicates that several females must have oviposited in the wood chips the previous year, 2011. But the presence of a sig-

nificant number of mature L3 larvae, 45, was a big surprise. Did this indicate that there was oviposition soon after the start of the experiment? The L2 development experiment and the monitoring at the end of September gave a clear answer to this question.

Second instar development

The cohort of L2 larvae set aside in late February reached the L3 stage by the end of July and in late September had an average weight of 6.8 ± 1.2 g ($n=16$). *Lucanus cervus* L3 larvae carry on growing until the winter sets in (Thomaes *et al.* 2022) and, quite likely, before then they could have reached weights ≥ 8.5 g. This indicates that of the L3 larvae found in February, the low weight larvae had overwintered in that stage once, but the mature L3 had overwintered twice. The development of the L2 stage was protracted and overlapped with the L3 stage. Therefore, there was oviposition in 2010 by more than one female, confirming that at that time they were actively searching for oviposition sites (Fremlin 2009), possibly even when the chips were still warm.



5. *Lucanus cervus* larvae (24.vi.2012): left, second instar, L2, next to a freshly moulted third instar, L3. Foto: Maria Fremlin

5. *Lucanus cervus*-larven (24.vi.2012): links, tweede stadium, L2, naast een vers vervelde derde stadium, L3.



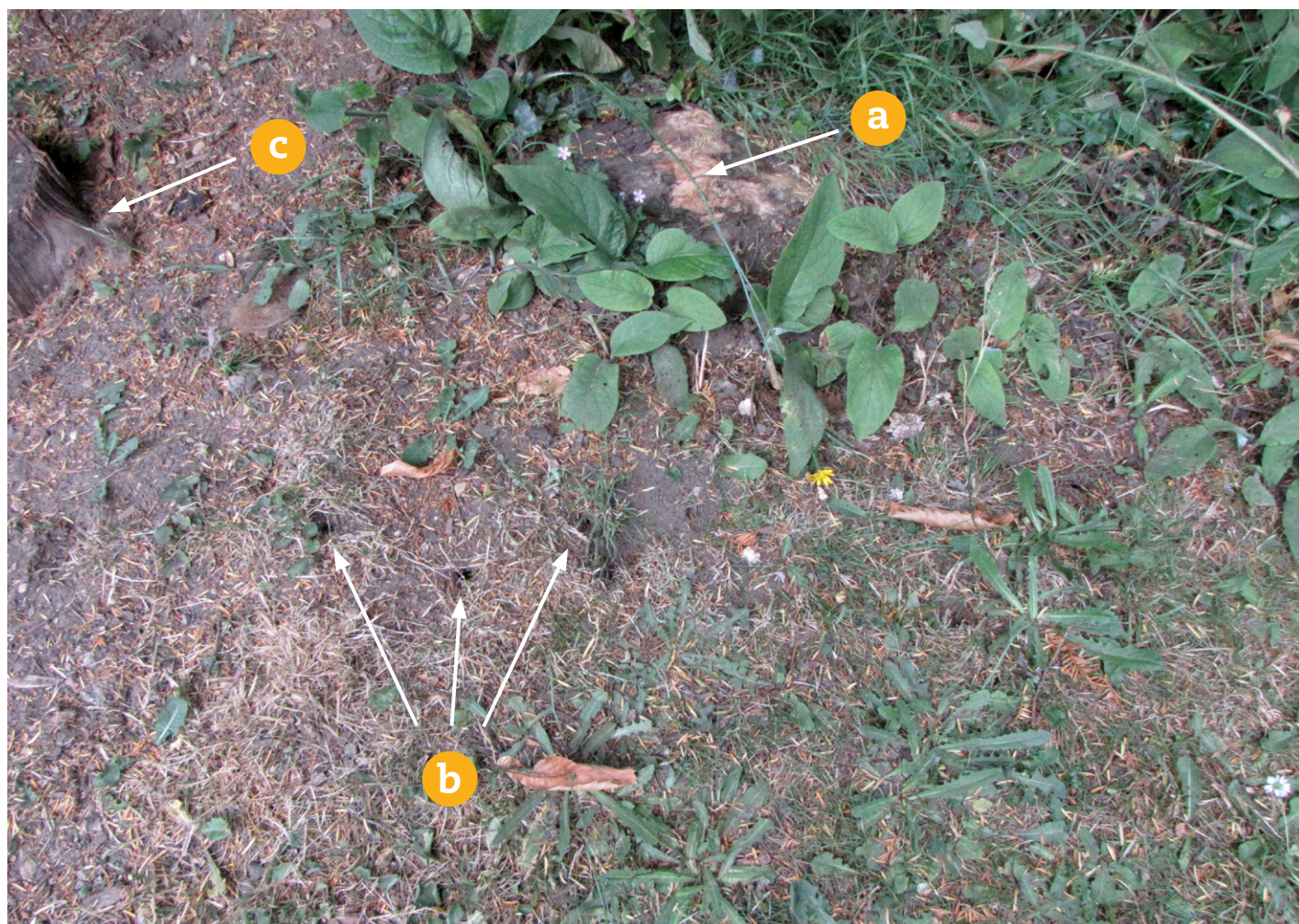
6. Teneral individuals of *Lucanus cervus*, five males and four females, and aborted male pupa. Lower left, *Cetonia aurata* imago's. Photo taken on 29.x.2012. Photo: Maria Fremlin
6. Verse individuen van *Lucanus cervus*, five mannetjes en four vrouwtjes, en geaborteerde mannelijke pop. Linksonder, *Cetonia aurata*-imago's. Foto gemaakt op 29.x.2012.

