

**REINALDO LUIZ CORRÊA BUENO**

**THE PHOTOPROTECTIVE ROLE OF THE PIGMENTED CUTICLE IN TERMITES**

Dissertação apresentada à  
Universidade Federal de Viçosa, como  
parte das exigências do Programa de  
Pós-Graduação em Entomologia para  
obtenção do título de *Magister Scientiae*.

Orientador: Og Fracisco F. de Souza

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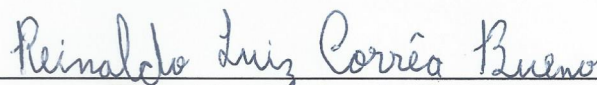
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Orientador

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## RESUMO

BUENO, Reinaldo Luiz Corrêa Bueno, M.Sc., Universidade Federal de Viçosa, fevereiro de 2020. **O papel fotoprotetivo da cutícula pigmentada em cupins.** Orientador: Og Francisco Fonseca de Souza.

Acredita-se que os animais pigmentados têm proteção contra os efeitos nocivos da luz, especialmente luzes como a UV. A pele pigmentada funciona como um filtro, preservando o metabolismo interno do calor e da oxidação. Os insetos que geralmente não se deparam a luz, como os cupins, não são pigmentados. No entanto, alguns cupins que encaram a luz do dia são bem pigmentados, como os alados e as espécies forrageadoras a céu aberto. Testamos a hipótese de que a cutícula pigmentada de cupins forrageadores a céu aberto serve como camada protetora contra os efeitos tóxicos da exposição à luz. Para fazer isso, comparamos a sobrevivência de cupins pigmentados e não pigmentados mantidos em arenas experimentais iluminadas ou não iluminadas. Testes intraespecíficos compararam soldados com operários. Testes interespecíficos contrastaram indivíduos, independentemente de sua casta, de *Cornitermes cumulans* e *Constrictotermes cyphergaster*. Os efeitos de luz de amplo espectro contrastaram luz branca e a escuridão. Os efeitos de luzes de comprimento de onda específicos contrastaram a luz vermelha, verde e azul usando a escuridão como controle. Todos os cupins mantidos na escuridão viveram mais tempo do que os cupins expostos à luz branca, indicando os efeitos nocivos da luz. Entre os afetados pela luz, os cupins pigmentados viveram mais tempo do que os não pigmentados, tanto em comparações intraespecíficas quanto interespecíficas. A sobrevivência dos cupins não foi afetada pela exposição isolada à luz vermelha, verde e azul. Nossos resultados sustentam a hipótese de que a pigmentação da cutícula protege os cupins contra os efeitos prejudiciais da luz, mas esses efeitos não podem ser atribuídos à ação isolada dos comprimentos de onda longo (vermelho), médio (verde) ou curto (azul). Portanto, qualquer que seja o mecanismo por trás da toxicidade da luz, este é dependente de uma combinação de comprimentos de onda de luz visível ou de um comprimento de onda de luz invisível específico (como ultravioleta). Esta conclusão encontra suporte no fato de que colunas de forrageamento de cupins pigmentados de *C. cyphergaster* são frequentemente vistas expostas à luz ao amanhecer, quando a composição da luz UV é menor e os

componentes RGB (Vermelho, verde e azul) são desiguais. Em resumo, a cutícula pigmentada pode facilitar o forrageamento de cupins a céu aberto. Testes que demandem imagens de vídeo podem ser usados com luzes vermelhas, verdes e azuis sem causar danos aos cupins.

**Palavras-chave:** Inseto. Cupim. Dano da luz.

## ABSTRACT

BUENO, Reinaldo Luiz Corrêa Bueno, M.Sc., Universidade Federal de Viçosa, February, 2020. **The photoprotective role of the pigmented cuticle in termites.** Orientador: Og Francisco Fonseca de Souza.

