The typical development cycle of the solitary bee *Colletes halophilus*

Marinus J. Sommeijer
Jos Neve
Chiel Jacobusse

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Nest building and larval development of the solitary bee *Colletes halophilus* were studied in a large nesting aggregation in 'Het verdronken land van Saeftinghe' ('sunken land of Saeftinghe', a tidal marsh in the province of Zeeland), The Netherlands. We collected brood cells at monthly intervals for a period of one year to analyze seasonal development of the juvenile stages. *Colletes halophilus* was found to overwinter in young and more advanced larval stages. Larval development was resumed in April. A quantitative analysis over the months shows the short duration of prepupal and pupal stages. Nest building and larval development of *C. halophilus* were compared with those of another closely observed *Colletes* species, *C. daviesanus*. The comparison reveals remarkable interspecific differences whose possible function are discussed. We present photographic documentation of nest building, stages of cell provisioning, larval and pupal development, adult emergence and mating of *C. halophilus*.

Introduction

The solitary bee *Colletes halophilus* Verhoeff (Apidae, Colletinae) occurs along the coasts of England, Germany, The Netherlands, Belgium, and Atlantic France (figure 1). Salt marshes and dunes are its habitat. *Colletes halophilus* builds nests, sometimes in large aggregations in the soil. Such aggregations occur in areas where sea aster (*Aster tripolium*) is abundant. Applying a palynological method for analysis of larval food from different aggregations, we earlier confirmed that *A. tripolium* is the major pollen source for the larval food in the aggregations in the province of Zeeland, The Netherlands. However, adult females and males were also found visiting other flowers (Sommeijer *et al*. 2009).

Colletes females spread glandular secretions on the wall of the excavated brood cells. After polymerization this forms a cellophane-like cell wall, typical for this group of bees (Michener 2000). The brittle and translucent cell can be readily separated from the soil. The provisions of most species of *Colletes* are a suspension of pollen in floral nectar and glandular secretion (O'Tool & Raw 1999, Michener 2000, Sommeijer *et al*. 2009).

The prepupa or the teneral adult is the overwintering stage for most solitary bees and the pupal stage is generally of short duration. Yocum *et al*. (2006) reported how the thermal history of prepupae of *Megachile rotundata* (Fabricius) influences post-diapause development into the pupal stage.

During the early spring of both 2004 and 2005, we first observed overwintering young larvae. Since this had not been previously reported as a general feature for species of this genus (Westrich 1990, Esser 2004), we undertook a series of observations on juvenile development to cover the period from oviposition to adult emergence. In this paper we present the results of these observations and in addition describe nest building, provisioning, emergence and mating.

Sites and sampling method

The observations were carried out in the nature reserve 'Het Verdronken Land van Saeftinghe' ('sunken land of Saeftinghe', a tidal marsh in the province Zeeland), where there is one of the largest aggregations of *C. halophilus* in The Netherlands (figure 2). General observations on *C. halophilus* behaviour were made from 2004 to 2009 and temporal larval development was quantitatively recorded during one season. From the commencement of adult activity in August 2005 regular samples of brood cells were collected on: 2 October and 7 November 2005, and 9 January, 3 March, 10 April, 7 May, 17 June and 14 July 2006. In September 2005, we marked plots of about 1 m2 in zones of the aggregation with a high density of nests. This allowed for the effective sampling of cells during winter, spring and summer with minimal disturbance to the aggregation. Additional observations on larval development were made in intervening months and the previous and ensuing years.

Larval development

Larval development was recorded by taking pictures of all the cells from each monthly sample. The brood cells of a sample were arranged in small, vertical, proximal batches close to each other, with the tops removed, to obtain a clear view on the inside of the cell. For the recording of juvenile development we distinguished between the following 'stages': (1) 'egg' (including first stage larva, as long as still attached to the cell wall), (2) 'young larva' (floating on larval food, reaching less than 50% of cell diameter), (3) 'advanced larva' (reaching more than 50% of cell diameter), (4) 'prepupa' (or defecated larva), and (5) 'pupa'.

