Unbalanced biparental care during colony foundation in two subterranean termites
Lou Brossette, Joël Meunier, Simon Dupont, Anne-Geneviève Bagnères, Christophe Lucas

To cite this version:
Lou Brossette, Joël Meunier, Simon Dupont, Anne-Geneviève Bagnères, Christophe Lucas. Unbalanced biparental care during colony foundation in two subterranean termites. Ecology and Evolution, Wiley Open Access, 2019, 9, pp.192 - 200. 10.1002/ece3.4710 . hal-02996395

HAL Id: hal-02996395
https://hal.archives-ouvertes.fr/hal-02996395
Submitted on 9 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.
Unbalanced biparental care during colony foundation in two subterranean termites

Lou Brossette1 | Joël Meunier1 | Simon Dupont1 | Anne-Geneviève Bagnères1,2 | Christophe Lucas1

1Institut de Recherche sur la Biologie de l’Insecte (UMR7261), CNRS – University of Tours, Tours, France
2CEFE, CNRS UMR5175, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

Correspondence
Christophe Lucas, Institut de Recherche sur la Biologie de l’Insecte (UMR7261), CNRS – University of Tours, Tours, France.
Email: christophe.lucas@univ-tours.fr

Funding information
Région Centre-Val de Loire, Grant/Award Number: APR-IA 2012 and APR-IR 2017-0017111 BioControleTermite; City of Paris, Grant/Award Number: CNRS 090306; GDR3658 MediatEC

Abstract
Parental care is a major component of reproduction in social organisms, particularly during the foundation steps. Because investment into parental care is often costly, each parent is predicted to maximize its fitness by providing less care than its partner. However, this sexual conflict is expected to be low in species with lifelong monogamy, because the fitness of each parent is typically tied to the other’s input. Somewhat surprisingly, the outcomes of this tug-of-war between maternal and paternal investments have received important attention in vertebrate species, but remain less known in invertebrates. In this study, we investigated how queens and kings share their investment into parental care and other social interactions during colony foundation in two termites with lifelong monogamy: the invasive species Reticulitermes flavipes and the native species R. grassei. Behaviors of royal pairs were recorded during six months using a non-invasive approach. Our results showed that queens and kings exhibit unbalanced investment in terms of grooming, antennation, trophallaxis, and vibration behavior. Moreover, both parents show behavioral differences toward their partner or their descendants. Our results also revealed differences among species, with R. flavipes exhibiting shorter periods of grooming and antennation toward eggs or partners. They also did more stomodeal trophallaxis and less vibration behavior. Overall, this study emphasizes that despite lifelong monogamy, the two parents are not equally involved in the measured forms of parental care and suggests that kings might be specialized in other tasks. It also indicates that males could play a central, yet poorly studied role in the evolution and maintenance of the eusocial organization.

Keywords
division of labor, foundation, parental care, social behavior, task allocation, termites

1 | INTRODUCTION

Parental care is a taxonomically widespread phenomenon across animals (Klug & Bonsall, 2010; Korb, Buschmann, Schafberg, Liebig, & Bagnères, 2012; Wong, Meunier, & Kölliker, 2013). It can last from a few days to several years, be performed before and/or after the emergence of juveniles and involve either the mother, the father or both parents (Smiseth, Kölliker, & Royle, 2012). From mammals
to insects, parental care can take multiple forms, such as egg and 
offspring attendance, nest building and burrowing and food provi-
sioning (Smiseth et al., 2012). All these forms typically provide ben-
efits to offspring by enhancing offspring survival, growth, and/or 
quality, as well as by improving their lifetime reproductive success 
(Klug & Bonsall, 2014; but see Kramer et al., 2017). However, in-
vesting into parental care may also go along with costs for parents. 
That is because it can entail an exaggerated loss of energy, as well 
as an increased risk of pathogen exposure and predation during off-
spring attendance, which all may ultimately curtail their survival rate 
and capability to invest into future reproduction (Alonso-Alvarez & 
Velando, 2012). The evolution of parental care therefore requires 
that its costs remain lower than its associated benefits for each fam-
ily member.

For parents, one way to reduce the costs of parental care is 
to share them with the other parent. The presence of two par-
ents with offspring has been reported in numerous birds, cichlid 
fishes, primates, and a few insects (Balshine, 2012; Trumbo, 2012). 
Although this mutual presence is typically associated with biparen-
tal care, a sexual conflict between mothers and fathers over their 
respective investment into care often emerges during family life, 
as each parent can maximize its own fitness by selfishly minimizing 
its investment into cares (Lessells, 2012). Such a selfish strategy 
allows males, for instance, to increase their investment into the 
search of additional partners and thus to maximize the number of 
offspring produced during a single reproductive season, while it 
allows females to reallocate their saved energy into future repro-
duction (Smiseth et al., 2012). The tug-of-war between mothers 
and fathers over parental investment has been shown to generally 
lead to a disequilibrium, during which one parent exhibits a lower 
investment compared to the other, while this latter does not fully 
compensate for this reduction (Harrison, Barta, Cuthill, & Szekely, 
2009).