Pigmented animals are thought to have protection against the harmful effects of light, especially lights such as UV. The pigmented skin would function as a filter, preserving the internal metabolism from heat and oxidation. Insects that usually don't face the light, such as termites, are not pigmented. However, some termites that face daylight are well pigmented, such as the alates and open forager species. We tested the hypothesis that the pigmented cuticle of open forager termites serves as a protective layer against the toxic effects of light exposure. To do so, we contrasted the survival of pigmented *versus* unpigmented termites which were kept in lightened or unlightened experimental arenas. Intra-specific tests contrasted soldiers with workers. Inter-specific tests contrasted individuals, irrespective of their caste, from *Cornitermes cumulans* and *Constrictotermes cyphergaster*. Broad spectrum light effects contrasted white light and darkness. Specific wavelength effects contrasted red, green, and blue light using darkness as a control. All termites kept under darkness lived longer than termites exposed to white light indicating harmful effects of light. Among those affected by light, pigmented termites lived longer than unpigmented termites, both in intra-specific and inter-specific comparisons. Termites' survival was not affected by red, green, and blue light isolated exposure. Our results support the hypothesis that cuticle pigmentation protects termites against damaging effects of the light but these effects cannot be attributed to the isolated action of long (red), medium (green), or short (blue) wavelengths. Hence, whatever the mechanism behind light toxicity, it is either dependent on a combination of wavelengths of visible light or to a specific invisible light wavelength (such as ultraviolet). This conclusion finds support on the fact that foraging columns of *C. cyphergaster* pigmented termites are often seen exposed to light at dawn, when UV light composition is lower and RGB (red, green and blue) components are uneven. In summary, pigmented cuticle can ease termite foraging in the open. Assays demanding video footage can be used with red, green and blue lights without causing harm to termites.

**Keywords:** Insect. Termite. Light damage.

## SUMÁRIO

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## 1 INTRODUCTION

The pigmentation in the skin of animals are thought to function as a blockade for light, minimizing the bad effects that light can cause in their internal metabolism, such as heat and oxidation. In humans, it is known that UV light from solar radiation causes damage to skin cells directly through DNA mutation and, indirectly, through oxidative stress (Ichihashi et al., 2003). This damage can ultimately lead to skin cancer (Gilchrest et al., 1999). Dark pigments protect the skin acting like a physical barrier against light as it absorbs more of it and reduces its penetration through the epidermis compared to light colored skins (Kaidbey et al., 1979). That is why humans with dark skin are less prone to develop skin cancer than humans with fair skin (Halder & Bang, 1988; Brenner & Hearing, 2008). Besides acting like a filter, dark pigments can have antioxidant properties (Bustamante et al., 1993).

Short wavelength lights are more deleterious than the long ones. For instance, UVB radiation (290-320 nm) is more toxic to cells than UVA radiation (320-400 nm) (Ichihashi et al., 2003). UV light is a short wavelength light ray as compared to visible light. Among the electromagnetic rays that compose visible light, blue light has shorter wavelength than green light and the red light. The latter has longer wavelength between them. Among the light rays in visible light, blue light is known to cause lethal effects on insects (Hori et al., 2014). Regarding termites, UV exposure can cause extreme mortality as compared to darkness exposure (Beard, 1971; Siderhurst et al., 2006).

Termites are insects that display cryptic habits. They live inside their nest and forage within tunnels and galleries (Eggleton, 2011). In some cases, termites live inside their source of food (e.g. soil-feeders or wood-eating termites). These microhabitats are under darkness. Therefore, termites do not face daylight at all. In fact, termites avoid light when exposed to incandescent or fluorescent lights in experiments (Cabrera & Rust, 1996; Park & Raina, 2005).

However, the alates, the workers and soldiers of a few species of termites are exceptions for this rule. The alates need to face daylight (or at least dusk light) in order to locate a sexual partner and found a new colony (Eggleton, 2011). Likewise, some termite species forage above the surface during the day (Kalshoven, 1958; Collins, 1979; Hoare & Jones, 1998; Martius et al., 2000). In general, termites that live and forage in the darkness are way less pigmented than the termites that face

daylight, these latter ones being typically darkly colored (Kalshoven, 1958; Collins, 1979; Hoare & Jones, 1998; Martius et al., 2000). The alates also are very dark in color. Since these termites can tolerate exposition to light, one could hypothesize that the dark cuticle of termites could help them to face daylight. This is reinforced by the fact that in termite species foraging in the open, workers tend to present pigmented cuticle. Examples include the Asian *Hospitalitermes* spp and the Neotropical *Constrictotermes* spp.

