Chapter

The Nymph Architect of the Cicada *Guyalna chlorogena*: Behaviours and Ecosystem

Claude François Béguin

Abstract

At the beginning of the last year of its larval life, the nymph of Guyalna chlorogena builds, from a vertical well, which is the result of a verticalization process from a deep horizontal gallery, a clay turret 20 to 40 cm high which appears as a regulating device of the physico-chemical conditions inside the burrow. The construction of the turret is remarkable for its finish. The nymph maintains, repairs and rebuilds it if necessary. It opens and closes it under certain circumstances. Before moulting, the nymph comes out at the top, opening it according to a set protocol and time schedule, using its chitins' forelegs. The burrow is associated in a commensal relationship with arborescent Fabaceae species (of the Tachigali genus) through its nutrition mode, the suction of the elaborated sap in fine roots, close to the meristems.

Keywords: behavior, building, burrow, cicada, clay, forelegs' hooked end, molt, nymph, regulating device, turret, urine, well, commensalism

1. Introduction

Over a large area of the Amazon rainforest, extending from the Brazilian state of *Para* to the south-east of *Peru* (*Madre de Dios* department), passing through *Surinam*, one can observe curious clay buildings, having the shape of turrets, or chimneys (**Figure 1a**), with a height of 20 to 40 cm and an internal diameter at their base of about 2 cm (**Figure 1b**). The turret surmounts a vertical well (**Figure 1c**) with a depth of up to about a meter, i.e. the thickness of the fertile soil layer. The surface inside the turret is perfectly smooth (**Figure 1d**).

Each turret is the visible part of the pupal burrow of the cicada *Guyalna chlorogena* (**Figure 2**), or *Fidicina chlorogena*, according to its old taxon [1]. Endoscopic exploration made it possible to observe the nymph in the well (**Figure 3**) and to verify that each burrow is occupied by a single nymph, male or female [2], which builds its turret (between December and February) a few months before moulting into a winged imago, and reproducing (between late July and early September).

Our research was conducted at the *Museu da Amazônia* (MUSA)[1], installed in the *Botanical Garden of Manaus*, on the edge of the *Adolfo Ducke Reserve* (**Figure 4**), in the northern area of Manaus, State of Amazonas, Brazil, in an area of about twenty hectares, around 59° 56′ 21.5" WO and 3° 0′ 19.7" S. A total of more than 250 burrows were observed, between November 2013 and September 2019. About 60 buildings

[1] Av. Margarita, 6305 - Cidade de Deus, Manaus - AM, 69088-265, Brésil.

Figure 1.
(a) View of a turret. (b) Turret removed. (c) Entrance to the well. (d) Inner surface of the summit.

were monitored daily. The observations made up to 2016 have been published [2]. The results obtained subsequently will be the subject of a second publication (Béguin, Gama and Ribamar Mesquita Ferreira, to be published).

2. Construction of the turret

The turret is constructed from the well, which has a double curvature near the ground surface (**Figure 5a**) and a single one in depth (**Figure 5b**), as revealed by cement casts.

From the moment it appears, the night-time growth of the turret is very rapid; 3–4 cm per night. The nymph uses a special technique that allows it to lengthen the top without ever opening it, so without exposing itself to predators. It softens the top with a mixture of its urine and clay drawn from the bottom of the well and loaded on its clypeus; then it pushes everything upwards [2].

When the nymph encounters obstacles, it continues its construction obliquely, but restores the verticality as soon as possible, manifesting an acute perception of gravity (**Figure 6**).

The monitoring of many buildings, after the construction of the turret and until the nymph abandons its burrow before moulting into a winged imago, has made it possible to identify various maintenance and rehabilitation behaviours, as well as to make hypothesis about the role of the turret.

Figure 2.
The cicada Guyalna chlorogena*; young imago after moulting (photography Vanessa Gama).*

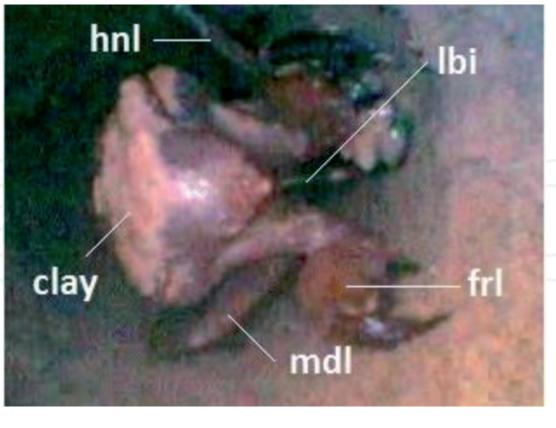

Figure 3.
Endoscopic images of the nymph in its well; lbi*: Labium,* frl*: Foreleg,* mdl*: Middle leg,* hnl*: Hind leg. Clay can be seen on the head of the nymph.*

3. Maintenance and rehabilitation

If a turret is damaged, the nymph fixes it without delay. It performs an occlusion with a mixture of clay and urine (**Figure 7**) if its turret was severed, before restoring the initial height (see below). Maintaining the sealing of the building appears to be a priority for the nymph; if one experimentally fractures a turret and then re-stack