Although most studies on sexual conflict explore its resolution 
in species where parents can do extra pair copulations and/or have 
novel mating partners at each reproductive season (Jennions, Kahn, 
Kelly, & Kokko, 2012), the expression and organization of biparental 
care remain unclear when the lifetime fitness of each parent tightly 
relies on its partner’s. This is the case, for instance, in the biparen-
tal family units often present in termites (Kramer & Meunier, 2018; 
Wilson, 1971). In this eusocial insect, mothers (queens) and fathers 
(kings) form pairs quickly after they reach adulthood and remain to-
gether during their entire lives, which can last decades (Boomsma, 
2009). Each couple typically lives in a dark nuptial chamber at the 
center of the colony, where queens produce eggs and kings regu-
larly inseminates queen(s); kings and queen having no direct contact 
with foreign individuals (Hartke & Baer, 2011). Because the termite 
royal couple has no opportunity of extrapair copulation, it has long 
been thought that parental care is equally shared between queens 
and kings especially at colony foundation (Bignell, Roisin, & Lo, 2011; 
Nalepa & Jones, 1991; Shellman-reeve, 1997). However, empirical 
support of this claim remains scarce (Rosengaus & Traniello, 1991; 
Shellman-Reeve, 1990).

In this study, we investigated how termite queens and kings share their investment into social interactions, as well as whether 
this share depends on the developmental stage of their offspring. 
Using an experimental setup allowing non-invasive and fine-scaled 
behavioral observations (Brossette et al., 2017), we analyzed the 
expression of grooming, antennation, trophallaxis (proctodeal and 
stomodeal), and body-shaking by queens and kings over the six first 
months of their colony foundation. Because we aimed at taking a 
broader perspective and exploring whether this biparental organi-
ization was species specific, we used two species of subterranean 
termites: the invasive Reticulitermes flavipes (Kollar, 1837) and the 
native R. grassei (Clément, 1978). If sexual conflict between males 
and females over their respective investment in parental care is ab-
sent in these species, we expected queens and kings to express a 
similar level of grooming, antennation, and trophallaxis toward their 
offspring. Note that body-shaking is a behavior that has been fre-
quently reported in termites, but for which the role is still unclear 
(Funaro, Bőröczky, Vargo, & Schal, 2018; Whitman & Forschler, 
2007). Our study will thus also provide novel insights into our un-
derstanding of its expression and function during colony foundation.

2 | MATERIAL AND METHODS

2.1 | Sampling and crossings

We investigated the behaviors of newly produced queens and kings 
originating from a total of four colonies of R. flavipes and four colo-
ries of R. grassei. The workers, nymphs (i.e., future queens and kings), 
and soldiers of each of these colonies were field sampled in March 
2014 in pine forests on Oléron Island in France and immediately 
transferred into plastic boxes (18 × 24 × 9.5 cm) with their own nest 
material and moistened sand (Brossette et al., 2017). These colonies 
were 100 m away from each other for R. grassei and 300 m for R. fla-
vipes, that is, distances that typically ensure colony independence 
(Perdereau, Bagnères, Dupont, & Dedeine, 2010). Back in the labora-
tory, these field-sampled colonies were maintained under standard 
conditions (80% relative humidity, 26°C, 13.5 L/10.5 D cycle) until 
nymphs became reproductive adults. To prevent uncontrolled sib-
mating, each colony was checked twice a day to collect the newly 
produced winged alates (females and males, i.e., future new queens 
and kings) and to transfer these individuals into sex-specific new 
plastic boxes (50 mm diameter; Starpack) containing moistened 
pure cellulose paper (47 mm diameter; Whatman, GE Healthcare; 
Brossette et al., 2017). Seven days after the emergence of the first 
winged alate, virgin males were paired with unrelated virgin females. 
To limit the risks of mating incompatibility between colonies, we 
paired individuals following 12 intercolonial combinations (later 
called cross ID), which were each replicated from 3 to 9 times (later 
called pair ID). This led to a total of 70 and 86 experimental pairs 
of R. flavipes and R. grassei, respectively. Each pair was then trans-
ferred to an experimental glass case allowing detailed behavioral 
observations (Brossette et al., 2017) and containing a food source 
composed of a pure cellulose disk (90 mm in diameter; Whatman,
GE Healthcare) supplemented with a solution composed of mineral salts, vitamins, and nitrogen (Argoud, Mocotte, & Sternalski, 1982). Over the subsequent six months of experiment, all pairs were maintained under standard laboratory conditions (80% relative humidity, 26°C) and complete darkness. Humidity was controlled with the use of potassium nitrate wells (35 ml KNO₃/100 ml H₂O; Thermo Fisher Scientific).