In this study, we aimed to test the hypothesis that the pigmented cuticle of open forager termites serves as a protective layer against the toxic effects of light exposure.

## 2 MATERIALS AND METHODS

The pigmented termite used in this study is the species *Constrictotermes cyphergaster* (Silvestri, 1901) (Isoptera: Termitidae). This is an arboreal termite, which forages in the open mainly at night, returning to the nest in the early hours of the day, just after sunrise. In closed canopy rainforests (such as Amazonian Rain forest) another species of this genus, *C. cavifrons*, can be seen foraging in the open during day hours (ODS, pers. Obs.). Termite nests of *C. cyphergaster* (Silvestri, 1901) were collected in the rural area of São José das Lajes (19°02'38.7"S 44°14'56.1"W), in the municipality of Cordisburgo, in the state of Minas Gerais, Brazil. The biome in this place is the Brazilian Cerrado, in which *C. cyphergaster* termites are found commonly in arboreal nests. The collected nests were transported to the Laboratory of Termitology facilities in the Federal University of Viçosa ('UFV' in Brazilian acronym), Brazil.

In the lab, the nests of *C. cyphergaster* were kept in plastic boxes 55 liters large. We offered water and food *ad libitum* to the colony. As food source we offered half of filter paper discs (total diameter = 90 mm) and barks of trees with lichen attached on the top surface. We also offered water in test tubes capped with a piece of cotton so that to allow the slowly diffusing water to be used by the termites. Every other day, we checked for old pieces of food and replaced them by fresh ones. By doing this, we tried to avoid proliferation of microorganisms. For the same reason, the test tubes with water were also replaced by new ones with the same time interval, as the humid cotton place in the opening of the tubes is a good spot for microorganism development. In doing these replacements, we could maintain the colony as alive and healthy as possible for several months.

The experimental tests with *C. cyphergaster* were made in August, October and November 2018. We transferred 15 individuals (12 workers + 3 soldiers) from each nest to Petri dishes (diam. = 55 mm) lined with filter paper and then, transported them to a BOD incubator. A light fixture was set up inside the BOD incubator to provide for the different light conditions. Then, we switched on the BOD incubator and adjusted the room temperature (25° C) inside it. To allow for acclimatization, the Petri dishes with termites were kept inside the incubator for 1 hour before the beginning of the tests. Right after, we switched on the light. We exposed groups of termites in closed Petri dishes to different light conditions (white, red, green and blue

light) and darkness. In each of the five light regimes (including darkness), we exposed three different groups of termites, each group from a different nest. In total, 15 nests of *C. cyphergaster* termite were used in this study. The lights sources used in this experiment were LED light bulbs.

Once the exposition to light or darkness started, we counted the number of alive and dead individuals hourly. Each hour, we opened the incubator to check them without opening the Petri dishes, and then we closed it again. We followed this routine, usually between 8:00 and 22:00 h, until all individuals died.

Unpigmented termites of the species *Cornitermes cumulans* were used as a control treatment. *C. cumulans* builds epigeous nests from where several foraging tunnels depart, always underground. Foraging proceeds by reaching tussocks and other foraging items from below. To do so, in August 2019, we collected different nest fragments from 15 different nests of the termite species *C. cumulans* in the *campus* of UFV. Once in the lab, 17 individuals (16 workers + 1 soldier) were extracted from the fragments of each nest, and placed in a Petri dish to set up an experiment in the same way we did for the *C. cyphergaster* termites.

The data were submitted to survival analysis under Weibull distribution, in R software, to inspect the effect of light regimes on the proportion of termites still alive at any given time along the experimental period. We started from a full model in which the response variable (proportion of termites still alive at a given time) was tested against the following explanatory variables: (1) the light regime in which the termites were exposed (dark or white light), as “light”; (2) the experimental arenas exposed to different light conditions as blocking factors, as “arena”; (3) the termite species that were subjected to the experiment (*Constrictotermes cyphergaster* and *Cornitermes cumulans*), as “spID”; (4) the caste represented by each termite individual confined in the experimental arenas (worker or soldier), as “caste”. We built a second full model in which the response variable (proportion of termites still alive at a given time) was tested against the same 4 explanatory variables cited above. But now, the categories of the “light” variable were dark, red, green and blue light.