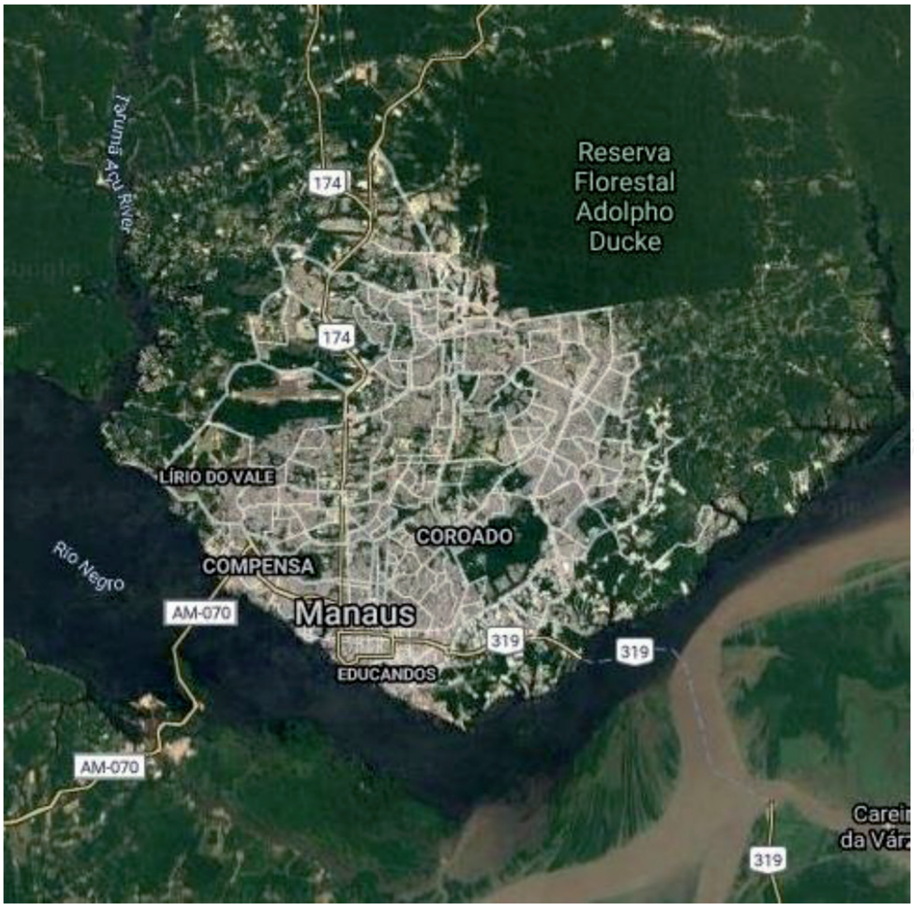

Figure 4.
Manaus and the Adolfo Ducke Reserve. *Google Maps https://www.google.ch/maps/place/Reserva+Florestal+Adolpho+Ducke/@-2.8580657,-60.0242213,71,452 m/data =!3 m1!1e3!4 m5!3 m4!1s0x926c1ec4d40d48b7:0x897d42e519777eb2!8 m2!3d-2.9633439!4d-59.9228331.*

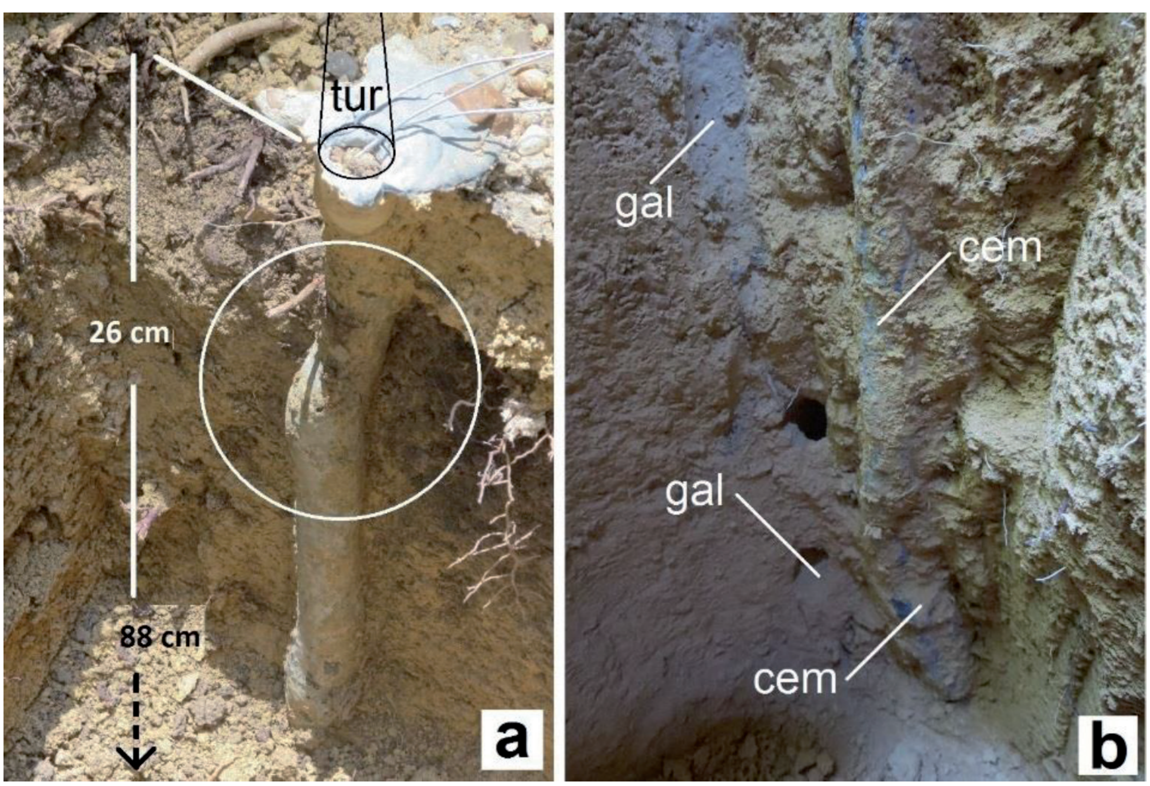

Figure 5.
(a) concrete moulding inside an 88 cm deep well, 26 cm of which have been excavated. The curvature (circle), just below the ground level, is clearly visible. The turret is traced (tur). (b) oblique galleries (gal) at the base of the well, oblique as well, up to a curvature at 15 cm from the bottom; cem*: Cement moulding.*

Figure 6.
A pile of stems and leaves became an obstacle during the construction of this turret; the nymph avoided it by raising the turret obliquely, but it reestablished the verticality as soon as the obstacle was passed.

Figure 7.
Occlusion in progress by the nymph with clay mixed with its urine (mcl) after its turret has been severed.

pieces over the base, the nymph plugs the interstices (**Figure 8**) by injecting soggy clay with its urine.

When a turret has been destroyed, or even when it tips over (**Figure 9**), the nymph rebuilds it completely.

Figure 8.
Sealing of interstices by injection of soaked clay (cl).

Figure 9.
Reconstruction of the turret after failover.

The experiment was carried out [2] to section a turret experimentally and to continuously monitor the repair; the nymph clogs the section and restores the original height within days using the same lengthening technique as when growing, and at the same rate of about 3 cm per night. The result of this experiment gives credence to the idea of the requirement of a minimum height necessary to maintain appropriate parameters (humidity, pressure, and O_2 and CO_2 levels) for the survival of the nymph in its burrow.

4. Spontaneous changes in height

A spontaneous increase in turret height to a value held constant thereafter has occasionally been observed, reflecting an increase in the minimum required height discussed above.

A spontaneous decrease in the height of the turret can also be observed, resulting from building a summit inside the turret, below the existing one, which, probably because it is no longer in contact with the moisture inside the burrow, dries up and crumbles (**Figure 10**), revealing the new top. After a few days, the parts above the new summit have completely disappeared and the result is a turret with reduced height.

Figure 10.
Spontaneous reduction in the height of the turret by construction of an internal top and drying out of the old one. The white line represents the old wall of the upper part of the turret.

The reasons leading to the performance of this operation by the nymph remain to be elucidated because, during experiments of artificial lengthening of a turret by transplanting fragments from another one, a nymph does not manifest a requirement of a maximum height; in the long run, it accommodates a higher turret than the one it has built itself; it does not practice the technique which has just been described, nor any other. On the other hand, it ensures the sealing of the modified turret by plugging with soaked clay the interstices between the base of its turret and the implants received, in the same way as described above (**Figure 8**).