2.2 | Behavioral recording

Over the six months of the experiment (from May to October), 12 pairs per species were randomly selected every 2 weeks to be video-recorded (Sony HDR CX700V). The chambers where the royal couple were settled with eggs and larvae were video-recorded for 30 min (after a five-min resting time, as the experimental glass cases were moved to the recording setup), under controlled environment (80% RH, 26°C) and total darkness using infrared lights (940 nm wavelength, 15 LEDs of 26 mm diameter, Kingbright). The presence of eggs and larvae in the royal chamber was assessed. Note that because the parents were the focal individuals, we discarded three videos with missing reproducibility from the statistical analyses. The resulting videos were analyzed with the freeware Boris v3.0 (Friard & Gamba, 2016) to quantify parental care behaviors between parents and between parents and descendants. This allowed us to disentangle behaviors that are specifically directed toward offspring (i.e., parental care) from behaviors that are directed toward all family members. In these analyses, donor individuals were defined as individuals expressing the behavior (queen or king), while recipients were defined as individuals receiving the behaviors (defined as either partners, eggs or descendants—this latter including larvae, nymphs, and workers). The recorded behaviors were (a) grooming and antennation (i.e., any contact from the head of a donor toward a recipient), (b) trophallaxis (either proctodeal or stomodeal, i.e., anal-to-mouth or mouth-to-mouth fluid transfer, respectively), and (c) body-shaking (rapid back and forth movement of the whole body with no contact with the substrate). Note that this latter behavior is not directed toward any recipient (Whitman & Forschler, 2007). Other behaviors were observed, but discarded from this study because they were not directly involved in parental care (e.g., dejections, selfgrooming, copulations, and food intake). For each video, queens and kings were discriminated by measuring the size of their seventh sternite (Zimet & Stuart, 1982). Videos were processed following a double blind procedure.

2.3 | Statistical analyses

The total duration of antennation and grooming behaviors (together) was analyzed using a general linear mixed effects model (LMM), in which the explanatory factors were the donors (Queens/Kings), the recipients (Partner/Offspring), the species (R. flavipes/R. grassei), and the developmental stage of the offspring (Eggs/Descendants). To interpret the resulting significant triple interaction involving recipients, species, and offspring developmental stage (see Section 3), the dataset was then split per developmental stage and the two resulting subsets were used to conduct two additional LMMs with the same explanatory factors (without the developmental stage factor). The observation of at least one type of trophallaxis (presence/absence) and the total duration of trophallaxis (when observed) were then tested using a generalized linear mixed effect model (GLMM) with binomial error distribution and a LMM, respectively. In these models, the explanatory factors were the donor, the recipient, the species, and the type of trophallaxis (proctodeal/stomodeal). Note that these models were restricted to the dataset where descendants were present, because trophallaxis is not possible toward eggs. Finally, the observation of at least one body-shaking (presence/absence) and the total number of body-shaking (when observed) were tested using a GLMM with binomial error distribution and a LMM, respectively. In these models, the explanatory factors were the donors, the species, the presence of eggs, and the presence of descendants.

In all the above statistical models, the cross ID and the pair ID (nested into the cross ID) were included as random factors to control for the fact that several kings and queens came from the same field colonies. The date of each video were also included as a random factor to control for the fact that parental behaviors may change over time, while providing an overview of the different behaviors over the six-month recording (i.e., the main goal of this study). To fit with homoscedasticity and normal distribution of model residuals, the total duration of antennation and grooming behaviors were log(+1)-transformed, while the total duration of trophallaxis and the total number of body-shakings were log-transformed. All GLMMs with binomial error distribution were fitted using the “cloglog” link-function to correct for the unbalanced representation of 1 and 0 (Crawley, 2012). All models were first tested with all possible interactions among explanatory variables and were then simplified step-by-step by removing the non-significant interactions (all p > 0.08). Note that some non-significant interactions are reported in the results to allow direct comparison between analyses, but their removal induces no qualitative changes. When required, we conducted post hoc pairwise comparisons within each model using model contrasts based on estimated marginal means. When appropriate, non-significant factors were pooled in the presented figures. All analyses were performed using the software R v3.4.3 (www.r-project.org) loaded with the packages lme4, car, and emmeans.