The candidate models were based on the competing biological hypotheses that termite survival depend on:

1. a single factor, i.e., models containing a single explanatory variable; or

2. the simultaneous action of the factors, i.e., models containing a given set of the explanatory variables.

These models were submitted to “model selection”, a statistical approach differing from traditional null hypothesis testing in that it can be used to identify a single best model, thus lending support to one particular hypothesis, or it can be used to make inferences based on weighted support from a complete set of competing models. Analyses followed recommendations by Burnham and Anderson (2002) and were performed under R version 3.5.3 R Core Team (2019), using package “MuMIn” (Bartón, 2016) applied to survival analysis under Weibull distribution. Initially, a global model was built to encompass all candidate models being thence subjected to model selection. The fit and complexity of each candidate model were measured using second-order Akaike information criterion ( $AIC_c$ ). Models were ranked to classify as the best the one presenting the lowest  $AIC_c$ . Inference on the existence of effects of explanatory variables on termites survival parameters was made based on the subset of models whose  $AIC_c$  differed from the best model’s values by less than 2 units. This final model was used to plot curves and derive the biological meaning explored further.

### 3 RESULTS

As soon as placed in the Petri dish, termites exhibited behaviors normally observed when they are confined together in experimental arenas. Individuals tended to walk around, meeting nestmates from time to time and performing trophalaxis and allogrooming. In many times the workers were spotted standing in a cluster, occupying one spot in the Petri dish. The workers tended to walk around more when the Petri dish was manipulated for the hourly tally. The soldiers usually were more mobile in the arenas, but sometimes were seen standing in the cluster. We also observed some vibration behavior while manipulating the Petri dishes. Both species fed on a small portion of the filter paper in some arenas. Necrophagy (cannibalism on dead nestmates) was present in a few arenas of *Cornitermes cumulans* but was absent in *Constrictotermes cyphergaster* arenas. When necrophagy happened, the whole body but the head was eaten. In some point, we noticed that the dead bodies were grouped as far as possible from the termites alive. It was also possible to see termites carrying nestmate corpses in their mandibles. This disposal of corpses is a well-known behavior in social insects (López-Riquelme & Fanjul-Moles, 2013). The disposal behavior was more eminent in the *C. cyphergaster* arenas. All these behaviors usually lasted for most of the duration of the experiments, but were more eminent in the beginning of the assays. As termites fed upon nestmates that were already dead, such a behavior did not affect our survival calculations directly.

When comparing both species, *C. cyphergaster* individuals moved faster in the arenas than the *C. cumulans* ones. As time went by, the termites alive slowed down their paces. The *C. cumulans* termites became immobile quickly than *C. cyphergaster* termites.

Termite species here assayed present differences in their baseline survival (that is, the survival under darkness) (Figure 1). *C. cyphergaster* individuals survived 5 to 6 times longer than *C. cumulans* individuals, regardless their caste (Table 1). This longevity reflected in the group as a whole: the moment when 50% of the group was still alive in *C. cyphergaster* termites occurred 5 to 6 times latter than in *C. cumulans*, regardless their caste. Within each species, the soldiers survived about 2 times longer than workers when they were kept in darkness.

**Table 1:** Number of hours since the beginning of the bioassay until death for termites confined in Petri dishes under distinct light regimes. Here we present the mean longevity of individuals and the mean time of death of 50% of the cohort.

Species	Caste	Longevity		50% dead	
		Dark	Light	Dark	Light
<i>Constrictotermes cyphergaster</i>	Soldier	120.1	99.8	134.5	111.7
	Worker	71.8	59.6	80.3	66.8
<i>Cornitermes cumulans</i>	Soldier	23.5	19.5	26.3	21.8
	Worker	14	11.7	15.7	13.1

This baseline survival was depressed when termites were subjected to white light (Figure 1, Table 2). Termites did not tolerate such an exposure for long periods of exposition dying faster when exposed to light than when kept in the darkness. Although presenting intolerance to white light as compared to a darkness regime, the assayed species did differ, with *C. cyphergaster* being far more tolerant than *C. cumulans*, by a factor of c.a. 5 times (Table 1). Within each species, workers were less tolerant to white light than soldiers and, again, such differences were less marked than differences between species.