5. Moving the turret

This action of the nymph is rarely observed, but its peculiarity makes it worthy of presentation. A turret emerges near another which later tips over and lies down on the ground. The communication with the well is either completely closed or in the process of being sealed with clay (**Figure 11a**). The hypothesis can be put forward (**Figure 11b**) that the new turret is built over a deviation made by the nymph from the exit of its well.

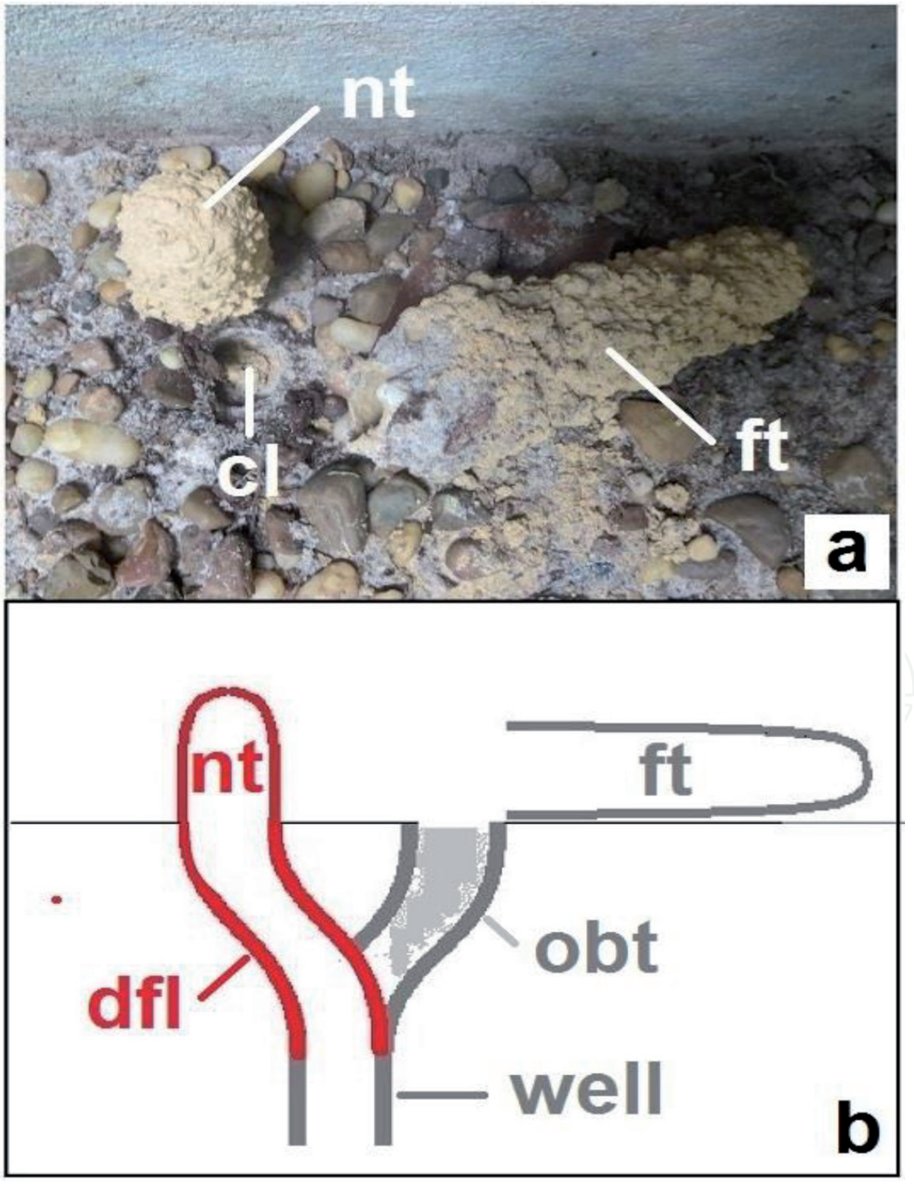

Figure 11.
(a) Spontaneous reconstruction of a new turret. (b) Diagram of deviation by the nymph of the outlet of the well: obt*: Filling with clay of the old outlet,* dfl*: Deviation made for a new outlet,* ft*: Former turret,* nt*: New turret.*

6. Role of the turret

A correlation has been established [2] and confirmed later (Béguin, Gama and Ribamar Mesquita Ferreira, to be published) between the appearance of intense rains and the simultaneous temporary opening of the turrets at their top. A succession of 3 episodes, between July 19 and 23, 2016, turned out to be particularly significant; many openings (**Figure 12**) appeared, which were then closed when the precipitation stopped (**Figure 13**). The openings vary in shape, from a small hole about 5 mm in diameter (**Figure 12a**) to a larger opening where the contour of the clypeus, eyes or anterior part of the pronotum (**Figure 12b**) can frequently