3 | RESULTS

Grooming and antennation were overall present in 86.3% of the movies. The total duration of grooming and antennation depended on a triple interaction between species (R. flavipes or R. grassei), recipients (offspring or partner), and offspring developmental stage (eggs or descendants; LR χ²₁ = 26.0, p < 0.0001). In the presence of eggs, R. grassei and R. flavipes adults spent the same amount of time grooming and antennating their partners (Table 1; Contrast, p = 0.9203), whereas R. grassei adults spent more time grooming
and antennating their eggs compared to *R. flavipes* adults (Contrast, *p* = 0.0247; Figure 1a). Nevertheless, both *R. grassei* and *R. flavipes* adults spent overall more time grooming and antennating their partner than their eggs (Table 1, Figure 1a). Conversely, in the presence of descendants, *R. flavipes* adults spent more time grooming and antennating descendants than partners (Table 1; Contrast, *p* = 0.0002), whereas *R. grassei* adults spent more time grooming and antennating partners than descendants (Contrast, *p* = 0.0091; Figure 1b). During that period, the total time spent grooming and antennating was higher in queens compared to kings, but independent of the species and the type of recipient (Table 1, Figure 1c).

At least one of the two types of trophallaxis (proctodeal and stomodeal) was present in 22.4% of the movies. Stomodeal trophallaxis was more likely to be observed in *R. flavipes* compared to *R. grassei* (Table 2; Contrast, *p* = 0.0430), whereas this difference was absent for proctodeal trophallaxis (Contrast, *p* = 0.2655; Figure 2a). Independent of the species and its type, trophallaxis was more likely to be expressed by queens than kings (Table 2; Figure 2b,e) and more likely to be received by descendants than partners (Table 2; Figure 2c,f). When at least one type of trophallaxis was observed, queens spent more time performing trophallaxis than kings (Table 2), descendants received trophallaxis for a longer total time compared to partners (Table 2) and proctodeal trophallaxis was overall expressed longer than stomodeal trophallaxis (Table 2). The total duration of trophallaxis was independent of any interaction among donors, recipient, and type of trophallaxis (all *p* > 0.0975).

Finally, body-shaking was observed in 39.2% of the movies. The observation of at least one body-shaking event depended on double interactions both between donors and eggs presence (Table 3) and between eggs and descendants presence (Table 3). In particular, queens were less likely to perform body-shaking in the presence compared to absence of descendants, but only in the presence of eggs (Figure 3b; Contrasts: eggs presence, *p* = 0.0023; eggs absence, *p* = 0.5270). Finally, when body-shaking was observed, its total number was overall higher in *R. grassei* compared to *R. flavipes* (Figure 3c), whereas it was independent of eggs and descendants presence, as well as of the type of donor (Table 3b).

### DISCUSSION

In this study, we compared the involvement of queens and kings in social interactions during colony foundation in the invasive *R. flavipes* and the native *R. grassei* termites. Our results first reveal that queens invest more in the measured forms of parental care than kings, as they overall performed more trophallaxis, grooming, and antennation (when descendants are present) than their partner. This sex-specific effect was independent of the species. Secondly, we showed that differences in parental care are species specific. In particular, *R. flavipes* exhibited less grooming/antennation toward...
eggs compared to partners, but more grooming/antennation toward descendants compared to partners. By contrast, *R. grassei* exhibited more grooming/antennation toward partners compared to both eggs and descendants. The two species also differed in their overall expression of stomodeal trophallaxis, which was more likely to occur in *R. flavipes* compared to *R. grassei*. This difference was absent in term of proctodeal trophallaxis. In both species, trophallaxis was preferentially directed toward descendants instead of partners and was overall more likely to involve proctodeal instead of stomodeal contacts. Finally, our results reveal that body-shaking depends on the species, the sex of the donor, and the developmental stage of the offspring. Body-shaking was overall more frequent in *R. grassei* compared to *R. flavipes*. Moreover, queens were more likely to perform body-shaking in the absence compared to presence of eggs, whereas this effect was absent in kings. When eggs were present, body-shaking was also more likely to occur in the presence compared to

**TABLE 2** Effects of recipient, donor, species and types of trophallaxis on (a) the presence of at least one trophallaxis event and on (b) the total duration of trophallaxis when present

|                  | (a) Presence/absence | (b) Total duration when expressed |
|------------------|----------------------|----------------------------------|
|                  | LR $\chi^2$ | $p$ | LR $\chi^2$ | $p$ |
| Recipient        | 24.8       | 0.0000 | 10.4 | 0.0013 |
| Donor            | 4.6 | 0.0321 | 7.9 | 0.0051 |
| Species          | 0.0 | 0.9445 | 0.8 | 0.3762 |
| Types of trophallaxis | 56.2 | 0.0000 | 24.6 | 0.0000 |
| Species:Types of trophallaxis | 6.8 | 0.0091 | 1.9 | 0.1682 |