Interestingly, termites did not present intolerance to some specific components of white light namely, red, green, and blue wavelengths (Table 3). As compared to the baseline survival (that is, under darkness) the survival under these wave lengths was not significantly depressed. In other words, the survival rates of termites under darkness, red, green and blue lights were the same.

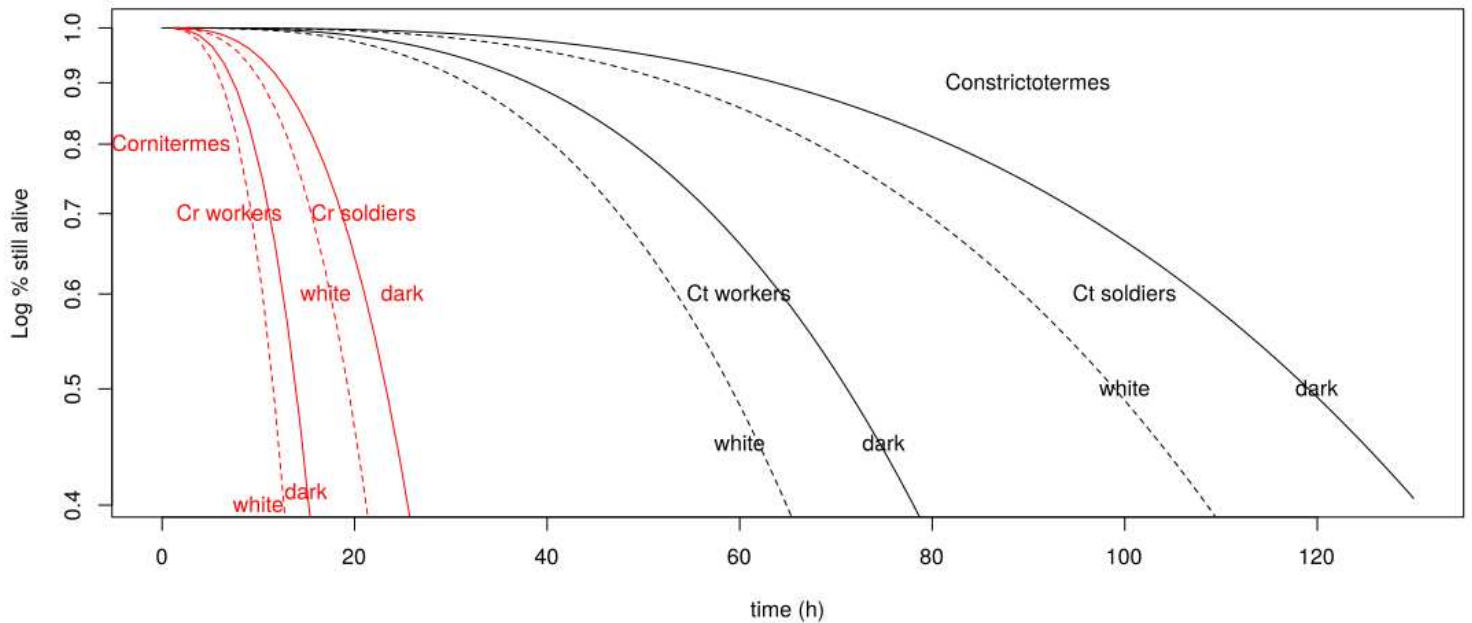
**Table 2:** Coefficients for the terms composing the model with substantial empirical support ( $\Delta < 2$ ), which predicts the mean time to death of soldier and worker termites subjected to two light regimes (white light and darkness) in a lab bioassay. The model depicted was the only one drawn from all candidate models used to describe all the competing hypotheses under test. This model refers to a right censored survival analysis performed under Weibull errors. Global model:  $y \sim \text{arena} + \text{caste} + \text{light} + \text{spID}$ , where  $y$  is the proportion of termites still alive at time  $t$ , arena is the arena ID (a blocking factor to control for intrinsic differences in termite groups), caste is the caste to which a given individual belonged to (either ‘worker’ or ‘soldier’), light is the light regime to which termites have been subjected (either ‘dark’ or ‘white light’), and spID is the species to which a given individual belonged to (either *C. cyphergaster* or *C. cumulans*). The coefficients for these variables are shown only for the significant variables in the model selected. In the name of the column variable, there is, in parenthesis, the category in which the coefficient corresponds to. Models are based on 192 individuals collected from 12 field nests. Statistical estimates are given under columns: df (degrees of freedom), logLik (log-likelihood), AIC (Akaike information criterion), delta (the AIC difference from the best model) and weight (this model’s weight).