1. Female *Colletes halophilus* at the nest entrance, carrying pollen on the hair-brushes (scopae) of the hind femora and coxae. Photo: M.J. Sommeijer
1. *Colletes halophilus* vrouwtje beladen met stuifmeel bij de nestingang. Het stuifmeel wordt getransporteerd in specifieke haarborstels ('scopae') die bij deze soort voorkomen onder de thorax en op de basale delen van de achterpoten

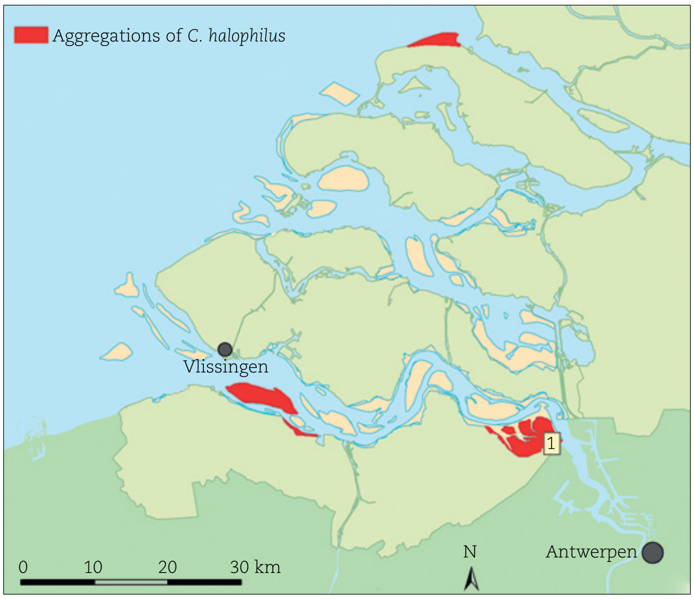
Our use of these 'stages' of larval development was based on the fact that the precise larval stages (instars) could not be determined. Shed larval skins are difficult to observe, particularly in cells that are kept intact. After observation, most cells could be returned to their natural habitat for further development. The results of the development stages in each of the samples are presented in figure 3 where the number of cells for each sample is given. Other behaviours of larvae, e.g. silk spinning and defecation, were analyzed through microscopic observation of live larvae in opened cells.

Results

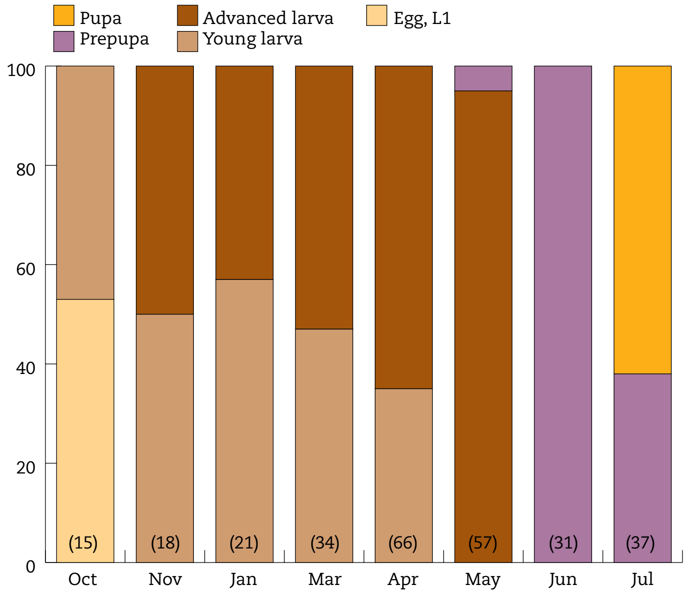
Nest building (observations 2004-2009)

Generally, adults of *C. halophilus* started to emerge from the soil in mid-August. Adult activity was synchronized with the flowering of sea aster. Adult flight activity could be delayed or interrupted for several weeks due to unfavourable weather. Nest building and foraging continued until mid-October.

The exit of the nest had a crater-shaped tumulus of excavated sand. Depending on the inclination of the surface, the tumulus was more or less bisymmetrical (figure 4a). In the



2. Southwest Netherlands, province of Zeeland, showing the important aggregations of *Colletes halophilus* (in red). 'Het Verdronken Land van Saeftinghe' is labelled 1.
2. Kaart van zuidwest Nederland (Zeeland) met de belangrijke aggregaties van *Colletes halophilus*. 1: 'Het verdronken Land van Saeftinghe'.