Note. Significant $p$-values are in bold.
absence of descendants, whereas this effect was not found in the absence of eggs. Somewhat surprisingly, our results reveal that queens and kings exhibit unbalanced investment in the measured forms of parental care during colony foundation in both *R. flavipes* and *R. grassei*. In particular, the involvement of queens into grooming/antennation and trophallaxis was overall higher than the one of kings. This finding both contrasts with the few results reporting an absence of sexual polyethism in incipient colonies of two other termite species, *Zootermopsis angusticollis* and *Z. nevadensis* (Rosengaus & Traniello, 1991; Shellman-Reeve, 1990), and provides no support for the general prediction of a tight association between lifelong monogamy and balanced investment of each parent into egg/offspring care (Boomsma, 2009). The higher investment of queens into direct interactions in both *R. grassei* and *R. flavipes* suggests that kings are either involved into other tasks and/or overall less active than queens during colony foundation. The success of colony foundation generally involves a broad set of tasks, such as nest construction and/or fights against predators and pathogens (Chouvenc, Efstathion, Elliott, & Su, 2013; Eggleton, 2010), or could be a dynamic response to local environmental changes (Shellman-Reeve, 1990), for which kings might indeed be more involved. The full task repertoire exhibited by termite queens and kings during colony foundation will be investigated in the future experiments taking into account other life traits like sexual size dimorphisms, physiological traits, or metabolite composition which might be part of the observed unbalanced biparental care.

While both *R. flavipes* and *R. grassei* show unbalanced levels of parental care, we found species-specific levels of parental investment for grooming/antennation depending on the presence of eggs or descendants. In particular, if we compare the duration of grooming/antennation toward eggs/descendants with the one toward partners (for both species), then *R. grassei* exhibited identical durations in the presence of eggs and descendants, whereas *R. flavipes* exhibited less grooming/antennation in the presence of eggs compared to in the presence of descendants. In social insects, grooming and antennation typically increase the development and survival of offspring (larvae and eggs) by mediating the application of chemical compounds preventing the risks of desiccation or microbial infections (Bulmer, Denier, Velenovsky, & Hamilton, 2012; Fujita, Minamoto, Shimizu, & Abe, 2002; Matsuura et al., 2002), by mechanically removing external pathogens from the cuticles (Rosengaus, Maxmen, Coates, & Traniello, 1998) and by facilitating ecdysis or egg hatching (Whitman & Forschler, 2007). It also allows to directly assess the nestmates needs and also increase social cohesion through exchange of chemical cues (Blomquist & Bagnères, 2010; Hoffmann, Gowin, Hartfelder, & Korb, 2014; Lucas et al., 2018;
Lucas, Pho, Fresneau, & Jallon, 2004, 2005; Soroker et al., 2003). The reported differences of grooming/antennation between R. flavipes and R. grassei suggest a species-specific role of parental care in the success of colony foundation, which might explain the differences in the colony foundation success observed between those two species (Brossette et al., 2017; Leniaud et al., 2011). Further studies should nevertheless be conducted to investigate whether the intrinsic quality of eggs and juveniles differ between R. flavipes and R. grassei, and whether parental care can mitigate the costs of these intrinsic differences in terms of foundation success.

Our results also reveal that parents exhibited more trophallaxis with their descendants compared to their partners, independent of both the sex of the parent and the species. In subterranean termites such as R. flavipes and R. grassei, trophallaxis between adults and juveniles typically mediate the transmission of symbionts that are necessary to digest wood (Fujita, Shimizu, & Abe, 2001). These symbionts are present in adults, but generally absent in newborn descendants (Nalepa, Bignell, & Bandi, 2001). Our finding thus suggests that both queens and kings are equally involved into the transmission of symbionts to the descendants in R. flavipes and R. grassei. Interestingly, our results also shed light on the occurrence of trophallaxis between parents. In addition to its potential role in the homogenization of gut microbial community among parents (Nalepa et al., 2001), this occurrence may also mediate the regular exchange of nutrients (particularly for larvae instars which are unable to feed themselves; Nalepa & Jones, 1991), nestmate recognition cues (Kirchner & Minkley, 2003; Soroker et al., 2003), and/or immune defenses between colony members (Bulmer, Bachelet, Raman, Rosengaus, & Sasisekharan, 2009; Chouvenc, Su, & Robert, 2009; Mirabito & Rosengaus, 2016). Our results also suggest that the nature of the compounds exchanged could be driven by the mode of transfer (proctodeal vs. stomodeal) and/or the donor (queens vs. kings). The absolute quantities of the fluids transferred are unknown; thus, the exact investment of each parent is difficult to assess.