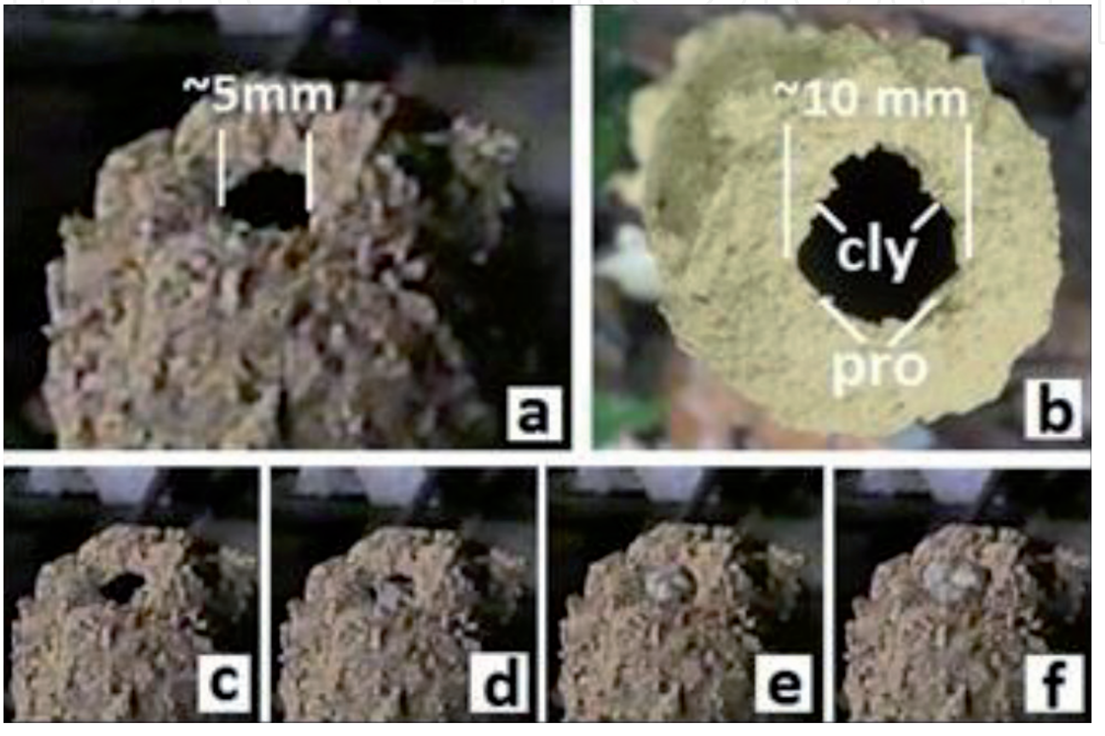

Figure 12.
(a) Circular orifice resulting from a slight pressure of the mass of soggy clay against the wall of the summit. (b) Orifice with imprint of clypeus (cly) and pronotum (pro) covered with soggy clay. (c–f) occlusion of the orifice shown in ***Figure 12a*** *after end of rainfall, by injection of soggy clay (captured images with the automatic camera* Brinno timelapseTLC200 Pro*).*

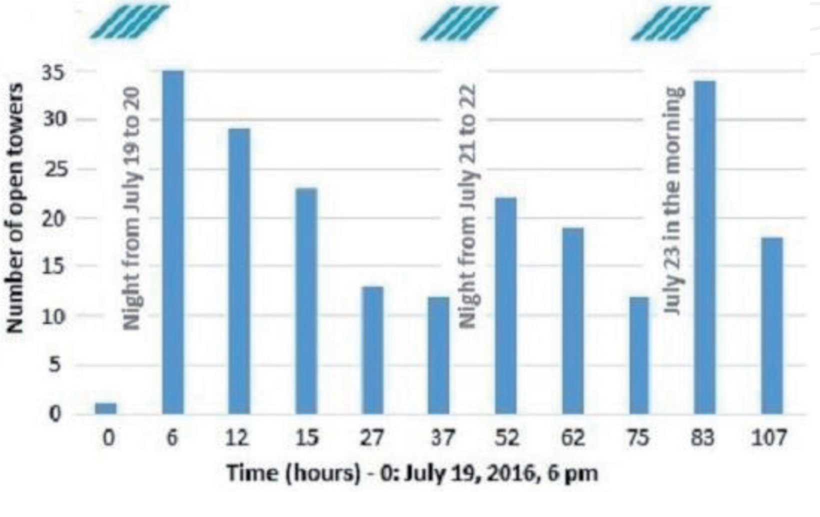

Figure 13.
Correlation between intense rainfalls (////) and temporary and simultaneous opening of 35 turrets, during 3 episodes, between July 19 and 23, 2016.

be observed, as a consequence of the liquefaction of the clay from the top wall by applying these parts covered with clay wet with urine. After the rain has stopped, the nymph closes these openings by injecting moist clay (**Figure 12c**–**f**).

When rainfalls are heavy, the soil becomes very wet and the moisture level in the burrow increases dramatically. In addition, rainwater in some places passes through a rapidly decomposing litter [3]. We can therefore imagine that the level of CO_2 also increases. The temporary opening of the turret would therefore lower these rates, as well as the concomitant increase in pressure. *The turret would thus appear as a regulating device of the physical–chemical conditions prevailing inside the burrow*.

7. Opening of the turret, exit and moulting

From the end of July begins the period of moults. The nymphs emerge from their turret after having opened it at the top, moult into a winged imago, on their own turret (**Figure 14a, b**) or on neighbouring vegetation (**Figure 14c**), then fly away for a brief adult life, during which males and females will mate.

We have identified three opening modes (Béguin, Gama and Ribamar Mesquita Ferreira, to be published), *each accomplished using the hook-shaped end of the forelegs*. It is therefore important to note that the opening behaviours of the top of the turret before moulting are totally distinct from those described above for the temporary opening of the top during intense rainfalls, and which are practiced by liquefaction of the top with soaked clay, without ever involving the front legs. *For the opening*

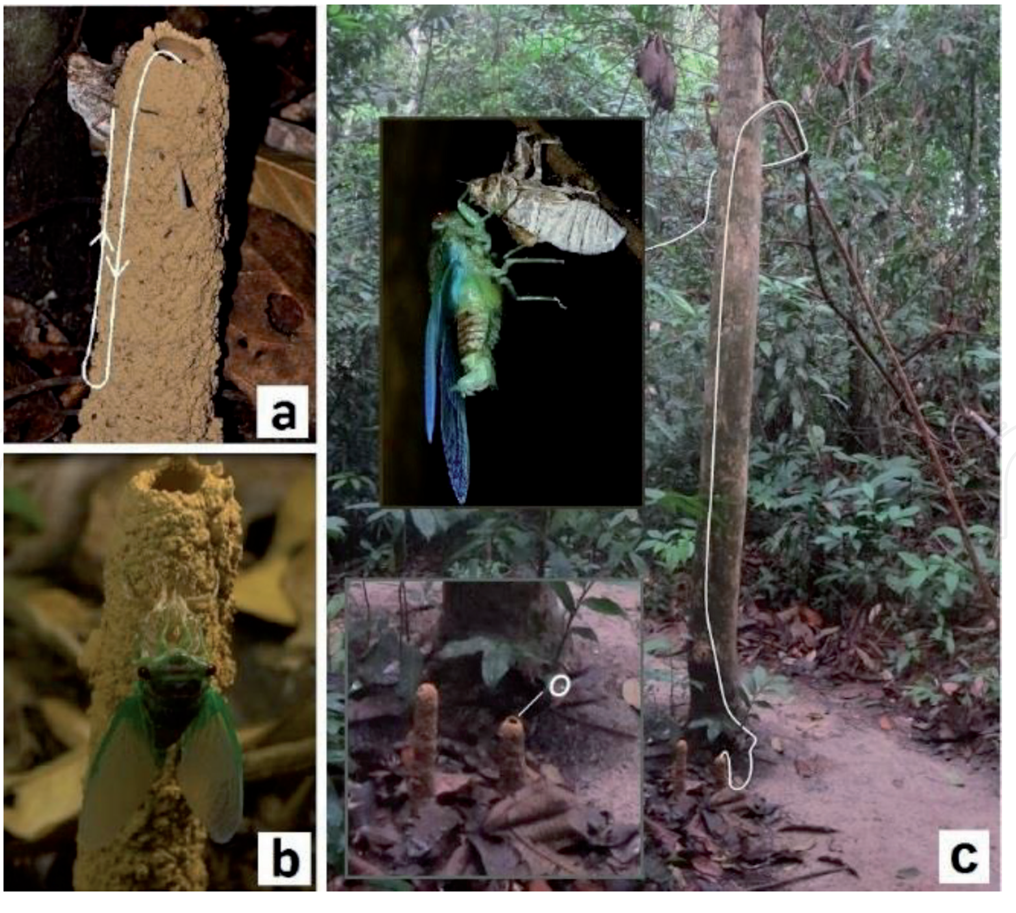

Figure 14.
(a) Exuvia attesting for the moulting of a nymph on its own building (photos Vanessa Gama). The white line represents the trip of the nymph between the opening at the top of the turret and the place where the moult took place. Note the rotation made by the nymph at the bottom of its turret. (b) imago from another nymph drying its wings after moulting on its own building. (c) Migration of a nymph from its turret to the branch where it has moulted. o: Opened turret.

