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RESEARCH ARTICLE

The relative importance of queen and king initial weights in termite colony foundation success

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Abstract

In termites, primary reproductives proceed through dispersal flight with finite metabolic reserves. During colony foundation, the mated pair requires just enough resources to produce the first few workers, through biparental care. When alloparental care is established, the primary reproductives are fully supported by their own offspring. It was, therefore, argued that the pressure to accumulate large quantities of metabolic reserves in termite imagoes was relaxed over evolutionary time, which resulted in a progressive reduction in alate size compared to ancestral wood roaches. However, such directional reduction in size may partially be countered if mated pairs with relatively large internal metabolic resources are more successful than mated pairs with relatively low internal resources. This hypothesis was tested with *Coptotermes gestroi* by establishing incipient termite colonies with a wide range of combinations of female and male initial weights in laboratory conditions. Both females and males depleted most of their internal resources within 9 months, and the combined initial weight of female and male explained 27% of the variation in incipient colony growth. Mature colonies that can invest into high-quality alates may have a slight fitness advantage; however, this advantage may be secondary to other environmental factors, as during large *Coptotermes* dispersal flights, a vast majority of alates die within the first few days, which would increase the fitness of colonies that invested in quantity over quality. Within a given termite species, the relative size of imagoes may, therefore, reflect a reproductive strategy trade-off emerging from the life history of the species.

Keywords Dispersal flight · Alates · Colony growth · *Coptotermes*

Introduction

Termite colony foundation is a critical event within the lifetime of a colony, as alates disperse from their original nest to find a mate and initiate a new colony (Nutting 1969). Termite colonies are usually founded by monogamous pairs of male and female alates following dispersal flight events (Nalepa and Jones 1991). In most instances, the success rate of colony establishment by a mating pair is extremely low (< 1%), as many factors can hinder the survival of the founding unit within the first few days of colony foundation (Nutting 1969; Chouvenc et al. 2017b). Environmental conditions during and after the dispersal flight directly influence the success of colony initiation. These conditions include alate densities, wind, temperature, humidity, predation, microbial habitat within the claustral chamber, initial access to resources, and luck (Nutting 1969; King and Spink 1975; Rosengaus and Traniello 1993; Chouvenc et al. 2017a; Kusaka and Matsuura 2018; Chouvenc et al. 2018). In addition, inherent morphological and physiological characteristics of the founders may influence initial colony success (Shellman-Reeve 1996; Matsuura and Nishida 2001; Mullins and Su 2018; Cole et al. 2018).

In various social insects, large body size of colony founders can have a positive impact on survival traits, mating success, fertility, or colony foundation success (Vargo and Fletcher 1989; Wiernasz and Cole 2003; Kovacs et al. 2008; Kovacs and Goodisman 2012). However, the influence of alate body size on dispersal flight abilities (Chouvenc et al. 2017b), mating success (Matsuura and Nishida 2001; Husseneder and Simms 2008), and colony foundation success and survival (Cole et al. 2018) in termites remains largely unexplored, as compared to social Hymenoptera (Hartke

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and Baer 2011). As with most other eusocial insects, colony foundation in termites is the only time within the life of the colony when primary reproductives are the sole providers of brood care toward their first emerged offspring. As a result, the overall quality of the founding female and male may influence initial colony growth (Oster and Wilson 1978; Shellman-Reeve 1990; Shimada et al. 2013; Chouvenc et al. 2015a, 2017a). In termites, the first few eggs laid during the foundation of the colony are solely reliant on the parental care of the king and queen (Shellman-Reeve 1990; Rosengaus and Traniello 1991; Matsuura and Kobayashi 2010). However, biparental care rapidly transitions to alloparental care as soon as the first functional workers are present in the colony (Nalepa 2015; Chouvenc and Su 2017). Therefore, queen and king initial reserves may be critical components of colony foundation success, and may be a limiting factor determining how much they can invest in their first brood (Shellman-Reeve 1997; Shimada et al. 2013; Johnston and Wheeler 2007; Cole et al. 2018).