Although body-shaking has been described as a response to disturbance in a large number of termites (Bagnères & Hanus, 2015; Howse, 1965), the modality of its expression remained unclear (Funaro et al., 2018) and was not previously studied in incipient colonies (Rosengaus & Traniello, 1991; Shellman-Reeve, 1990). Our results reveal that body-shaking is a relatively frequent behavior exhibited by both parents at colony foundation, and that its expression depends on the species, the sex of the parent and the presence/absence of eggs and descendants. In particular, body-shaking was overall more frequent in R. grassei compared to R. flavipes, in the presence compared to the absence of descendants, and finally less frequently expressed by queens in the presence compared to absence of eggs. Termites are known to use vibration communication to quickly transmit information throughout the entire colony (Hunt & Richard, 2013). Body-shaking might be part of this communication system and mediates the rapid spread of a social signal. The importance of egg presence on its expression suggests that the body-shaking might be used to transmit information on the reproductive state of the incipient colony to the other member of the colony, either independently or in complement with other potential chemical signals. Indeed, the presence of eggs or descendants could represent a proxy of the reproductive state of the incipient colony that could modulate social organization. More investigations are needed to fully explain the observed interactions between the body-shaking and the presence of eggs or descendants and to explore all factors possibly involved in its expression. Those studies would also allow to explain why this behavior was conserved over several termite species (Bagnères & Hanus, 2015).

Overall, this study sheds light on unbalanced investment into parental care by queens and kings during colony foundation, as well as on species-specific patterns of social interactions between the invasive R. flavipes and the native R. grassei termites. These findings emphasize that despite lifelong monogamy, the two parents are not equally involved in the measured forms of parental care and instead suggest that kings are specialized in other tasks and/or overall less active. Second, the presence of species-specific patterns of social interactions may provide important insights into our understanding of the invasive success of R. flavipes (Brossette et al., 2017; Perdereau et al., 2010; Perdereau, Dedine, Christidès, Dupont, & Bagnères, 2011). More generally, the sex-specific organization of parental care during termites’ colony foundation emphasizes that males could play a central, yet poorly studied role in the evolution and maintenance of the eusocial organization.

ACKNOWLEDGMENTS

We are grateful to C. Company for her comments on the English translation. This work was supported by the Région Centre-Val de Loire (APR-IR 2017-00117111 BioControleTermite; APR-IA 2012), the city of Paris (CNRS 090306), and the GDR3658 MediatEC. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