3. Monthly frequency distribution of the various development stages per sample. Sample sizes (numbers of cells) are given in parentheses.
3. Frequentieverdeling van de ontwikkelingsstadia in de cellen op basis van de maandelijkse monsters. Het aantal cellen per monster staat tussen haakjes.

4. *Colletes halophilus* nest building. (a) A freshly excavated crater 'tumulus' of sand around the nest entrance of *Colletes halophilus*. On inclined surfaces this has a bisymmetric conical shape, whereas on horizontal surfaces it is radially symmetrical. After rain or wind the excavated sand may be washed away. (b) An inverted block of soil viewed from the underside to show terminal cells of the same nest in situ. These cells are at the end of lateral branches of the main vertical tunnel and most cells of one nest are at the same depth. A comparison with figure 4c shows the exact orientation of the cells in the nest. (c) Side view of cells at the end of lateral branches of the major burrow. (d) Protruding extension of the cell wall which is always considerably higher up than the multi-layered cover of the cell contents. (e) The rare case of two cells in the same tunnel. The bottom of the upper cell (right) is partly enclosed in the upward protruding extension of the collar of the lower cell (left). This connection is very loose and such cells can easily be separated. (f) Cells of distinctly different sizes. The larger cells usually contain females and the smaller ones males. (g) After the emergence of the adult bee, the empty cell disintegrates over a period of time. Such empty cells often become filled with sand. Photos: M.J. Sommeijer

4. *Colletes halophilus* nestbouw. (a) Verse kratervormige 'tumulus' van uitgegraven zand rond nestingang van *Colletes halophilus*. Deze tumulus is tweezijdig symmetrisch vanwege de hellende bodem. Op horizontale ondergrond is de tumulus ronder van vorm. Door regen en wind kan de krater snel verdwijnen. (b) De bodems van enkele cellen, behorend tot hetzelfde nest, in een omgekeerd blok aarde, van onderaf bezien. Deze cellen zijn gebouwd aan het uiteinde van zijgangen van de vertikale hoofdgang. De meeste cellen van een nest zijn ongeveer op eenzelfde diepte. Figuur 4c completeert het beeld van de positie van de broedcellen aan de einden van zijgangen van de hoofdtunnel. (c) Cellen aan het eind van zijgangen van de hoofdgang van het nest, van opzij gezien. (d) De cellen hebben een verhoging van de zijwand die uitsteekt boven het meerlagig deksel van de cel. Deze verlenging van de celwand omhult een prop aarde waarmee de tunnel boven het celdeksel is gevuld. (e) In zeldzame gevallen zijn twee cellen tegen elkaar aan in dezelfde gang gebouwd. De cellen vallen los van elkaar als de omgevende aarde wordt verwijderd.
(f) Er is een duidelijk verschil in grootte van de cellen. In het algemeen zijn de grote cellen voor vrouwtjes en de kleinere zijn altijd voor mannetjes. (g) Nadat de adulte bij uit de cel is gekropen blijft het overblijfsel van de lege cel nog enkele weken intact. De lege cel is dan gevuld met zand.

centre of the aggregation the soil layer was dark with roots of plants up to 10-15 cm deep. Cells were mostly at a depth of around 20 cm in the deeper layer of pure sand (figure 4b). The deepest cells were at about 25 cm. Nearly all cells were built at the end of lateral burrows branching from the main vertical tunnel (figure 4c). Eveline Rooijakkers (personal communication) who filled nest tunnels with plaster of Paris for subsequent excavation and measurement, further confirmed the typical nest architecture of *C. halophilus* with single cells at the end of lateral tunnels.

Completed cells, provisioned and containing eggs, had a cover of various layers of cellophane-like material. The lining of the lateral cell wall extended upwards beyond the cover and so included a plug of soil, normally enclosing the burrow above the cell (figure 4d). Very rarely cells were constructed on top of each other in the same burrow (<0.5% of cases). In this case the cells appeared to be tightly attached to each other, but after removing adhering sand, they separated easily (figure 4e). The bimodality in cell size (small 'male' and large 'female' cells) was distinct (figure 4f). The phenomenon of offspring sex determination that is controlled by the female is discussed in Rooijakkers & Sommeijer (2009), see also Esser (2004).

