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Research article

Male or female soldiers? An evaluation of several factors which may influence soldier sex ratio in lower termites

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Abstract. In termites, the soldiers' sex ratio is often biased toward one sex. Unlike in the Hymenoptera, this bias cannot easily be explained by relatedness asymmetries because termites are diploid. Matsuura proposed that when large body size is adaptive for colony defence (e.g. in case of phragmotic defence) then the larger sex (given sexual size dimorphism exists) should be more likely to reach a threshold size and develop into soldiers. This would explain biased sex ratios. Matsuura validated his hypothesis for four *Reticulitermes* species. Here, we tested his hypothesis for two species of *Cryptotermes* with phragmotic defence. These drywood termites have a life type that is thought to be ancestral in termite's evolution, thus giving us potential insights into the evolution of the soldier caste. In one of these species, the sex ratio of soldiers was highly female biased, but we could not support Matsuura's hypothesis. Both species lacked sexual size dimorphism in all castes. Additionally, in both species, the sex ratio of helpers and sexuals did not deviate from a 1:1 ratio, and hence can also not account for the bias observed in soldiers. However, this study showed that there were behavioural differences between the sexes in both species, which could shed some light on biased sex ratio in soldiers. Our findings also indicate that the developmental pathway taken by individuals reflects a 'decision' at the colony level. The discovery of behavioural differences between sexes in termites should open the way to similar studies in other taxa with helpers/ workers of both sexes, as it might reveal more task partitioning in colonies than previously thought and it raises questions concerning the selective pressures that acted on caste evolution in termites.

Keywords: Cryptotermes, sex ratio, sexual dimorphism, sexual specialization, soldiers.

Introduction

Eusociality often implies that some individuals permanently forego reproduction to the benefit of others, resulting in reproductive and non reproductive (altruistic) castes. A central question in the study of eusociality concerns the mechanisms leading to the evolution of these altruistic castes, amongst which is the soldier caste. The soldier caste in termites is unique both in its exclusive defensive function and its development. Soldiers are ancestral in termites and evolved prior to a true worker caste (i.e. a helper caste with reduced reproductive potential). Unlike the soldiers found in other social insects, this caste has a single origin in termites (Noirot and Pasteels, 1987). Our purpose here is to investigate potential mechanisms involved in the differentiation of soldiers from immature individuals, thus unveiling key processes in soldier caste evolution.

In lower termites, the soldier caste is the only completely sterile caste (see below) and the sex ratio of this caste is often biased (Matsuura, 2006). Until recently, there was no explanation for this bias: as termites are diploid, theories based on relatedness asymmetries (Trivers and Hare, 1976), similar to those for social Hymenoptera, cannot be easily applied to termites (with the exception of some species with chromosomal translocations to sex chromosomes; Roisin, 2001). But recently Matsuura (2006) proposed sexual size dimorphism as a potential explanation for skewed sex ratios in soldiers. In termites, fecundity is often correlated with female body size, usually resulting in females being larger

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than males (Noirot, 1990). Assuming this size difference also occurs in workers (which can potentially develop into soldiers, see below), species for which large soldiers are adaptive should have a soldier sex ratio that is biased toward the larger sex. This would result because large individuals, which have a high probability of belonging to the larger sex, would be more likely to reach a threshold size and develop into soldiers than small individuals. In termites, large soldiers might not be adaptive for all species (e.g. in species with mass defence), but in species with phragmotic defence, large body size seems to offer advantages. These species have soldiers with plug-like heads, and when the colony is attacked, the soldiers block the nest entrances with their head. A large head should be more efficient at blocking the colony's tunnels than a small one, and thus large soldiers should be selected during evolution (Matsuura, 2006).