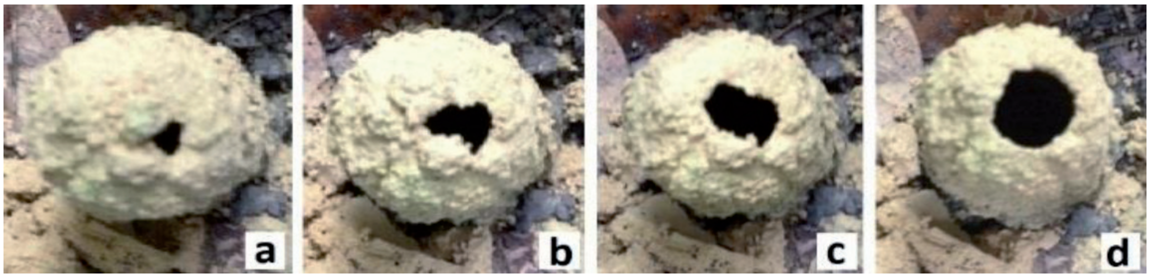

Figure 15.
Four stages of opening a turret. (a) Beginning of the draft work (6:21 a.m.). (b) draft in progress (9:58 a.m.). (c) Draft completed (10:43 a.m.). (d) Equalisation of the border completed (11:35 a.m.). Observation on 19.08.2019.

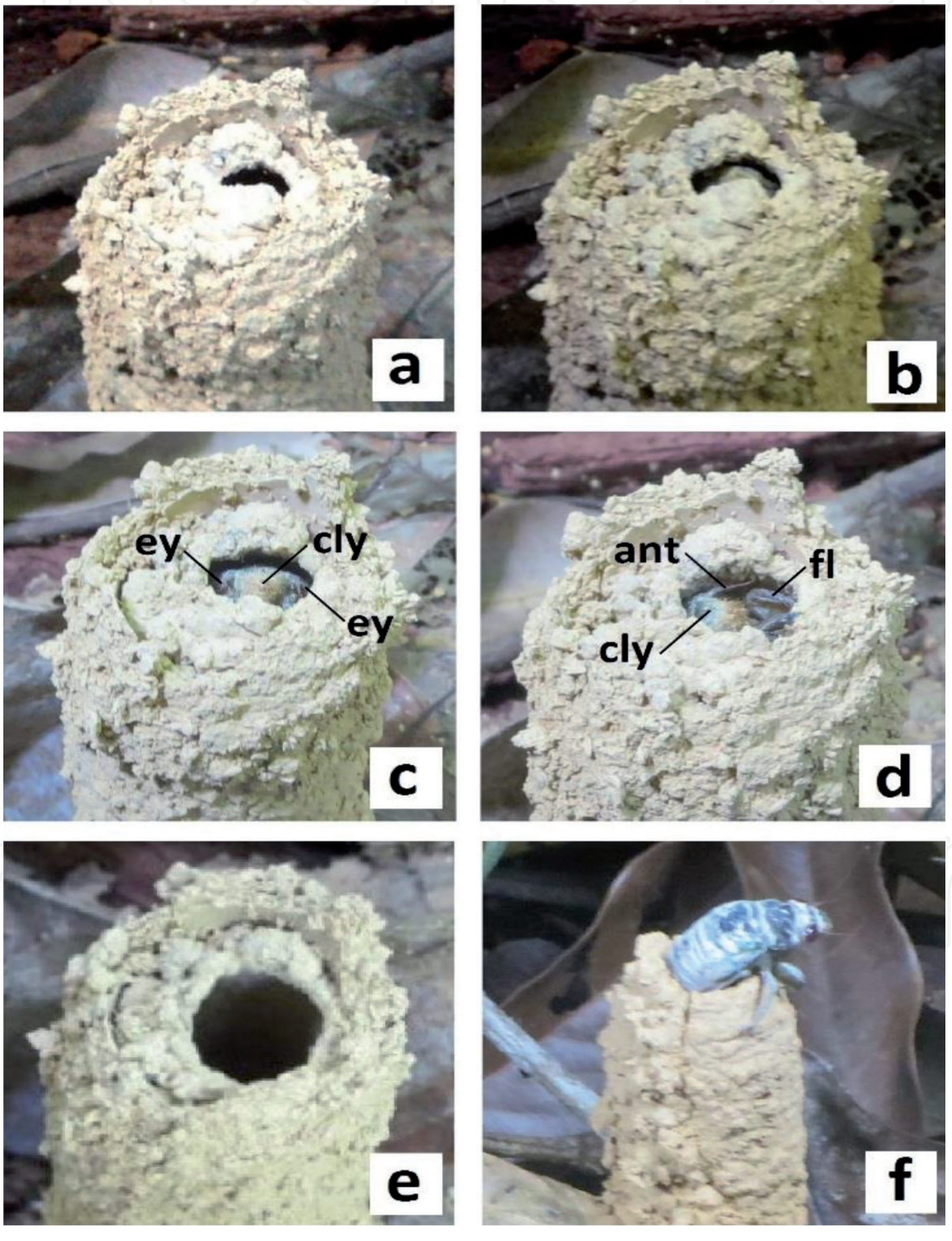

Figure 16.
(a) 6:59 a.m.: Opening resulting from the enlargement of a small perforation, such as that shown on ***Figure 15a****. (b) 7:03 a.m.: Continuation of the enlargement; the nymph is discernible. (c) 8:44 a.m.: The enlargement is finished; the nymph appears, on can distinguish its eyes (ey) and its clypeus (cly). (d) 9:38 a.m.: The nymph, gripped at the opening, is equalising the edge by scratching with the hook-shaped end of its forelegs (fl); one distinguishes also an antenna (ant) and the clypeus (cly). (e) 10:05 a.m.: The equalisation of the edge is complete, the opening is perfectly circular and the nymph withdrew. (f) 6:08 p.m.: The nymph leaves its building. Observation on 01.09.2019.*