In many social insects, mating with relatively small partners can be disadvantageous for colony success, and may sometimes result in some forms of sexual selection (Schlüns et al. 2003; Couvillon et al. 2010). However, in termites, there is little evidence for sexual selection, or at most, the importance of sexual selection may be secondary to more critical selective pressures during and after dispersal flight events (Matsuura and Nishida 2001; Hartke and Bear 2011; Chouvenc et al. 2018b; Kusaka and Matsuura 2018). Nalepa (2011) argued that in incipient termite colonies, the rapid switch from biparental care of the first brood to alloparental care of subsequent broods resulted in relaxed selection for the accumulation of large metabolic reserves in imagoes, because queen and king fecundity is maintained despite a relatively small body size (when compared to their ancestral wood roaches). The directional reduction of body size in termite imagoes may, therefore, have allowed mature colonies to increasingly invest into the number of alates, so as to optimize their alate dispersal success rate.

The limited metabolic reserves of termite alates during colony foundation leave little room for inefficiency. Chouvenc and Su (2017) showed that 5 months after termite colony foundation, the shift to alloparental care was already irreversible, as the royal pair was not able to compensate for the loss of their alloparents. The quality of the first brood is important for colony foundation success (Chouvenc et al. 2015a) and the initial input from the queen and king in the form of biparental care (Shellman-Reeve 1997), symbiotic microbes (Shimada et al. 2013), nitrogen resources (Mullins and Su 2018), and immunocompetence (Cole et al. 2018) are critical to jump-start the colony. Thus, there are potentially two selective pressures pulling the evolution of the size of alates in opposite directions: despite directional selection for relatively small size of imagoes in termites owing to their eusociality (Nalepa 2011, 2015), contrary selection forces may maintain a relatively large size in alates of both sexes, by favoring mature colonies that invest in "high quality alates", because of the critical need for initial resources during the upcoming incipient colony phase.

The high intra- and intercolonial variability of the size of alates produced by mature colonies during a termite dispersal flight (Chouvenc et al. 2017b) may influence the success of founding events. Since primary reproductives invest most of their reserves in their initial brood, there may be a positive correlation between the initial reserves of the queen and king and long-term colony success. This study investigates the importance of the initial body weight of alates in *Coptotermes gestroi* (Blattodea: Isoptera: Rhinotermitidae) on the success of colony foundation.

Materials and methods

Coptotermes gestroi incipient colony foundation

Coptotermes gestroi is a termite species originating from Southeast Asia, and is now invasive in many parts of the neotropics, where it has a major economic impact (Scheffrahn and Su 2005). Alates from *C. gestroi* dispersal flights were collected in Broward County (Florida, USA) on the evening of 6 March 2015 with a single light trap, as described by Chouvenc et al. (2015b). More than 27,000 termite alates were collected within 45 min at dusk, were placed in a 35 × 24 × 17 cm container with moist corrugated cardboard, and brought to the laboratory on the morning after the dispersal flight. Owing to the high colony density of this invasive species in the sampled area (Chouvenc et al. 2016), it is presumed that alates originated from a multitude of closely related colonies. The sex of dealates was determined morphologically, as only females have their last abdominal sternites fused to form a genital plate. More than 200 male and 200 female dealates were randomly picked from the general pool, sorted, and kept in separate 10 cm diameter Petri dishes in groups of ≈ 100 termites, with a moist filter paper on the bottom, for up to 4 h before being used for colony foundation. One male and one female were haphazardly selected from their respective groups, weighed independently on a microscale at the 0.1 mg precision level, then paired and introduced in a rearing unit. The number of replicates for rearing units was progressively increased ($n = 175$) until a wide range of female-male weight combinations was obtained, as shown in Fig. 1.

Rearing units were made of 37.5 ml cylindrical vials (2.5 cm diameter × 7.8 cm height), containing organic soil, wood pieces (*Picea* sp.) and a layer of 3% agar, which provided sufficient moisture for the duration of the experiment. Rearing units ($n = 175$) were stored at 2 °C for 9 months.