model ID	(Intercept)	arena	Caste (worker)	Light (white)	SpID (Cornit)	df	logLik	AIC	delta	weight
15	4.90		-0.514	-0.185	-1.632	5	-717.2	1444.4	0.0	0.931

**Table 3:** Coefficients for the terms composing the model with substantial empirical support ( $\Delta < 2$ ), which predicts the mean time to death of soldier and worker termites subjected to four light regimes (red, green and blue lights and darkness) in a lab bioassay. The model depicted was the only one drawn from all candidate models used to describe all the competing hypotheses under test. This model refers to a right censored survival analysis performed under Weibull errors. Global model:  $y \sim \text{arena} + \text{caste} + \text{light} + \text{spID}$ , where  $y$  is the proportion of termites still alive at time  $t$ , arena is the arena ID (a blocking factor to control for intrinsic differences in termite groups), caste is the caste to which a given individual belonged to (either ‘worker’ or ‘soldier’), light is the light regime to which termites have been subjected (either ‘dark’ or ‘white light’), and spID is the species to which a given individual belonged to (either *C. cyphergaster* or *C. cumulans*). The coefficients for these variables are shown only for the significant variables in the model selected. In the name of the column variable, there is, in parenthesis, the category in which the coefficient corresponds to. Models are based on 384 individuals collected from 24 field nests. Statistical estimates are given under columns: df (degrees of freedom), logLik (log-likelihood), AIC (Akaike information criterion), delta (the AIC difference from the best model) and weight (this model’s weight).

model ID	(Intercept)	arena	Caste (worker)	Light	SpID	df	logLik	AIC	delta	weight
4	3.52	+	-0.588			32	-1389.33	2842.7	0.0	0.696

**Figure 1:** Termite survival curves under exposition to dark and white light: x-axis represents time in hours and y-axis represent the logarithmized proportion of individual still alive. Black lines represent *Constrictotermes cyphergaster* survival curves while red lines represent *Cornitermes cumulans* survival lines. Solid lines represent termites' survival under darkness, while dashed lines represent termites' survival under white light. The survival curves for the two different castes are depicted in this graph. Ct stands for the genus *Constrictotermes* and Cr stands for the genus *Cornitermes*.



## 4 DISCUSSION

Our results support the hypothesis that cuticle pigmentation protects termites against damaging effects of the light. This conclusion derives from two main facts: (i) all termites here assayed lived longer in the dark than when subjected to white light, and (ii) sclerotized termites (*Constrictotermes cyphergaster*) lived way longer than unsclerotized ones (*Cornitermes cumulans*) under exposure to white light as compared to darkness (Tables 1 and 2, Figure 1). This pattern was further confirmed by the fact that, within the same species (hence, ruling out phylogenetic effects), individuals more sclerotized (soldiers) also tolerated white light better than their less sclerotized nestmates (workers).

Whether or not this damaging effect arises from phototoxicity or from some indirect correlate to light (such as stress) is still unresolved. Nevertheless, we now know that monochromatic lights (red, blue and green lights) did not affect termite survival in either species under study (Table 3). This is particularly relevant if one considers how harmful blue light can be to animals and, particularly, to insects (Godley, et al., 2005; Hori et al., 2014). Thus, whatever the mechanism behind harmful effects of white light to these termites, it is not expressed by any of these light components alone. Or, stated in another way, if these wavelengths are deleterious to termites, they do so only when applied simultaneously. This could explain why the sclerotized termite *C. cyphergaster* can forage under light conditions in the first hours of daylight: the relative contribution of red, green and blue lights composition to daylight varies within the day. From morning until evening, the relative contribution of blue light decreases while the red and green light contributions increase as time goes by (Thorne et al., 2009). Additionally, it is in the early hours of the day that other light components (such as UV wavelengths) are less abundant.