Matsuura (2006) found substantial support for his hypothesis in four *Reticulitermes* (Rhinotermitidae) species with phragmosis. Species with sexual size dimorphism in sexuals also had sexual size dimorphism in workers and the sex ratio of the soldier caste was biased towards the larger sex. Here, we test his hypothesis for two *Cryptotermes* species (Kalotermitidae) with a life type that is thought to be ancestral in termite evolution (Roisin, 2000; Thorne and Traniello, 2003; Korb, 2007a; Inward et al., 2007b). They are one-piece nesters, i.e. they live in a single piece of dead wood that serves both as nest and food. In contrast, *Reticulitermes* belongs to the multiple-pieces nesters that forage outside the nest (Roisin, 2000). Associated with the one-piece nesting type is a flexible development in which all 'workers' are totipotent to explore all caste options (Lüscher, 1974; Roisin, 2000; Korb and Katrantzis, 2004). Hence, there is no genuine worker caste (Roisin, 2000; Korb, 2007b). They build the platform from which three permanent castes develop: (i) sterile soldiers, (ii) winged sexuals that leave the nest and found new colonies as primary reproductives or (iii) neotenic replacement reproductive that inherit the natal breeding position when the same-sex reproductive of the colony dies or becomes unhealthy. Thus, in contrast to what was recently found for a *Reticulitermes* species (Hayashi et al., 2007), caste development is not determined genetically. Each individual is totipotent and caste development is a conditional tactic, depending on environmental conditions, such as food availability, colony size, or the presence/absence of other castes (e.g. Roisin, 2000; Korb et al., 2003; Korb and Lenz, 2004). Because these immature members of the colony retain the ability to develop into sexuals and because new evidence for *Cryptotermes* indicates that they are less engaged in helping to raise siblings (Korb, 2007b), they are referred to as 'false workers' in this study (Roisin, 2000). The only imagos in a colony are the soldiers and the sexuals. Soldiers are sterile, and thus are the only individuals in a colony to forego all hope of reproduction (Roux and Korb, 2004).

Cryptotermes' life-type, selective regime and mechanisms of soldier caste determination might be similar to those found in termites' ancestors. Thus, this genus might provide insights into soldier caste evolution. The two species studied here, *Cryptotermes secundus* and *C. domesticus,* were chosen for their close phylogenetic position (Thompson et al., 2000) and their similar ecological requirements (J. Korb, unpubl. results).

In addition to testing Matsuura's hypothesis, this work will also consider other factors that might influence the sex ratio of soldiers. Firstly, due to the capacity of false workers to develop into soldiers, biased sex ratios in soldiers could simply reflect biased sex ratio in false workers. Secondly, this study will also enable us to discuss behavioural differences between the sexes in termites in the light of soldier and worker/false worker evolution. Whereas workers are exclusively female in social Hymenoptera (maybe because brood care was done exclusively by females in their solitary ancestors), in *Cryptocercus* wood cockroaches (the sister group of the termites; Nalepa, 1994; Inward et al., 2007a), both sexes participate in brood care.

Materials and methods

Collection of colonies

Between 2000 and 2004, *Cryptotermes* colonies were collected from dead *Ceriops tagal* trees from mangroves in Darwin Harbour (Northern Territory, Australia). Some of these colonies were preserved in 100% ethanol, while others were set up in wood blocks (*Pinus radiata*) adjusted to colony size (Korb and Lenz, 2004). The latter were transferred to Germany and stored in climatic chambers at 28 °C and 70% relative humidity with a 12 day/night cycle (for more details see Korb and Katrantzis, 2004; Korb and Schmidinger, 2004). These conditions are appropriate for *Cryptotermes* and do not affect growth or development of colonies (for more details Korb and Katrantzis, 2004; Korb and Schmidinger, 2004).