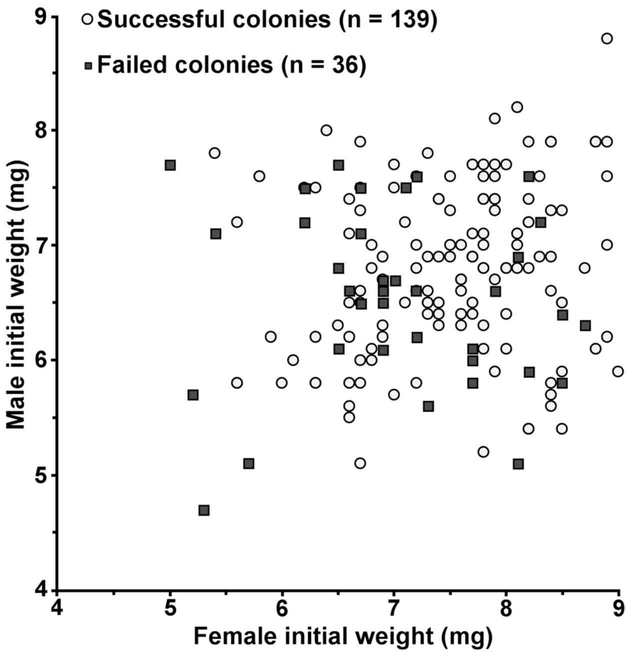

Fig. 1 Distribution of all *Coptotermes gestroi* female-male parings by weight ($n=175$ colonies) in this study. Black squares indicate pairings that resulted in failed colonies at 9 months ($n=36$ colonies), while white circles indicate pairings that resulted in successful colonies at 9 months ($n=139$ colonies)

After 9 months of development, all 175 rearing units were opened and processed to count all castes (eggs, larvae, workers, soldiers, queen, and king). The entire termite colony biomass was measured, and the final king and queen weights were also measured, if present.

Statistical analysis

In this study, at the 9-month census, a colony was determined as "successful" if it contained both the primary reproductives (king and queen), viable brood and a viable workforce (numerous workers and soldiers). If a colony was missing at least one of the two primary reproductives, or did not possess any brood (no larvae, workers or soldiers), it was determined as a "failed" colony. The "female + male" weight corresponds to the added weight of both reproductives in a given rearing unit. To determine if the initial weight of kings and queens was significant factors for colony foundation success, the initial weight of females, males, and female + male from successful colonies were, respectively, compared to the initial weight of females, males, and female + male from failed colonies, using independent Student *t* tests. Weight values in the text represent the mean ± SE.

In each of the 139 successful colonies, the weight loss of the king and queen during the 9 months of the experiment was determined by subtracting the final individual weight from their initial weight at day 0. To test if the loss of weight was significant in females, males, and females + males, a paired Student *t* test was used for each factor. To determine if weight loss of individuals at 9 months was a function of their initial weight, a Spearman correlation ρ (rho) test and a linear model (R Core Team 2018, version 3.5.0) were used with initial weight as a factor and weight loss as a variable, for each independent sex and their added weight.

Finally, as the numbers of eggs, larvae, workers, soldiers, and soldier ratio were highly variable, depending on the degree of development of each colony at 9 months (no significant correlation for the number of eggs, larvae, worker, and soldiers, with initial queen and king weights, data not shown), the total colony biomass was used as a proxy for the overall colony growth. As above, a linear model was used to determine if the initial weight of females, males, and females + males were significant predictors of colony growth at 9 month after foundation. In addition, to disentangle the relative contributions of the initial female weight and initial male weight on colony growth, the relative importance of each initial weight was determined by following the method developed by Grömping (2006), using the default method "lmg" in the "relaimpo" R package (R Core Team 2018), and the variability of the two regressor estimates was tested with bootstrapping (1000 runs) and by comparing their 95% CI overlap.

Results

Sexual dimorphism in alates

The initial weights of females and males of *C. gestroi* were highly variable (Fig. 1), with females ranging from 5.00 to 9.00 mg and males ranging from 4.70 to 8.80 mg. However, a significant sexual dimorphism was observed between females (7.40 ± 0.07 mg) and males (6.75 ± 0.06 mg), as males were in average 8.8% smaller than females (*t* test, $t=7.34$, $df=348$, $p<0.001$).

Influence of initial queen and king weights on colony success

Out of the 175 colonies, 36 failed and 139 had successfully established within 9 months after foundation (79.4% foundation success rate). Among the 36 failed colonies, 22 had lost both the queen and king, 7 colonies were missing the male, 6 colonies were missing the female, and only 2 colonies still had both a live queen and king, but had no brood (Table 1). No colony, successful or failed, produced nymphs or secondary reproductives (Chouvenc et al. 2015c). When comparing the initial weight of the reproductives in successful and failed colonies, both females (7.49 ± 0.07 mg) and males

Table 1 Status of colonies regarding the presence of the king, the queen, and brood by 9 months ($n = 175$ colonies)