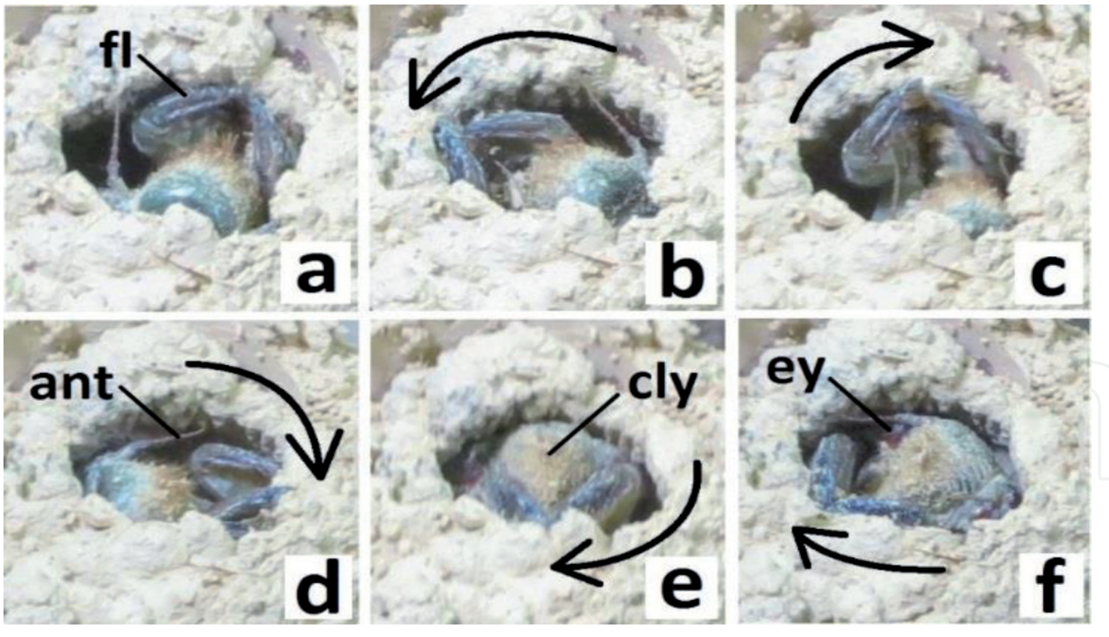

Figure 17.
Six snapshots illustrating the nymph's rotations when equalising the edge of the opening with its forelegs. (a) 9:15 a.m. (b) 9:35 a.m. (c) 9:37 a.m. (d) 9:38 a.m. (e) 9:41 a.m. (f) 9:45 a.m.. Arrows represent the rotations from the previous snapshot; ant*: Antenna,* fl*: Foreleg,* cly*: Clypeus. Observation on 01.09.2019.*

Moulting period	**Late July - early September (maximum frequency during the first week of August)**
First perforation for the opening of the top of the turret	Before 7:00 a.m.
End of opening (before equalising the edge) - program *A*	Between 8:30 and 11:00 a.m.
Equalisation of the edge completed - program *A*	Between 10:00 and 12:00 a.m.
Exit of the nymph through the opening at the top of its turret	Between 6:00 and 6:10 p.m.
Immobilisation before moulting	Between 6:45 and 7:00 p.m.
Downtime to moult	About 2 hours
Downtime after moulting (drying the wings)	About 5 hours
Taking flight	After 2 a.m.

Table 1.
Work schedule of the nymph during its moult to imago.

of its turret, the nymph therefore has a register of behaviours specific to the function performed.

The most common method of opening before moulting (named program A) is worth explaining here. It takes place in two phases: a draft of the opening (**Figure 15a–c**), then an equalisation until the opening is remarkably circular (**Figure 15d**).

Continuous monitoring makes it possible to describe in detail the behaviour of the nymph which creates the roughing by enlarging (**Figure 16a–c**) the initial perforation (**Figure 15a**) by a scraping carried out with the chitins' end of its forelegs, up to obtain an elongated opening with irregular edges (**Figure 16c**). Working from the inside, the nymph is almost invisible. When the roughing is complete, the nymph appears (**Figure 16c**) and undertakes the work of equalisation, which is accomplished by scraping the edge with the chitins' end of its forelegs (fl) also (**Figure 16d**), at the same time as it performs rotations. During this phase, the nymph's head is clearly visible, and one can easily recognise its *antennae* (ant), *front legs* (fl) and *clypeus* (cly). Once the equalisation is complete (**Figure 16e**), the nymph disappears until its exit (**Figure 16f**) which takes place with a remarkable precision between 6 p.m. and 6:10 p.m. (local time). The 6 pictures in **Figure 17** illustrate the rotations that the nymph performs at the same time as it levels the edge of the opening with its forelegs.

The monitoring of two individuals, from the exit of the nymph from its turret, until the flight of the imago, made possible to establish a detailed time schedule (**Table 1**).

8. Ecosystem

Each time an edifice of *G. chlorogena* was discovered on the site we studied, an arborescent *Fabaceae* of the genus *Tachigali* has been identified in the vicinity (Béguin, Gama and Ribamar Mesquita Ferreira, to be published). The building of the nymph is usually the much farther from the tree the larger this one is. This fact is not surprising when one takes into account: 1°) that a cicada nymph can plant its tiny rostrum [4] to suck up the elaborate sap on which it feeds, only in radicular extremities of comparable size, close to the meristems; 2°) that the root ends of trees, in the Amazon rainforest where the layer of fertile soil is very small (of the order of 1 meter), instead of plunging in depth, spread out [5], forming a "root disc" whose radius is all the greater as the size of the tree is large.

During the 2 years 2018 and 2019, we identified 132 buildings of *G. chlorogena* distributed among 14 trees of the genus *Tachigali*; 11 from the species *chrysophyllum* and 3 from the species *venusta*. We therefore measured, for each building, the distance separating it from the tree[2], as well as the diameter of the trunk of this latter[3].

The results were reported on two graphs relating the diameter of a tree with: a) the distances to all the buildings associated with it (**Figure 18a**); b) the average distance to them (**Figure 18b**). The trend lines calculated with *Excel* by the smallest squares indicate clearly, on each of the graphs, a proportionality between the diameter of the trunk of the tree and its distance to a building of *G. chlorogena*, thereby providing a logical-mathematical support to the association between the nymphs of *G. chlorogena* and these *Fabaceae*[4]. *G. chlorogena* apparently being the main, if not the only, beneficiary of this relationship, we admit that this is a case of *commensalism* [6].

The graph with plotting of all distances (**Figure 18a**) shows that part of the buildings are located near the trunk. We will be re-examining our statistics to determine if the location of the buildings is related to the *Tachigali* species (*chrysophyllum* or *venusta*). One thing is obvious; nymph buildings (i.e. nymphs feeding) close to the trunk involve root ramifications down to the level of the meristems from the proximal roots, particularly the buttresses. We recently discovered, at another place in the *Adolfo Ducke reserve*, a *Tachigali* station of a species (yet to be identified) which is neither *chrysophyllum* nor *venusta*, with nymph buildings (the species to which their hosts belong has not yet been confirmed as *G. chlorogena*) close to the trunk. In Santarém (*Pará*, Brazil), edifices of *Fidicina chlorogena*, a taxon since identified with *G. chlorogena* [1] have been described [7] near the base of the trunk; the

[2] More precisely of the estimated center of its implantation surface.