Second monitoring

By the end of September there was an abrupt decline of *L. cervus* larvae because of the rats' predation (table 1). Despite that, several larvae were able to pupate successfully after their arrival in May. Perhaps by then some mature larvae had already left the mould to pupate in the ground or the rats did not burrow too

deep. The presence of nine teneral imago's proved conclusively that the field duration of the immature stage for the first generation was two years, leading to a three-year life cycle.

The fact that there was one L2 larva, plus a few immature ones, indicates that there was oviposition for the third time, 2012, but since it was not possible to source more wood chips it



7. Buried apple stump (a) close to an oak log (c) and emergence holes (b) downwards from it, 30.vi.2013. Photo: Maria Fremlin
7. Begraven appelstronk (a) dichtbij een eikenhouten stam (c) en uitkomstgaten (b), 30.vi.2013.

became increasingly difficult to follow up the second and third generations in such an impoverished habitat.

Regarding *C. aurata*, their larvae were far more numerous, all from oviposition in the current season. They seem to have escaped the rats' predation probably because they were still too small when they arrived. The presence of three imago suggests that, like the mature *L. cervus* larvae, they also had started making their pupal chambers when the rats arrived (Fremlin 2020).

Predation

As been mentioned before, both habitats were predated. In the 2011 Spring an animal dug near the apple stump, most likely a fox *Vulpes vulpes*, probably in search of larvae. Foxes with their acute senses can easily detect stag beetle breeding grounds, because the larvae stridulate (Harvey et al. 2011b, Sprecher-Uebersax & Durrer 1998) and they might have a characteristic scent. There are a lot of foxes in this urban area and at that time of the year they are rearing their cubs and food can be very short. In the past they have upturned the log on top of the holly nest to get at the larvae underneath. They also prey on the imago active above the ground.

The wood chips experiment was particularly vulnerable to rodents; rats almost destroyed it. Rats like foxes, have acute senses and there were far too many larvae in a readily accessible container. Over the years, rats have occasionally visited that composting area even though no animal products are composted there as a rule.

Wood mice *Apodemus sylvaticus* are settled residents in the containers; their aggregations of gnawed nuts and pips are very common. Not sure if they predate on larvae; but the larvae of both species are regularly found in this composting area, albeit in very small numbers, in particular *L. cervus*. House mice *Mus musculus* once ate all the *C. aurata* larvae (n=13) in a terrarium indoors thus destroying an experiment.

Conclusion

These experiments provided direct field data about the life cycle duration – a minimum of three years in Colchester, UK. The development of the three instars is very variable possibly reflecting a lengthy oviposition period. The first instar, L1, has the shortest duration, the second instar may last until July of the following year. All larvae overwinter for the second time in the third instar, L3. The larvae enter the pre-pupation stage at about the same time that the imago become active above the ground. By mid-August the teneral imago are fully formed. They overwinter in a quiescent stage and become active above the ground in late May-early June; after reproducing they die. Possibly in a shadier place or cooler years, or geographical locations with a cooler climate, the duration of the larval stage might be longer (Rink & Sinsch 2008, Thomaes et al. 2022).

This study confirmed that *L. cervus*, in a favoured area, can respond promptly to newly created habitats. This is supported by the fact that this saproxylic species thrives in areas which are actively managed (Bowdrey 1997, Fremlin 2013, Hachtel et al. 2007, Percy et al. 1998, Rink & Sinsch 2006, Tini et al. 2017). The impact of active habitat management in the soil mycobiome needs to be studied further because it seems to be crucial for their conservation. At the same time, when creating stepping-stone habitats with logs, adding wood chips and inoculating the area with the soil and mould from active oviposition sites in order to pass on the mycangium symbiotic yeasts might increase the chances of tempting such a 'honkvast' (stay at home) beetle to disperse.

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Summary

De levenscyclus van het vliegend hert *Lucanus cervus* beslaat in het veld minimaal drie jaar (Coleoptera: Lucanidae)

Van het vliegend hert *Lucanus cervus* worden lange ontwikkelingscycli gerapporteerd. Kweekexperimenten waarbij natuurlijk omstandigheden werden nagestreefd, laten zien dat het de kever drie of vier jaar kan kosten om volwassen te worden. Om dit in het veld te meten, werden in 2010 twee kunstmatige leefgebieden ingericht. In maart werd een stobbe van een appel ingegraven op een laag van houtsnippers en eind juni werden twee hopen met verse houtsnippers van Noorse esdoorn aangelegd. De plekken werden spontaan gekoloniseerd door het vliegend hert. De onvolwassen stadia in de houtsnipperhopen werden in 2012 gemonitord. In februari werden vele larven van verschillende stadia gevonden, wat duidde op twee generaties. De eerste generatie larven (uit 2010) overwinterde twee keer, hetgeen bevestigd werd door verse volwassen dieren eind september 2012. De larven van de tweede generatie (2011) ontwikkelden geleidelijk; eind juli 2012 had het grootste deel het derde larvenstadium bereikt. Een paar onvolwassen larven werden eind September gevonden, hetgeen aangaf dat er een derde keer eieren waren afgezet. In 2013 werden de eerste uitkomstgaten gevonden bij de appelstobbe. Zo reageerden vrouwtjes snel op beide leefgebieden en werd tweemaal een levenscyclus van minimaal drie jaar aangetoond.

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