Individual status	Colony status							
	Successful	Failed						
Queen present	Yes	Yes	Yes	No	Yes	No	No	No
King present	Yes	Yes	No	Yes	No	Yes	No	No
Brood present	Yes	No	Yes	Yes	No	No	Yes	No
Number of colonies	139	2	3	2	3	4	0	22

(6.81 ± 0.10 mg) from successful colonies were significantly heavier than females (7.04 ± 0.16 mg, i.e., 6.1% smaller) and males (6.53 ± 0.13 mg, i.e., 4.1% smaller) from failed colonies, respectively (*t* test, $t = 2.81$, $df = 173$, $p = 0.005$, and $t = 2.01$, $df = 173$, $p = 0.046$, respectively) (Fig. 2a). In addition, the initial weight of females + males was also a significant predictor for colony success, as successful colonies had an higher combined weight of their primary reproductives (14.30 ± 0.10 mg) than failed colonies (13.57 ± 0.20 mg, i.e., 5.2% smaller) (*t* test, $t = 3.25$, $df = 173$, $p = 0.001$).

Queen and king weight losses within 9 months after colony foundation

Nine months after colony foundation, both the queen (6.62 ± 0.05 mg) and king (5.55 ± 0.04 mg) from successful colonies had lost significant weight (Fig. 2b) compared to their initial weight at day 0 (paired *t* test, $t = 18.44$, $df = 138$ $p < 0.001$, and $t = 24.59$, $df = 138$, $p < 0.001$, respectively). However, kings had lost significantly more weight (1.27 ± 0.05 mg loss) than queens (0.86 ± 0.05 mg loss) (*t* test, $t = 5.71$, $df = 276$ $p < 0.001$). Proportionally, kings lost 18.01% of their initial weight, while female lost 11.14% of their initial weight. Cumulatively, queen + king weight (12.17 ± 0.05 mg) at 9 months was significantly lower (14.9% weight loss) than their initial weight (paired *t* test, $t = 27.85$, $df = 138$, $p < 0.001$). Finally, strong positive correlations between the initial weight of the queen and king and their final weight loss were found (Fig. 3a, b), and overall, the added queen + king initial weight was also positively correlated with their added weight loss (Fig. 3c).

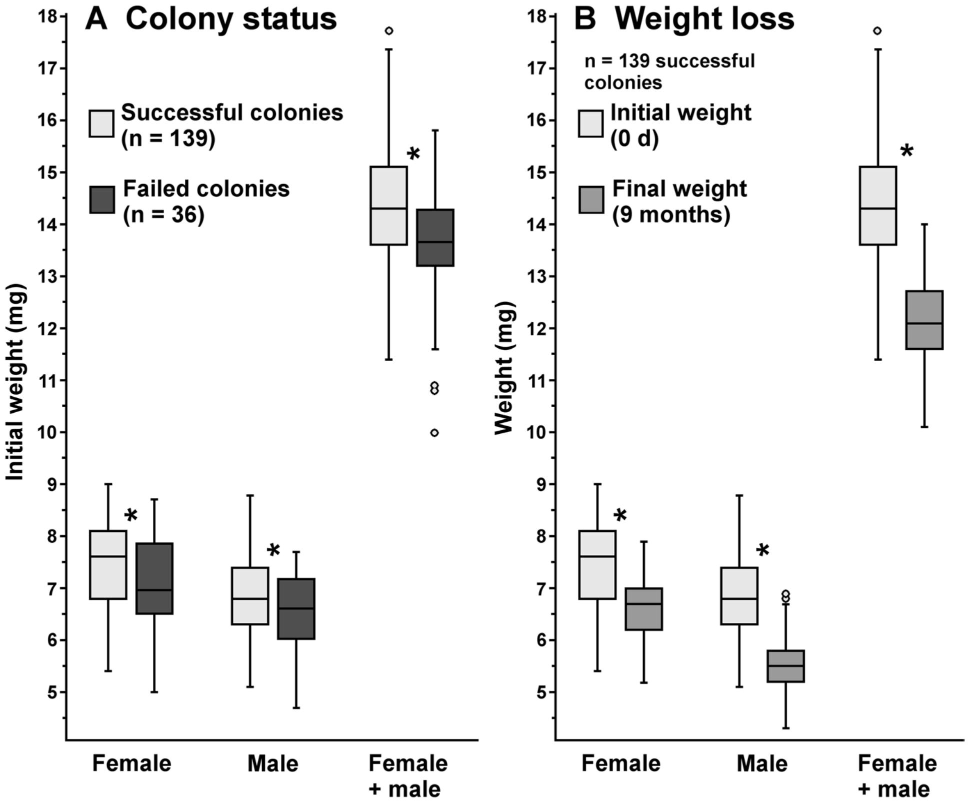

Fig. 2 Importance of individual initial weight on colony success at 9 months. **a** Status of the colonies in relation with the initial weights of individuals ($n = 175$ colonies), **b** weight loss between day 0 and 9 months in successful colonies ($n = 139$ colonies), *significant weight loss over time (paired *t* test, $p < 0.05$)