The experiment was designed by CL, LB, and AGB. SD, CL, and LB performed the field work. LB, CL, and SD performed the termite crossings and transferred royal couples to the glass cases. LB followed colony development and analyzed the movies. JM, LB, and CL conducted the statistical analyses. JM, CL, LB, and AGB wrote the manuscript. All the authors read and approved the final version of the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vs6md76.
REFERENCES
Alonso-Alvarez, C., & Velando, A. (2012). Benefits and costs of parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), The evolution of parental care (pp. 40–61). Oxford, UK: Oxford University Press.
Argoud, M., Mocotte, J., & Sternalski, R. (1982). Mise au point d’une microtechnique de laboratoire destinée à produire un matériel biologique de qualité pour rechercher et contrôler des produits de préservation du bois. Bois Et Forêts Des Tropiques, 196, 46–50.
Bagnères, A.-G., & Hanus, R. (2015). Communication and social recognition in termites. In L. Aquiloni, & E. Tricarico (Eds.), Social recognition in invertebrates (pp. 193–248), Cham, Switzerland: Springer.
Balshine, S. (2012). Patterns of parental care in vertebrates. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), The evolution of parental care (pp. 62–80), Oxford, UK: Oxford University Press.
Bignell, D. E., Roisin, Y., & Lo, N. (2011). Biology of termites: A modern synthesis, 2nd ed. London, UK: Springer.
Blomquist, G. J., & Bagnères, A.-G. (2010). Insect hydrocarbons: Biology, biochemistry, and chemical ecology. Cambridge, UK: Cambridge University Press.
Boomsma, J. J. (2009). Lifetime monogamy and the evolution of eusociality. Philosophical Transactions of the Royal Society of London. Series B, 364, 3191–3207. https://doi.org/10.1098/rstb.2009.0101
Brossette, L., Bagnères, A.-G., Millot, A., Blanchard, S., Dupont, S., & Lucas, C. (2017). Termite’s royal cradle: Does colony foundation success differ between two subterranean species? Insectes Sociaux, 64, 515–523. https://doi.org/10.1007/s00040-017-0571-x
Bulmer, M. S., Bachelet, I., Raman, R., Rosengaus, R. B., & Sasisekharan, R. (2002). Molecular cloning of lysozyme-encoding cDNAs expressed in the salivary gland of a wood-feeding termite, Reticulitermes speratus. Insect Biochemistry and Molecular Biology, 32, 1615–1624. https://doi.org/10.1016/S0965-1748(02)00100-5
Fujita, A., Shimizu, I., & Abe, T. (2001). Distribution of lysozyme and protease, and amino acid concentration in the guts of a wood-feeding termite, Reticulitermes speratus (Kolbe): Possible digestion of symbiotic bacteria transferred by trophallaxis. Physiological Entomology, 26, 116–123. https://doi.org/10.1046/j.1365-3032.2001.00224.x
Funaro, C. F., Böröczky, K., Vargo, E. L., & Schal, C. (2018). Identification of a queen and king recognition pheromone in the subterranean termite Reticulitermes flavipes. Proceedings of the National Academy of Sciences of the United States of America, 115, 3888–3893.
Gamboa, G. J., Reeve, H. K., & Holmes, W. G. (1991). Conceptual issues and methodology in kin-recognition research: A critical discussion. Ethology, 88, 109–127. https://doi.org/10.1111/j.1439-0310.1991.tb00267.x
Harrison, F., Bart, A., Cuthill, I., & Szekely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. Journal of Evolutionary Biology, 22, 1800–1812. https://doi.org/10.1111/j.1429-9101.2009.01792.x
Hartke, T. R., & Baer, B. (2011). The mating biology of termites: A comparative review. Animal Behavior, 82, 927–936. https://doi.org/10.1016/j.anbehav.2011.07.022
Hoffmann, K., Gowin, J., Hartfelder, K., & Korb, J. (2014). The scent of royalty: A P450 gene signals reproductive status in a social insect. Molecular Biology and Evolution, 31, 2689–2696. https://doi.org/10.1093/molbev/msv021
Howse, P. (1965). On the significance of certain oscillatory movements of termites. Insectes Sociaux, 12, 335–345. https://doi.org/10.1007/BF02222723
Hunt, J., & Richard, F.-J. (2013). Intracolony vibroacoustic communication in social insects. Insectes Sociaux, 60, 403–417. https://doi.org/10.1007/s00040-013-0311-9
Jennions, M. D., Kahn, A. T., Kelly, C. D., & Kokko, H. (2012). Meta-analysis and sexual selection: Past studies and future possibilities. Evolutionary Ecology, 26, 1119–1151. https://doi.org/10.1007/s10682-012-9567-1
Kirchner, W., & Minkley, N. (2003). Nestmate discrimination in the harvester termite Hodotermes mossambicus. Insectes Sociaux, 50, 222–225. https://doi.org/10.1007/s00040-003-0667-3
Klug, H., & Bonsall, M. B. (2010). Life history and the evolution of parental care. Evolution, 64, 823–835. https://doi.org/10.1111/j.1558-5646.2009.00854.x
Klug, H., & Bonsall, M. B. (2014). What are the benefits of parental care? The importance of parental effects on developmental rate. Ecology and Evolution, 4, 2330–2351. https://doi.org/10.1002/ece3.1083
Korb, J., Buschmann, M., Schafberg, S., Liebig, J., & Bagnères, A.-G. (2012). Brood care and social evolution in termites. Proceedings of the Royal Society of London, Series B: Biological Sciences, 279, 2662–2671. https://doi.org/10.1098/rspb.2011.2639
Kramer, J., & Meunier, J. (2018). The other facets of family life and their role in the evolution of animal sociality. Biological Reviews, https://doi.org/10.1111/brv.12443
Kramer, J., Körner, M., Diehl, J. M., Scheiner, C., Yüksel-Dadak, A., Christi, T., ... Meunier, J. (2017). When earwig mothers do not care to share: Parent-offspring competition and the evolution of family life. Functional Ecology, 31, 2098–2107. https://doi.org/10.1111/1365-2435.12915
Leniaud, L., Darrouzet, E., Dedeine, F., Ahn, K., Huang, Z., & Bagnères, A.-G. (2011). Ontogenetic potentialities of the worker caste in two sympatric subterranean termites in France. Evolution & Development, 13, 138–148. https://doi.org/10.1111/j.1525-142X.2011.00464.x
Lessells, C. (2012). Sexual conflict. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), The evolution of parental care (pp. 150–170). Oxford, UK: Oxford University Press.

Orcid
Joël Meunier. https://orcid.org/0000-0001-6893-2064
Christophe Lucas. http://orcid.org/0000-0003-2839-7583
Lucas, C., Brossette, L., Lefloch, L., Dupont, S., Christidès, J.-P., & Bagnères, A.-G. (2018). When predator odor makes groups stronger: Effects on behavioral and chemical adaptations in two termite species. Ecological Entomology, 43(4), 513–524.