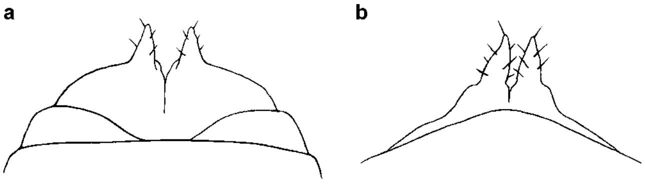
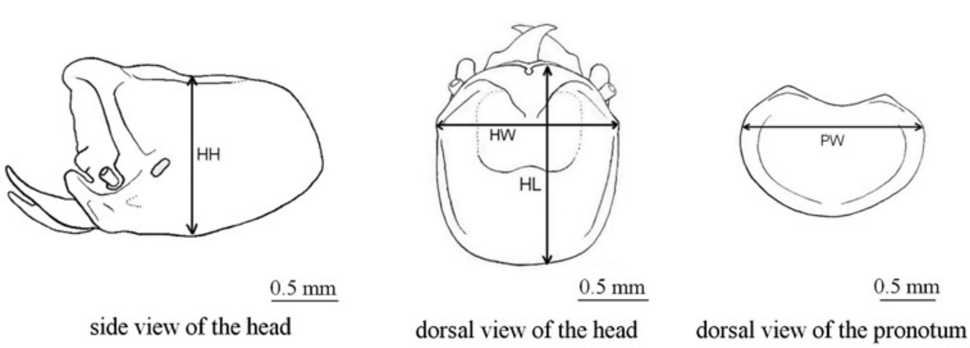


Figure 1. Schematic drawing of the ventral view of the distal end of the abdomen of *Cryptotermes* immatures showing the styli on the IXth sternite. **a.:** female immature and **b.:** male immature.

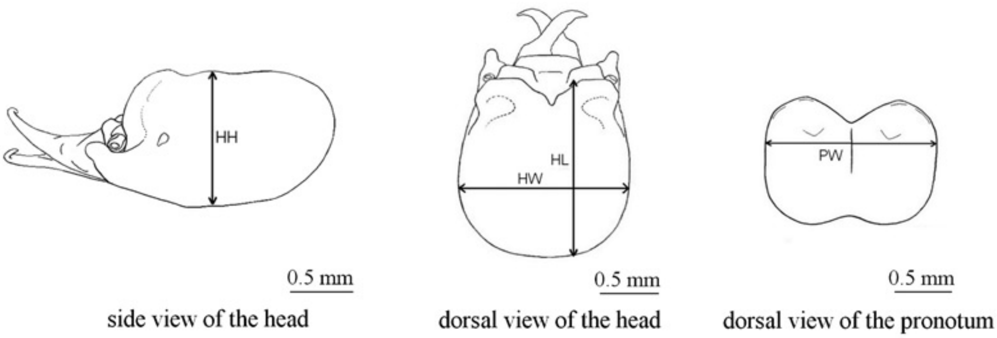
Sex identification and sex ratio

Sex identification in Kalotermitidae is based on the shape or presence of styli, which are structures found on the IXth sternite of the abdomen. For imagos, the presence of styli indicates the male sex (Lebrun, 1967). In immatures, both sexes possess styli. Whereas a characteristic ridge separates the female's styli, the space between the male's styli is smooth (Fig. 1). For identification, individuals were placed in standard position toward a light source and ethanol-preserved specimens were superficially dried prior to the identification. When necessary, the VIIIth sternite was removed on dead specimens to make the styli visible. Live specimens were immobilised using a notch in a wet sponge.

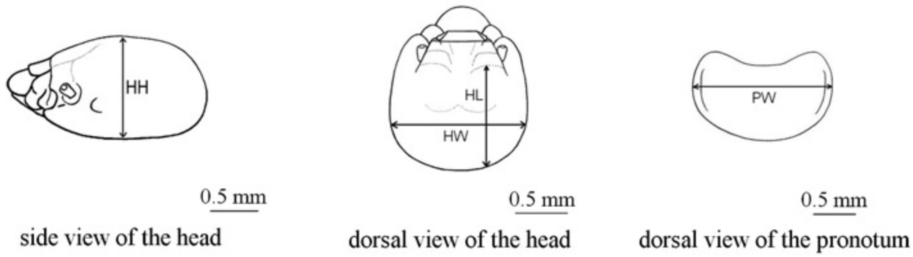
The sex ratio was determined for ethanol-preserved colonies only. Six *C. secundus* and five *C. domesticus* colonies were completely sexed.