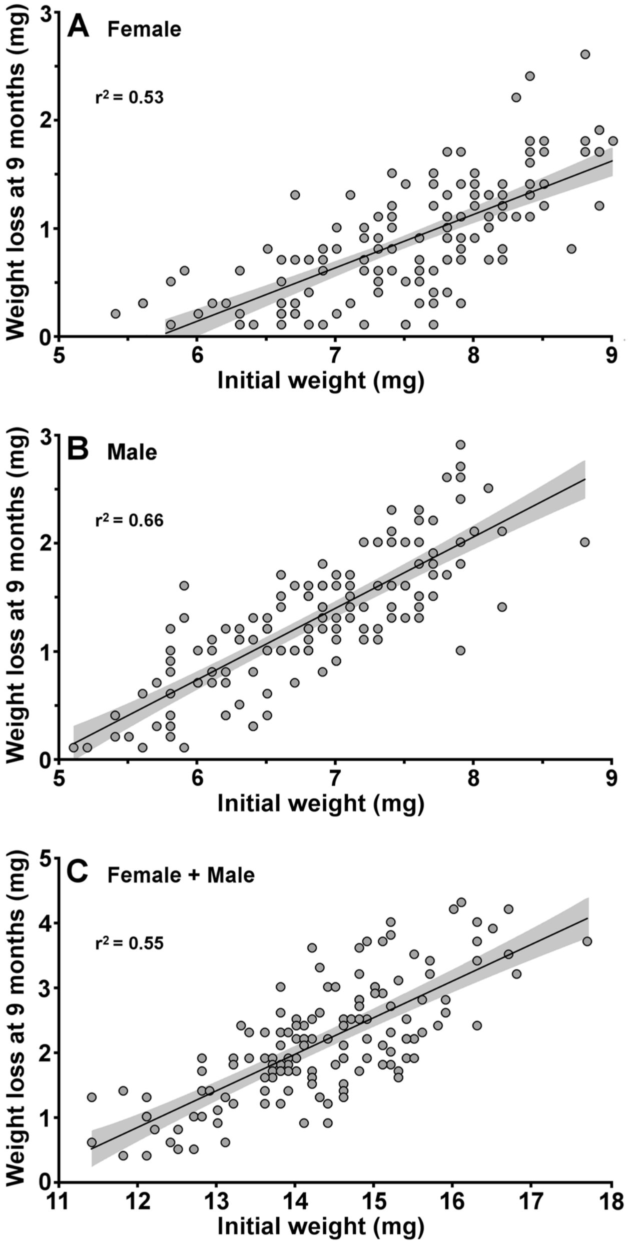

Fig. 3 Relationship between primary reproductive initial individual weights and their weight loss at 9 months in successful colonies ($n = 139$ colonies). **a** Females (Spearman $\rho = 0.75$, $p < 0.001$), **b** males (Spearman $\rho = 0.81$, $p < 0.001$), **c** females + males (Spearman $\rho = 0.72$, $p < 0.001$). Linear models are presented with their 95% CI and their coefficient of determination