Stages of development in monthly samples and related observations

August-October In August, we still found some pupae of the former season together with just provisioned and oviposited cells. In August, September and October we encountered the residues of old cells from which bees had eclosed and that were now

5. *Colletes halophilus* development stages. (a) A cell where provisioning has yet to be started. This can be observed in the early weeks of the period of flight activity. (b) A cell containing the first part of the larval food provisions. (c) A cell with the egg deposited against the wall just above the surface of the larval food. Young larvae remain attached to the wall for some time. The emerging larva on this photo bends toward the food before contact with the wall is lost. (d) October cells contain either eggs or young larvae (length <50% of cell diameter). (e) November cells with either young larvae (length <50% of cell diameter) or advanced larvae (>50%). Young and advanced larvae are present in about the same numbers. (f) January cells contain either young or advanced larvae, in similar proportions as in November and March. (g) April cells with either young or advanced larvae, 65% of the larvae at the advanced stage. Larval development is now progressing. (h) June cells contain only prepupae. (i) July cells containing 38% in the prepupal stage (example on the left). The numerous pupae are all young (not tanned; top). In August cells all pupae are fully tanned (bottom). Photos: M.J. Sommeijer

5. *Colletes halophilus* ontwikkelingsstadia. (a) Een cel waar de bevoorrading nog moet beginnen. Dit stadium kan aangetroffen worden in de eerste weken van de vliegactiviteit. (b) Een cel die nog maar een deel van het larvale voedsel bevat. (c) Het ei wordt tegen de celwand afgezet net boven het larvale voedsel. De larve van deze foto komt net uit het ei en buigt zich naar het voedsel toe. Daarna komt de larve los van de wand. (d) Een voorbeeld van de cellen in oktober. Er zijn dan alleen eieren en jonge larven. De lengte van de gekromde larven is <50% van de celdiameter. (e) Enkele cellen van november: jonge larven (<50% van de celdiameter) en gevorderde larven (>50%) aanwezig in ongeveer gelijke aantallen. (f) De cellen in januari bevatten uitsluitend jonge en gevorderde larven, in ongeveer gelijke aantallen. Dit komt overeen met de ontwikkelingsstadia van november en maart. (g) Enkele cellen uit april, met alleen jonge en oudere larven. Maar deze maand maken de oudere larven 65% uit van het totaal. De ontwikkeling gaat nu weer verder. (h) Alle cellen van het juni monster bevatten prepoppen. (i) In juli is 38% van de juvenielen nog in het prepopstadium (links). De talrijke poppen zijn nog erg jong en niet uitgekleurd (bovenste helft). In augustus zijn alle poppen donker gekleurd (onderste helft).

filled with sand (figure 4g). Cells where provisioning yet had to be started and those that were still partly provisioned are illustrated in figures 5a and 5b. Ovipositing females attach the egg to the cell wall just above the larval food, but not touching the food mass. Upon hatching, the first instar bends downwards and can now reach the food store (figure 5c). Soon after this, the larva detaches from the wall and is from now on floating on the larval food, to feed and develop in this position for several months. Cells of the October sample contained eggs, first-stage larvae and young larvae exclusively (figure 5d).

November, January, March, April In the November sample we encountered only larval stages, both young and more advanced (figures 5e). It is remarkable that the January (figure 5f), and March and April (figure 5g) samples, were exclusively of these stages. Young larvae and advanced larvae occurred in similar proportions in the samples of November, January and March ($\chi^2 = 0.533$, d.f. = 2, P = 0.77). In April, 65% of the larvae were in the advanced stage, compared to November, January and March ($\chi^2 = 3.543$, d.f. = 1, P = 0.006) (figure 3).

May By May all the larvae were in the advanced stage, and prepupae were already present in 5% of the cells.

June, July, August In June all cells contained prepupae (figure 5h). Pupae appeared first in the July sample, but instantly in considerable numbers (38% prepupae and 62% pupae). In July, the pupae were still young and non-pigmented (figure 5i). A representative sample was not taken in August since a number of adults had already emerged and recently oviposited cells were present. The pupae that we found to be still present in this month were all fully pigmented (figure 5i).