***C. domesticus* soldier**



***C. secundus* soldier**



Both species false workers

Figure 2. Measured morphometric traits. HH: head height, HL: head length, HW: head width, PW: pronotum width. The head and pronotum of sexuals correspond to those of of false workers, therefore they are not shown here. Antennae are truncated.

To obtain a sufficient number of *C. domesticus* soldiers for statistical analyses, additional individuals from other colonies were used, raising the total number of *C. domesticus* soldiers to 52.

Behavioural observations

Prior to observation, each colony was extracted from the wood block by splitting it with hammer and chisel. The individuals extracted were counted and the colony composition was recorded according to the presence of the following castes: primary or neotenic reproductives, alates (winged sexuals), nymphs (individuals with pronounced wing buds), false workers (their wing buds, if any, were not visible with the naked eye), larvae (instar I, II and III) and soldiers (for classification details see Korb and Katrantzis, 2004). Only colonies containing both reproductives and at least one soldier were used for behavioural observations. All individuals of one colony were set up in an observation chamber of adjusted size that had been drilled in a *P. radiata* wood block (for more details see Korb and Schmidinger, 2004).

The individuals to be observed were sexed and then marked with two dots of non-toxic Revell® enamel paint (Revell, Germany). Using focal sampling, the duration or frequency of several interactive and non-interactive behaviours was recorded for 30 minutes. For interactive behaviours the role of the observed individual (whether it was the actor or the recipient of a behaviour) as well as the caste of the partner was recorded. The interactive behaviours recorded were: jerking (rapid back- and forward movements aimed at another individual), allogrooming, proctodeal trophallaxis (anal feeding) and antennation (for more details see Korb and Schmidinger, 2004). The non-interactive behaviours recorded were ‘moving’ (running or building) and resting/feeding (these were combined as they were difficult to separate unambiguously with the naked eye).

For each colony, all soldiers, both reproductives and two false workers (one of each sex) per soldier were observed. In total, 10 soldiers, 20 false workers and 14 reproductives from seven colonies were observed for *C. secundus* and 11 soldiers, 22 false workers and 8 reproductives from four colonies were observed for *C. domesticus.*

Morphometric measurements

For morphometric measurements, we used 10 male and 10 female false workers, arbitrarily selected from each of the preserved colonies (N = 6 for *C. secundus* and N = 5 for *C. domesticus*). Forty-six *C. secundus* soldiers were measured as well as all soldiers (N = 31) found in these colonies for *C. domesticus.* In order to increase the number of *C. domesticus* soldiers, additional soldiers (N = 29) present in other *C.*

domesticus colonies (N = 7) were used (total N = 60). For each individual, four morphological traits were measured: head length, head width, head height, and pronotum width (Fig. 2). The measurements were all done with a micrometric scale on a dissecting microscope (80x) with recordings to the nearest 0.01 millimetre. Whenever antennae were present, the number of antennal segments was recorded as an indicator of the developmental instar.

Data analyses

All statistical analyses were performed with SPSS 14.0. All tests were two-tailed and the alpha level was set to 0.05, except for sex ratio analyses where the same data set was analysed twice and thus the alpha level was adjusted to 0.025.

First, we tested for both species and all castes separately, the null hypothesis that the sex ratio did not deviate significantly from a 1:1 ratio using chi^2-test. This was done first for all colonies separately and then all colonies were pooled.