[3] If the trunk is connected to a buttress by its base, its diameter is measured above.

[4] It is due to this situation to meet, at the Botanical Garden of Manaus for example, buildings in a built area near the forest. This is the case with the one shown in **Figure 11**.

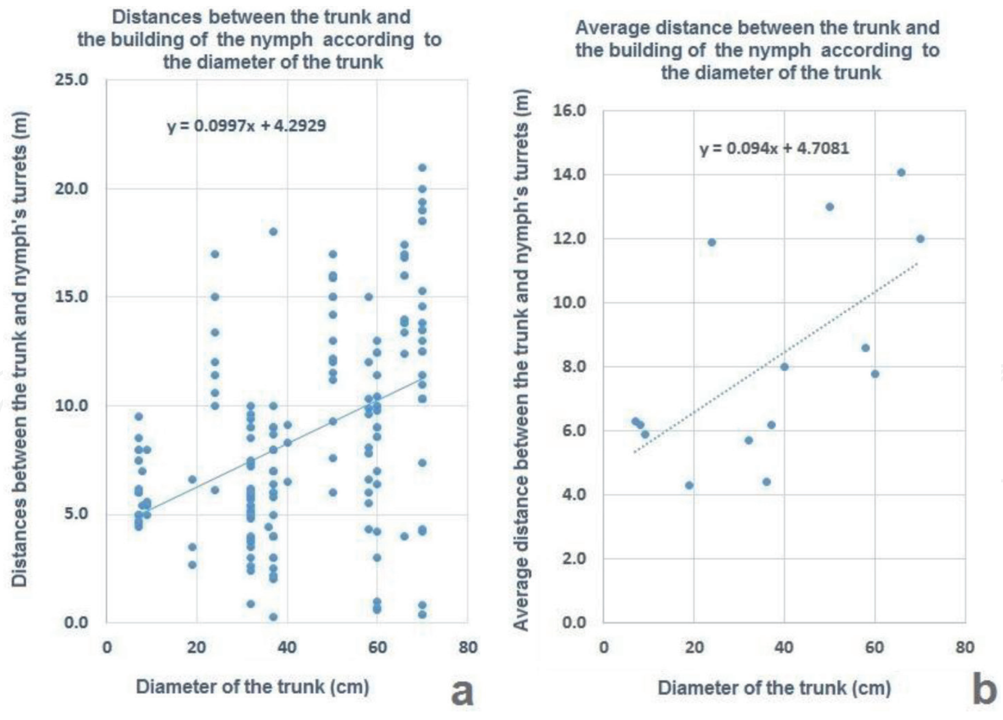

Figure 18.
Relationship between Tachigali's trunk diameters and distances to G. chlorogena's edifices. (a) Plotting distances to all the buildings associated with a given tree. (b) Plotting the average distance to the buildings associated with a given tree.

species name of the tree was not reported. The same disposition was observed [8] for *Orialella aerizulae* (Boulard), which could also feed on *Tachigali* sp. as well as possibly on *Tabebuia* sp. This aspect of the dependency relationship between cicadas and their foster trees has to be explored in more detail.

9. Reproductive cycle

The nymphs spend several years underground, moving to reach the fine roots (less than 2 mm) from which they suck, with their rostrum, the elaborate sap on which they feed (see above). They move forward by digging galleries with their forelegs, throwing the excavated material behind them.

On can consider [9] the beginning of the reproductive cycle at the time of mating (**Figure 19a**), after the nymph has emerged from its burrow and moulted into an imago (**Figure 19h, i**). The winged adults, stimulated by singing males, mate in trees. Then the females search for a stem in which they will plant their ovipositor several times [10] to deposit their eggs under the bark (**Figure 19b**). The larvae hatch on the twigs and then fall to the ground (**Figure 19c**) where they sink (**Figure 19d**). No one has yet observed their behaviour during this first phase of underground life. No one either knows the duration of the underground life until the exit to moult into a winged imago; it is estimated at several years.

From excavations undertaken after moulding with cement (see above), which revealed an inclination of the deepest zone of the well, as well as in its vicinity traces of oblique galleries of intermediate inclinations (**Figure 5b**), one can envisage the upwards digging of a vertical well from a deep horizontal gallery (**Figure 19e**) by digging successive oblique galleries more and more inclined (**Figure 19f**).

The digging of deep horizontal galleries giving access to fine roots that the nymphs can use to feed themselves (see above), is consistent with the presence of a