6. Faecal cell coating. (a) The dark brown coating of the inner cell wall extends high up but does not reach the cover of the cell. (b) The coating extends to form a ceiling over the pupa. There is a space between the faecal-ceiling and the cell cover and there is always a hole in the middle of that faecal-ceiling. Photos: M.J. Sommeijer

6. De celwandbekledende laag ontlasting. (a) De donkerbruine laag reikt hoog langs de zijwand van de cel, maar komt niet tot aan het celdeksel. (b) De ontlasting is als een plafond over de pop gevormd. Er is altijd ruimte tussen het fecale plafond en het celdeksel en er is altijd een venster in het midden van het plafond.

Final larval stage, defecation and pupation

In May, a small proportion (5%) of the mature larvae commenced defecation. At this stage, the larva (now called a prepupa; Michener 2000) becomes a little smaller and less flaccid with the segments more constricted. In the mid-June sample all larvae had developed into prepupae.

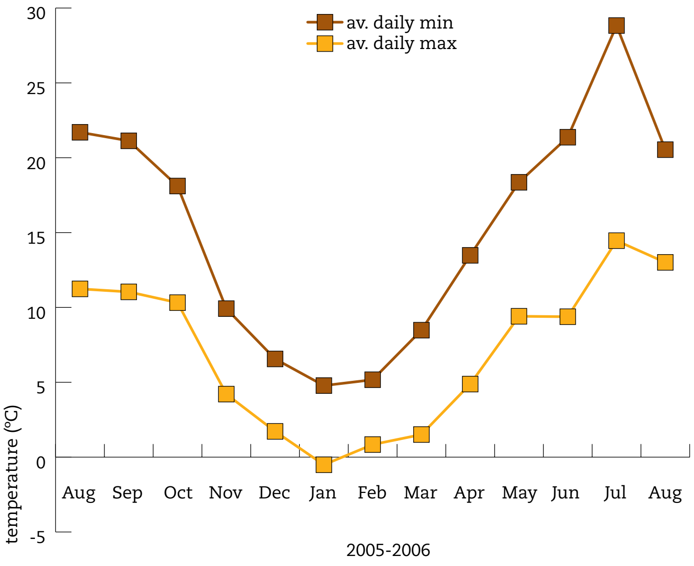
The faecal pellets are deposited in strings that form a framework, initially against the bottom and the lateral walls of the cell. At the sides of the cell this takes the shape of a thick, opaque layer around the larva. The faecal material on the sides of the cell extends much further up towards the top of the cell than the level attained by the liquid larval food at the onset of larval feeding. This, together with the dark shade of brown which the faecal lining quickly develops in, gives the cell a distinct outside appearance compared to one containing an early juvenile stage (cf. figures 5c and 6a).

Faecal material is also deposited as a ceiling above the larva, but not attached to the roof of the cell, leaving a free space between the cell cover of layered cellophane-like material and the faecal ceiling (figures 6a and 6b). There was always a central opening in the faecal ceiling through which the prepupa could be seen in opened cells (figure 6b).

Silk spinning was weak but evident, the faecal pellets being interwoven with fibres of silk. We could not establish precisely the very onset of spinning and defecation, but clearly observed the spinning of fibres through very recently voided faecal material.

7. (a) 'Mating ball', several males simultaneously attempt to mate with the same female. (b) Females are able to move and even to fly short distances with an attached male during copula. Photos: M.J. Sommeijer

7. (a) Meerdere mannetjes proberen elkaar weg te duwen om een goede paringspositie op het vrouwtje te verkrijgen. (b) Vrouwtjes zijn in staat om met een gekoppeld mannetje te lopen en zelfs kort te vliegen



8. Maximum and minimum field temperatures (°C) from October 2005 until July 2006. Values represent monthly averages of daily maximum and minimum temperatures (based on data KNMI [= Royal Dutch Meteorological Institute] station Westdorpe, 7 km from Saeftinghe).
8. Gemiddelde temperatuur in de onderzoeksperiode oktober 2005 – juli 2006. De waarden geven de maandelijkse gemiddelden voor maximum- en minimumdagtemperatuur (gebaseerd op gegevens van het KNMI-station Westdorpe, 7 km van Saeftinghe).