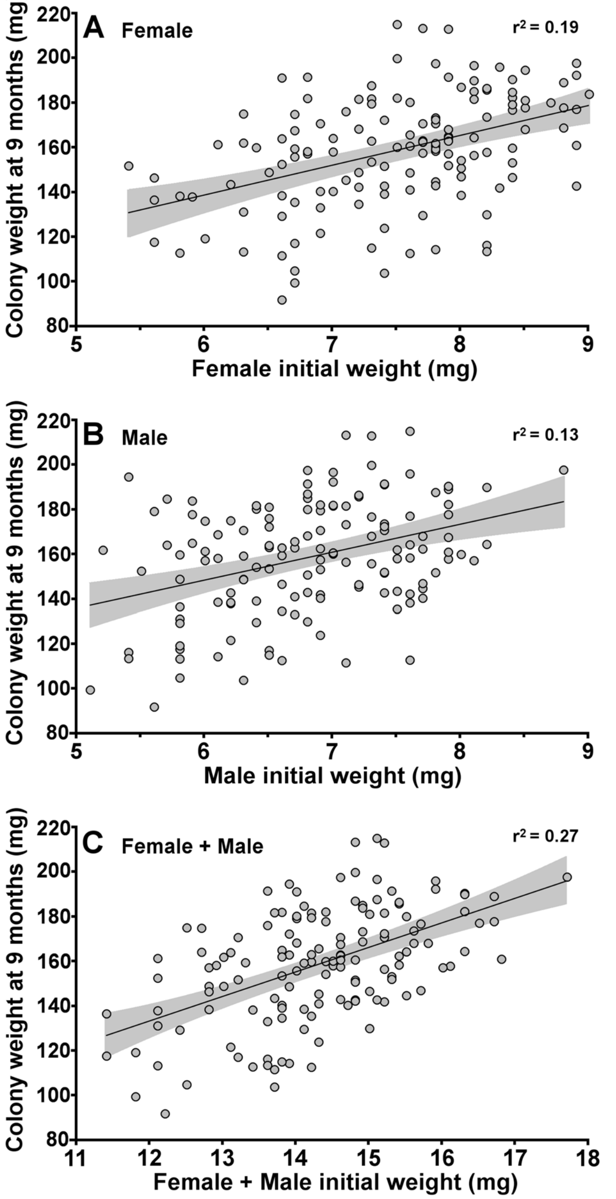

Fig. 4 Relationship between primary reproductive initial individual weights and colony growth at 9 months in successful colonies ($n = 139$ colonies). **a** Females (Spearman $\rho = 0.44$, $p < 0.001$), **b** males (Spearman $\rho = 0.31$, $p < 0.001$), **c** females + males (Spearman $\rho = 0.71$, $p < 0.001$) (additive effect only, with both initial weight being equally important contributors for colony growth, see text). Linear models are presented with their 95% CI and their coefficient of determination

Role of the initial weight of the queen and king on colony growth

Total colony biomass was used as a measurement of colony growth at 9 months. Again, both female and male initial weights were independent significant predictors for colony growth (Fig. 4a, b). However, the linear models provided relatively weak coefficients of determination ($\rho = 0.44$, $R^2 = 0.19$ for females, and $\rho = 0.31$, $R^2 = 0.13$ for males) owing to a large variance of colony growth (from 91.2 to 214.5 mg) and the female and male initial weights as confounding factors. When combined, the female + male initial weight was a more robust predictive factor ($\rho = 0.71$, $R^2 = 0.27$) (Fig. 4c). From this last linear model, the relative contributions of the female and male initial weights on colony growth were determined (Grömping 2006), and female initial weight explained 16% of the colony growth variability, while the male initial weight explained 11% of the colony growth variability (Fig. 4c). The importance of both female and male weights was significantly different from 0, while the interaction of the two factors was not, based on the 95% CI overlap of the regressor estimates tested with bootstrapping (1000 runs). Therefore, the contribution of the female and the male weights to colony growth was simply additive. Finally, it was not possible to fully disentangle the relative contribution of the female and the male initial weights as assessed by the overlap of their 95% CI. This indicated that the relative contribution from the females (16%) and the males (11%) was not significantly different, implying that both female and male initial weights were equally important contributors for colony growth ($n = 139$).