Lucas, C., Pho, D. B., Fresneau, D., & Jallon, J. M. (2004). Hydrocarbon circulation and colonial signature in Pachycondyla villosa. Journal of Insect Physiology, 50, 595–607. https://doi.org/10.1016/j.jpinsphys.2004.04.006

Lucas, C., Pho, D. B., Fresneau, D., & Jallon, J. M. (2005). Role of cuticular hydrocarbons in the chemical recognition between ant species in the Pachycondyla villosa species complex. Journal of Insect Physiology, 51, 1148–1157. https://doi.org/10.1016/j.jpinsphys.2005.06.003

Matsuura, A., Yao, M., Aizawa, T., Koganesawa, N., Masaki, K., Miyazawa, M., ... Nitta, K. (2002). Structural analysis of an insect lysozyme exhibiting catalytic efficiency at low temperatures. Biochemistry, 41, 12086–12092.

Miranbito, D., & Rosengaus, R. (2016). A double-edged sword? The cost of proctodeal trophalaxis in termites. Insectes Sociaux, 63, 135–141. https://doi.org/10.1007/s00040-015-0448-9

Nalepa, C., Bignell, D., & Bandi, C. (2001). Detritivory, coprophagy, and the occurrence of colony fusion in a European population of the American termite Reticulitermes flavipes. Insectes Sociaux, 48, 194–201. https://doi.org/10.1007/PL00001767

Nalepa, C. A., & Jones, S. C. (1991). Evolution of monogamy in termites. Biological Reviews, 66, 83–97. https://doi.org/10.1111/j.1469-185X.1991.tb01136.x

Perdereau, E., Bagnères, A.-G., Dupont, S., & Dedeine, F. (2010). High occurrence of colony fusion in a European population of the American termite Reticulitermes flavipes. Insectes Sociaux, 57, 393–402. https://doi.org/10.1007/s00040-010-0096-z

Perdereau, E., Dedeine, F., Christidès, J.-P., Dupont, S., & Bagnères, A.-G. (2011). Competition between invasive and indigenous species: An insular case study of subterranean termites. Biological Invasions, 13, 1457–1470. https://doi.org/10.1007/s10530-010-9906-5

Rosengaus, R. B., Maxmen, A. B., Coates, L. E., & Traniello, J. F. (1998). Disease resistance: A benefit of sociality in the dampwood termite Zootermopsis angusticollis (Isoptera: Termopsidae). Behavioral Ecology and Sociobiology, 44, 125–134. https://doi.org/10.1007/s002650050523

Rosengaus, R. B., & Traniello, J. F. (1991). Biparental care in incipient colonies of the dampwood termite Zootermopsis angusticollis Hagen (Isoptera: Termopsidae). Journal of Insect Behavior, 4, 633–647. https://doi.org/10.1007/BF01048075

Shellman-Reeve, J. S. (1990). Dynamics of biparental care in the dampwood termite, Zootermopsis nevadensis (Hagen): Response to nitrogen availability. Behavioral Ecology and Sociobiology, 26, 389–397. https://doi.org/10.1007/BF00170895

Shellman-reeve, J. S. (1997). Advantages of biparental care in the wood-dwelling termite, Zootermopsis nevadensis. Animal Behavior, 54, 163–170. https://doi.org/10.1016/anbe.1996.0412

Smiseth, P. T., Kölliker, M., & Royle, N. J. (2012). What is parental care? In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), The evolution of parental care (pp. 1–17). Oxford, UK: Oxford University Press.

Soroker, V., Lucas, C., Simon, T., Fresneau, D., Durand, J.-L., & Hefetz, A. (2003). Hydrocarbon distribution and colony odour homogenisation in Pachycondyla apicalis. Insectes Sociaux, 50, 212–217. https://doi.org/10.1007/s00040-003-0669-1

Trumbo, S. T. (2012). Patterns of parental care in invertebrates. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), The evolution of parental care (pp. 81–100). Oxford, UK: Oxford University Press.

Whitman, J., & Forschler, B. (2007). Observational notes on short-lived and infrequent behaviors displayed by Reticulitermes flavipes (Isoptera: Rhinotermitidae). Annals of the Entomological Society of America, 100, 763–771.

Wilson, E. O. (1971). The insect societies. Cambridge, MA: Belknap Press of Harvard University Press.

Wong, J. W., Meunier, J., & Kölliker, M. (2013). The evolution of parental care in insects: The roles of ecology, life history and the social environment. Ecological Entomology, 38, 123–137. https://doi.org/10.1111/een.12000

Zimet, M., & Stuart, A. M. (1982). Sexual dimorphism in the immature stages of the termite, Reticulitermes flavipes (Isoptera: Rhinotermitidae). Sociobiology, 7, 1–7.

How to cite this article: Brossette L, Meunier J, Dupont S, Bagnères A-G, Lucas C. Unbalanced biparental care during colony foundation in two subterranean termites. Ecol Evol. 2019;9:192–200. https://doi.org/10.1002/ece3.4710