Emergence and mating

The weather conditions were poor in the period of emergence but nevertheless, protandry was evident, male emergence being only a few days before that of the females. Usually, in the first days of the emergence period, males were seen patrolling in large numbers over the ground at a height of only 5-20 cm in search for females. In years with favourable weather conditions, they were observed as a 'blanket' of bees flying around with intense activity. Such males rapidly seize females that have just emerged. Visual stimuli appear important for the very first contact, since males were also observed to seize other objects than females, e.g. other males. Odour may play a role in the following steps of the behavioural sequence of mating. Receptive females may be simultaneously seized by a number of males. These males compete actively for the proper mating position on the female by trying to push other males to the side. This results in 'mating-balls', clusters of males on one female (figure 7a). On favourable days we observed up to five mating-balls per m^2. A female in copula appeared to be able to walk with the attached male for some distance. She even could fly with the coupled male for a distance up to about 2 m (figure 7b). As soon as females had mated, their attractiveness to males changed. Males only briefly seized such non-receptive females.

Discussion

A major conclusion is that *C. halophilus* overwinters in early stages of development, i.e. as larvae. Larval development is fully resumed after the winter period. The prepupal and particularly the pupal period are of short duration. Many other species of solitary bees overwinter in the prepupal stage and some as adults. The detailed observations of Esser (2004) on *C. daviesanus* in Germany facilitate a comparison of the life cycles of *C. halophilus* and *C. daviesanus*. The food-plant of *C. daviesanus* is *Tanacetum vulgare*, which flowers in July and August. A major difference with *C. halophilus* is that the development of *C. daviesanus* has shifted forward in time and it overwinters as a prepupa.

The observed overwintering of *C. halophilus* as young juveniles cannot be explained as merely the consequence of an occasional severe winter. During the winter period of our sampling period (2005-2006) the weather was mild (figure 8); but of course larval development will be retarded in colder winters (see also Yocum *et al.* 2006).

Michener (2000) indicates that cocoon spinning is lost in most short-tongued bees, which are often protected by the cell lining secreted by the mother bee. *Colletes daviesanus* does not spin a cocoon (Esser 2004), neither does *C. halophilus* spin a typical cocoon. The clearly observed spinning may have a function in the weaving of strings with faecal pellets into a thick protecting mass of faecal material around the larva.

Another interspecific difference was apparent in nest building. Brood cells of *C. daviesanus* are built in linear rows in the same burrow, whereas cells of *C. halophilus* are built at the end of lateral burrows. Males and females of *C. halophilus* emerge from cells that are built in loose sandy soil and do not need to re-use old nest tunnels. They can dig their own emergence exit by burrowing through the sand directly above their cell. In this species protandry is therefore not constrained by nest architecture. This may be different in *C. daviesanus*. Esser (2004) reports that this species nests in hard substrates (even excavates burrows in 'Sandstein'). We may conclude then that differences in nest building and associated behaviours between these two species are related to characteristics of their respective nesting substrates.

The typical overwintering in the larval stage of *C. halophilus* in conjunction with the later flowering period of the food plant, is possibly due to the generally mild winters in the coastal Atlantic region where this species occurs. The evolutionary choice of *C. halophilus* for the late-blooming sea aster as a food plant, determines habitat, including soil type, as well as the timing of adult activity and possibly larval development in this species. This suggests that bee species feeding on other plants may evolve different nest architecture as well as developmental phenology. Further comparative studies on relations between life cycle, food plants and nest-architecture are needed to elucidate this.