Besides that, when the *C. cyphergaster* termite face daylight, the foraging bout is returning to the nest and tends to be exposed to light at a maximum of 2 hours (personal observation). Here, these termites were exposed continually to light until they died in usually, five days of light exposure.

The effects of light in animals in general and in termites in particular are already reported as damaging. Godley et al. (2005) and Kuse et al. (2014) reported the damage blue light causes to the retinal cells in vertebrates. Regarding insects, Hori et al. (2014) reported the lethal effect blue light cause in Diptera and Coleoptera

insects. For the specific case of termites, UV light is supposed to trigger the phototoxic effect of an alkaloid called norharmane, present in the termite body (Larson et al., 1998; Siderhurst et al., 2005). When exposed to UV light, termites show high mortality compared to termites kept in the darkness (Siderhurst et al., 2006; Beard, 1971). This could explain why our results did not point out to harmful effects of blue light but showed such effects from white light. The termite workers and soldiers from the species here studied, being blind, do not possess any light receptor structure comparable to the retina and that can prevent them to suffer from blue light. But UV wavelengths are among the components of white light. Therefore, UV light could be responsible for the survival decrements here observed under white light.

Additional damaging effects of light could come from indirect correlates, of which desiccation is a candidate often called upon. Insofar as termites depend on high moisture, desiccation by light exposure could be indeed harmful. However, in our assays, we used LED bulbs (which produce only negligible rise of temperature) and kept the termites in closed Petri dishes (hence hindering water loss). It is hence unwise to attribute to light-driven desiccation the harm experienced by the assayed termites.

Among the implications of the results here achieved, one is of immediate use: assays demanding video footage (*e.g.*, for behavioral analysis) could be carried out using wavelengths that combine low disturbance to termites and suitable light to filming. In doing so, less sophisticated cameras can be used, lowering experimental costs while keeping footage quality.

In a biological front, our results reinforce the protective role pigmented skin or cuticle has against deleterious effects of daylight. This is not only true for mammals, but also to insects. Darker pigmentation might be an adaptive trait for insects in order to face daylight.

Concluding, we have shown evidences that pigmented termites tolerate light exposure better than unpigmented ones, implying hence that pigmentation in these insects can ease foraging in the open. It remains to be shown the actual mechanism behind such a result. Candidate hypotheses would include pigmentation as a filter to prevent light to harm internal body parts or light-sensitive body fluids. Another set of hypotheses could inspect indirect effects of light, such as desiccation. It also remains to be tested how termites with intermediary pigmentation would survive under exposition to light.

## REFERENCES

- Bartón, K. (2016). **MuMIn: Multi-Model Inference**. R package version 1.15.6.  
<https://CRAN.R-project.org/package=MuMIn>
- Beard, R. L. (1971). **Lethal action of UV irradiation on insects**. *Journal of Economic Entomology*, 65; 650-654.
- Brenner, M. & Hearing, V. J. (2008). **The protective role of melanin against UV damage in human skin**. *Photochemistry and Photobiology*, 84; 539-549.
- Burnham, K. P. & Anderson, D. R. (2002) **Model selection and multimodel inference: A practical information-theoretic approach**. New York: Springer.
- Bustamante J., Bredeston, L., Malanga, G. & Mordoh, J. (1993). **Role of melanin as a scavenger of active oxygen species**. *Pigment Cell & Melanoma Research*. 6; 348-353.
- Cabrera, B. J. & Rust, M. K. (1996). **Behavioral Responses to Light and Thermal Gradients by the Western Drywood Termite (Isoptera: Kalotermitidae)**. *Environmental Entomology*, 25; 436-445.
- Collins, N. M. (1979). **Observations on the foraging activity of *Hospitalitermes umbrinus* (Haviland), (Isoptera: Termitidae) in the Gunong Mulu National Park, Sarawak**. *Ecological Entomology*, 4; 231-238.
- Eggleton, P. (2011). **An Introduction to Termites: Biology, Taxonomy and Functional Morphology**. In: Bignell, D. E., Roisin, Y. & Lo, N. (Eds.), *Biology of Termites: A modern synthesis*.
- Gilchrest, B. A., Eller, M. S., Geller, A. C. & Yaar, M. (1999). **The pathogenesis of melanoma induced by ultraviolet radiation**. *The New England Journal of Medicine*, 340; 1341–1348.
- Godley, B. F., Shamsi, F. A., Liang, F., Jarret, S. G., Davies, S. & Boulton, M. (2005). **Blue Light Induces Mitochondrial DNA Damage and Free Radical Production in Epithelial Cells**. *The Journal of Biological Chemistry*, 208; 21061-21066.
- Halder, R. M. & Bang, K. M. (1988). **Skin cancer in blacks in the United States**. *Dermatologic Clinics*, 6; 397–405.
- Hoare, A. & Jones, D. T. (1998). **Notes on the foraging behaviour and taxonomy of the southeast Asian termite *Longipeditermes longipes* (Termitidae: Nasutitermitinae)**. *Journal of Natural History*, 32; 1357-1366.
- Hori, M., Shibuya, K., Sato, M. & Saito, Y. (2014). **Lethal effects of short-wavelength visible light on insects**. *Scientific Reports*, 4: 7383.