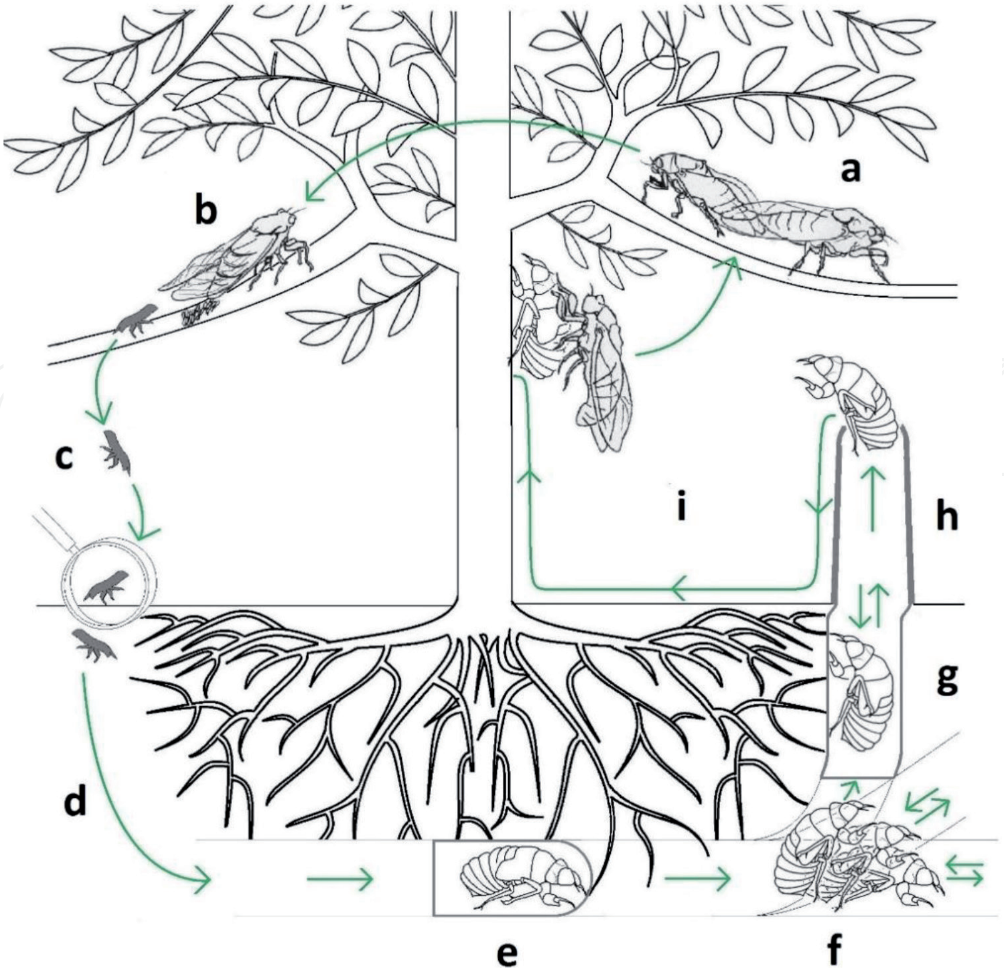

Figure 19.
Life cycle of G. chlorogena. (a) Mating. (b) Lay eggs. (c) After hatching, the tiny larvae (~ 2 mm) fall to the ground. (d) They bury themselves in the ground. (e) The nymph digs its gallery at the same time as it feeds on the sap of the roots. (f) As it moves forward and back, the nymph changes direction until it is vertically oriented. (g) The nymph digs the well which is a vertical gallery. (h) the turret is built from the well. (i) The nymph comes out of the turret to turn into an imago.

significant biomass of fine roots in the deep soil layer of the Amazon rainforest, as recent research has shown [11]. The digging of successive oblique galleries more and more inclined implies a capacity of the nymph to back up into an already dug burrow. Such a capacity is observed when one surprises, by the withdrawal of its turret, a nymph near the exit of its well. It can also be observed in experiments where the nymph is placed in a glass tube.

10. Role of urine

The key role mentioned above of urine in *G. chlorogena*, has been underlined in connection with the construction of the turret and the various maintenance activities described; in experiments where the turret was replaced by a glass tube [2], the observation was made of the rise of the urine soaked mass of clay that the nymph loads on its head. The role of urine, in European species of cicadas, was demonstrated [12] for digging underground burrows; abdominal gutters redirect urine to the anterior part of the body and allow the nymph to use it to soften the soil with its forelegs. In the case of *G. chlorogena*, urine is used to soften the clay [2]. Urine from cicadas also contains *mucin*, a *glycoprotein*, which strengthens the walls of burrows after drying [13].

Figure 20.
(a) Lacertilian *on an open turret. (b) Perforations (p) following passage of* Legion ants *on an open turret after an episode of heavy rainfall;* o: *Opening in the shape of its clypeus practiced by the nymph in response to rainfall. (c) Perforations (p) following a passage of army ants on a turret that the nymph closed with a clay occlusion (clc) after the cessation of precipitation. (d) Bottom of a well after passage of ants; the remainder of the hook of the end of a front leg (fl) is visible. (e)* Ant *in the bottom of a well.*

11. Predators

Different reptiles, such as Lacertilians (**Figure 20a**), can be supposed as predators when a nymph opens or leaves its building. However ants, known by the vernacular name of *Legion ants*, or *Formigas de coreção* according to the local name, are the most dangerous (**Figure 20b–e**). They invade (**Figure 20e**) towers which have been opened (**Figure 20b**) following heavy rainfalls (see above: the role of the turret), and even manage to perforate the walls (**Figure 20c**). Entering a building, they devour the host, leaving only the chitins' organs, such as the hook-shaped ends of the forelegs (**Figure 20d**).

12. Conclusions

This article has presented the activities of the nymph of the cicada *G. chlorogena* during its last year of larval life, in relation to its burrow, the visible part of which is a clay turret built from a well whose depth can reach one meter. The clay with which the turret is built probably comes from the base of the well, from the volcanic bedrock on which the fertile soil rests. The nymph mixes this clay with its urine and transfers the mixture to its forelegs and then to its clypeus, through its abdominal and thoracic "gutters" [9]. It can then climb this mortar to the surface and build its turret. By replacing a turret with a glass tube, it was possible [2] to observe the rise of a nymph with a mass of soggy clay on its clypeus.

The existence of a one meter deep well, dug vertically from the bottom thanks to a process of verticalization of a horizontal gallery (**Figure 19f**), validates the representation of the digging by the nymph of paths below the root base of the tree with which it is associated, in order to find appropriate roots to introduce its rostrum and feed on elaborated sap [10], which is confirmed, as mentioned above, by the recent demonstration [11] of a significant biomass of fine roots in the deep soil layer of the Amazon rainforest. To dig, the nymph shovels with its chitins' forelegs, tears off earthy fragments which it impales on the bristles of its clypeus and deposits behind it [12]. It thus advances in a short gallery, which it opens in front of it and closes behind (**Figure 19e**). One question remains to be clarified; at what moment, and consecutively to which signals (external and/or endogenous), does the nymph begin its process of verticalization.

The well therefore has the status of a gallery, from which it is however distinguished by the fact that, after closing off the bottom, it is not closed as the nymph digs it, vertically and from bottom to top, until reaching the ground surface. The turret, for its part, is an additional device. Maintained sealed by the nymph (**Figure 8**), it appears to be devoted to maintaining appropriate conditions for the survival of the nymph in its burrow (see above; Role of the turret). As already mentioned, a minimum height of the turret is required by the nymph, which repairs or rebuilds it if necessary.

A behaviour, considered as motor coordination, involves [14, 15] stimuli (external and/or endogenous), as well as a recognition mechanism which is a neuronal structure. The observed richness of the nymph's behaviours is therefore concomitant with an important perceptual component in its nerve system. The realisation of similar tasks (opening the top of the turret, for example) by different behaviours according to the circumstance, can be considered as falling under an elementary cognitive system. The execution, without learning, of complex motor sequences, such as the opening of the top of the turret before moulting, according to a straight defined time schedule, is the result of highly perfected innate programming.

The dependence of *G. chlorogena* on arboreal *Fabaceae* of the genus *Tachigali* is a very important aspect of its reproductive cycle. In this regard, an important question arises: do the very young larvae which have just burrowed (**Figure 19b**), have the same mode of nutrition? If so, are they also related to *Tachigali* to find fine root ends near the soil surface?

Many questions still remain open about cicadas, insects as popular as their biology is poorly understood.

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Author details

Claude François Béguin
Museu da Amazônia (MUSA), 69060-060, Manaus, AM, Brasil

*Address all correspondence to: claude.beguin@gmail.com;
claudefb@museudaamazonia.org.br

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