Discussion

This study showed that in controlled laboratory conditions, the initial weight of founders in *C. gestroi* is a relevant factor for successful colony establishment. Successful incipient termite colonies had larger queens and kings than failed colonies, and among successful colonies, there was a positive correlation between the initial weights of the reproductives and colony growth at 9 months. In addition, there was a positive correlation between the primary reproductives initial weights and their respective weight loss after 9 months, suggesting that large primary reproductives were able to provide more resources to their offspring than small primary reproductives. Overall, both the female and male initial weights were significant factors for colony growth, which supports the importance of biparental care in termite incipient colonies (Nalepa 1994, 2015; Rosengaus and Traniello 1991; Shellman-Reeve 1997). In *C. gestroi*, the initial weights of the female and the male are equally important factors during colony foundation, although even when combined, the primary reproductive weights only explained 27% of the observed colony growth variability. Such a result highlights that, even in highly standardized rearing conditions with a high survival rate (~ 80%), the quality of the brood (here measured from the colony biomass) was highly variable, and 73% of such variability was not explained by the initial body weight of the queen and the king. Other factors such as stress during dispersal flight, the unknown level of inbreeding among the mating pairs, variable quality of the biparental brood care behaviors, and other potential biological incompatibilities between the mated pair, could also influence the initial colony growth. In addition, the initial hydration levels among alates may have differed, resulting in the high variability observed in the relationship between initial weight and colony success. However, such confounding factors could not be disentangled in the current study owing to the destructive nature of the protocol to obtain initial dry weights. Nonetheless, this aspect deserves further investigation.

Sexual dimorphism is common in termite alates. Females tend to be larger than males, as females potentially require more resources than males for the initial egg production compared to sperm production (Nutting 1969; Thorne 1983; Matsuura 2006). The current study showed that *C. gestroi* male alates were on average 8.8% smaller by fresh weight than their female counterparts. However, both primary reproductives lost significant weight in the first 9 months of colony foundation, and males proportionally lost more weight than females. Such observations reinforce the importance of the male contribution (direct or indirect) to the brood in a termite incipient colony (Shellman-Reeve 1990; Matsuura and Nishida 2001; Brossette et al. 2018). Queens apparently lost less weight than males, although by 9 months, queens have already initiated the maturation of their ovaries toward early physogastry (Higa 1981) and likely have started to regain some weight as a consequence of an established alloparental care. In addition, there was a strong positive correlation between individual initial weight and weight loss at 9 months for both queens and kings. This suggests that the primary reproductive pairs have invested (and potentially depleted) most of their internal reserves, regardless of their initial weight. Both reproductives have depleted most of their initial reserves by 5 months post-foundation (Chouvenc and Su 2017), and the current study suggests that the initial input of a given primary reproductive toward the first brood may be directly limited by its initial body weight.

This study confirmed that during colony foundation in laboratory conditions, the initial weight of *C. gestroi* females and males has a role in colony foundation establishment rates and initial colony growth (Matsuura and Nishida 2001; Cole et al. 2018). However, in field dispersal flights, where the vast majority of alates do not survive more than a few days, and where founding conditions are highly heterogeneous and hazardous, the importance of alate weight may be secondary to many other environmental factors (Nutting 1969). The current study also showed that even relatively small primary reproductives still had a chance to establish and initiate colony growth and that despite limited metabolic resources, they were sufficient to start a colony. As previously suggested (Hartke and Bear 2011), sexual selection for large alate body size in termites during and after large dispersal flights may be extremely weak, and secondary to a wide variety of other selective pressures. Nalepa (2011) made the case that throughout the evolution of termites, rapid transition to alloparental care in incipient colonies relaxed the need for the accumulation of large reserves in alates, progressively resulting in a reduction of termite alate relative body size. However, as the mating pair still requires a bare minimum of initial metabolic resources to initiate efficient colony foundation and provide biparental care, the reproductive strategy in the production of alates by mature colonies of a given species may have reached an evolutionary compromise between the two opposite selective forces driving for alate body size.

Mating flights in *C. gestroi* termites can comprise hundreds of thousands of alates (Chouvenc et al. 2017b), where the large quantity of alates produced may be more relevant for the final number of established incipient colonies, than the marginal advantage that relatively large alates may have during colony foundation. Such a reproductive strategy primarily relies on "inundative" dispersal flights, which may also have reduced the importance of alate weights during colony foundation. The trajectory of the reproductive strategy of a given termite species may partially be reflected in the current size of their imagoes, in a balanced investment into reproduction which reflects the life history of the species. Over evolutionary time, termite colonies have optimized this quality/quantity trade-off in alate production, which varies greatly among species. On one hand, mature colonies may have an incentive to invest in high-quality alates (which would be metabolically expensive to produce) to increase their foundation success rates during dispersal flights. On the other hand, they also have a competing incentive to invest just the bare minimum of resources in alates (which would be cheap to produce) to maximize the quantity of alates produced. In the light of its remarkable invasive abilities (Chouvenc et al. 2016), *C. gestroi* may be a termite species that was able to efficiently optimize such balanced investment and adapt to various environmental pressures during dispersal flights and colony foundation.

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