Ichihashi, M., Ueda, M., Budiyo, A., Bito, T., Oka, M., Fukunaga, M., Tsuru, K. & Horikawa, T. (2003). **UV-induced skin damage**. *Toxicology*, 189; 21-39.

Kaidbey, K. H., Agin, P. P., Sayre, R. M. & Kligman, A. M. (1979). **Photoprotection by melanin — a comparison of black and Caucasian skin**. *Journal of the American Academy of Dermatology*, 1; 249-260.

Kalshoven, L. G. E., 1958. **Observations on the black termites, *Hospitalitermes spp.*, of Java and Sumatra**. *Insectes Sociaux*, 5; 9-30.

Kuse, Y., Ogawa, K., Tsumura, K., Shimazawa, M. & Hara, H. (2014). **Damage of photoreceptor-derived cells in culture induced by light emitting diode-derived blue light**. *Scientific Reports*, 4 : 5223, 1-12.

Larson, R. A., Marley, K. A., Tuveson, R. W. & Berenbaum, M. R. (1998).  **$\beta$ -Carboline alkaloids: Mechanisms of phototoxicity to bacteria and insects**. *Photochemistry and Photobiology*, 48, No. 5; 665-674.

López-Riquelme GO, Fanjul-Moles ML. (2013). **The funeral ways of social insects. Social strategies for corpse disposal**. *Trends Entomol.* 9, 71 –129.

Martius C., Amelung, W. & Garcia, M. V. B. (2000). **The Amazonian forest termite (*Isoptera:Termitidae*) (*Constrictotermes cavifrons*) feeds on microepiphytes**. *Sociobiology*, 35; 379-383.

Park, Y. & Raina, A. (2005). **Light sensitivity in workers and soldiers of the formosan subterranean termite, *Coptotermes formosanus* (*Isoptera: Rhinotermitidae*)**. *Sociobiology*, 45: 367-376.

R Core Team (2019). **R: A language and environment for statistical computing**. Vienna, Austria: R Foundation for Statistical Computing.

Siderhurst, M. S., James, D. M. & Bjostad, L. B. (2006). **Ultraviolet Light Induced Autophototoxicity and Negative Phototaxis in *Reticulitermes* Termites (*Isoptera: Rhinotermitidae*)**. *Sociobiology*, 48; 27-49.

Siderhurst, M. S., James, D. M., Rithner, C. D., Dick, D. L. & Bjostad, L. B. (2005). **Isolation and Characterization of Norharmane from *Reticulitermes* Termites (*Isoptera: Rhinotermitidae*)**. *Journal of Economic Entomology*, 98, 5; 1669-1678.

Thorne, H. C., Jones, K. H., Peters, S. P., Archer, S. N. & Dijk, D. (2009). **Daily and seasonal variation in the spectral composition of light exposure in humans**. *Chronobiology International*, 26 (5); 854-866.