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Samenvatting

De typische ontwikkelingscyclus van de schorzijdebij, *Colletes halophilus*

Volgend op onderzoek naar het larvale voedsel, het foerageergedrag en het bouwen van specifieke mannelijke en vrouwelijke broedcellen, beschrijven we nu de levenscyclus van de schorzijdebij, *Colletes halophilus* Verhoeff. De Colletinae (zijdebijen) zijn solitaire bijen met een korte, tweelobbige tong die dient om kliersecreet uit te smeren over de binnenwand van de uitgegraven celholte. Het materiaal polymeriseert tot de voor deze bijen typische perkamentachtige celwand. Vrouwtjes transporteren stuifmeel in opvallende 'scopae' (gespecialiseerde haarvelden) vooral op de femur en tibia van de achterpoten, maar ook op de metasomale sterna en de zijkant van het propodeum. Het onderzoek naar de larvale ontwikkeling en de wijze van overwinteren is uitgevoerd in het Verdronken Land van Saeftinghe (Zeeland). Hier verzamelt *C. halophilus* bijna uitsluitend pollen op zulte (zeeaster), *Aster tripolium*. De resultaten betreffende de nestbouw zijn verkregen door waarnemingen in de periode 2005-2010. Van augustus 2005 tot juli 2006 werd specifiek het verloop van de larvale ontwikkeling bestudeerd: maandelijks werd een aantal broedcellen opgegraven om de vordering van de juveniele stadia te bekijken. Hiervoor werden alle cellen van een maandelijks monster geopend en van bovenaf in groepjes gefotografeerd. De vliegperiode is van midden augustus tot begin oktober. Broedcellen worden door het vrouwtje één voor één gebouwd, van larvaal voedsel voorzien en belegd. De cellen liggen meestal alleen aan het eind van een zijgang van de centrale verticale tunnel (trosvormig nest). De cellen van één nest reiken vaak tot eenzelfde diepte. De meeste cellen bevonden zich op ongeveer 20 cm in de grond. Het ei-stadium duurt ongeveer een week. De larven groeien langzaam. Het is opmerkelijk dat bij deze soort slechts jonge en halfvolgroeide larven in de cellen overwinteren. Na de winter groeien de larven verder en pas in juni vindt de overgang naar het 'prepop'-stadium plaats. Dit is het moment waarop de volgroeide larve de ontlasting afscheidt in een ketting van 'fecale korrels'. Hoewel er geen duidelijke cocon voorkomt, worden er wel draden gesponnen, waarmee de ontlastingslierten worden verweven en in een compacte laag tegen de celwand worden geplakt. Cellen met prepoppen of poppen zijn van buitenaf goed te herkennen. Door de doorzichtige celwand zien we dat de bruine laag ontlasting veel hoger langs de wand reikt dan de gele massa van larvaal voedsel in cellen met de jongere stadia. De verpopping begint eind juli. Medio augustus kunnen de bijen uit de grond kruipen. Jürgen Esser (2004) heeft voor *C. daviesanus* (boerenwormkruidbij) in Duitsland een beschrijving gegeven van de ontwikkeling, die zich leent voor vergelijking. Het verloop in de tijd van de larvale ontwikkelingscyclus van *C. halophilus* blijkt op belangrijke punten te verschillen. Een verschil is dat *C. daviesanus* als prepop overwintert. Dit is een meer algemene manier van overwinteren voor solitaire bijen. Verder is ook de nestbouw van *C. daviesanus* verschillend, namelijk met gangen waarin de cellen achter elkaar worden gebouwd. Deze soort nestelt in harde substraten en kan zelfs nesttunnels 'boren' in zandsteen. Wij veronderstellen een samenhang tussen genoemde verschillende nestbouwtypen en de kenmerken van de bodem waarin nesten gegraven worden. *Colletes halophilus* heeft zich in de loop van de evolutie gespecialiseerd op de laatbloeiende zulte. Dit is bepalend voor habitat en vliegtijd en mogelijk dus ook voor de larvale ontwikkeling. Bij bijensoorten die op andere planten en in andere perioden van het jaar fourageren kunnen andere nestarchitectuur en andere larvale ontwikkelingsschema's ontstaan. De typische overwintering van *C. halophilus* in de vorm van larven kan samenhangen met het exclusief voorkomen van deze soort langs de Atlantische kust, waar de winters gematigd zijn.

Marinus J. Sommeijer
Utrecht University
Behavioural Biology
PO Box 80.086
3508 TB Utrecht
The Netherlands
m.j.sommeijer@uu.nl

Jos Neve & Chiel Jacobusse
Stichting Het Zeeuwse Landschap
Postbus 25
4450 AA Heinkenszand
The Netherlands