Both the behavioural and the morphological data were analysed using parametric statistics as the data met the appropriate assumptions. Linear Mixed Models are a powerful tool for the analysis of unbalanced hierarchical data, i.e. when an unequal number of cases are clustered within larger units and information should be analyzed at both the case and the larger unit level (Norusis, 2005). Here the observed and measured individuals were males and females that were nested into colonies. Therefore, we built mixed effect models for each observed behaviour or morphometric trait for *C. secundus* and for *C. domesticus*. Morphometrical data were analysed separately for soldiers and false workers using the morphological trait as dependent variable, colony as random factor, number of antennal segments as fixed covariate and sex as fixed factor. Behavioural observations were analysed using each behaviour as dependent variable, colony as random factor and sex and caste as fixed factor. As suggested by Norusis (2005) for such a design we used an unstructured covariance type in all models.

Results

Sex ratio

In *C. secundus,* the false worker and nymph sex ratio did not differ significantly from a 1:1 ratio, neither when all colonies were analysed separately nor when all individuals were pooled (χ^2-tests: always $p \geq 0.39$; Fig. 3). The soldiers' sex ratio differed significantly from a 1:1 ratio for three of the four colonies containing enough soldiers to perform a test (col1: $\chi_1^2 = 7.1$, $p = 0.008$; col2: $\chi_1^2 = 1.0$, $p = 0.32$; col3: $\chi_1^2 = 12.8$, $p < 0.001$; col6: $\chi_1^2 = 13.37$, $p < 0.001$). The soldiers' sex ratio also differed significantly from a 1:1 ratio, when all colonies were pooled (Fig. 3). There were four times more female than male soldiers.

In *C. domesticus*, the false worker, nymph and soldier sex ratio did not differ significantly from a 1:1 ratio, neither when all colonies were analysed separately, nor when they were pooled (χ^2-tests: always $p \geq 0.16$; Fig. 3). However, 60 % of the soldiers were males ($N_{males} = 31$ and $N_{females} = 21$).

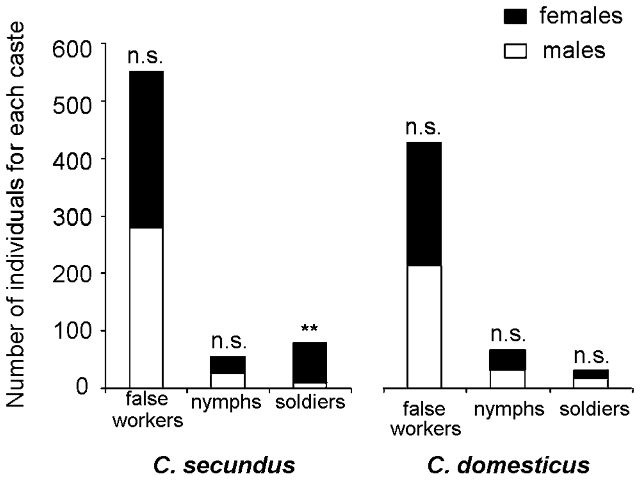


Figure 3. Total number of males and females for false workers, nymphs and soldiers of both species with the result of the χ^2-tests: **: $p < 0.001$.

Morphometric measurements

In *C. secundus*, for soldiers and false workers, none of the morphometric traits measured (pronotum width, head width, head length and head height) differed significantly between sexes (linear mixed models: always $p \geq 0.11$; Fig. 4). This confirms the findings of Roux (2004) for soldiers. However, with the exception of head length in soldiers, all morphometric traits in false workers and soldiers increased significantly in size with the number of antennal segments, and thus with the instar (linear mixed models: always $p \leq 0.002$).

Figure 4. Mean size (±S.E; in mm) of morphometric traits for *C. secundus.* Note: The large standard error observed for male soldiers traits can be explained by the small number of male soldiers found (N = 6).

In *C. domesticus*, for soldiers and false workers, none of the morphometric traits (pronotum width, head width, head length and head height) differed significantly between sexes (linear mixed models: always $p \geq 0.37$; Fig. 5). In both false workers and soldiers, pronotum

Figure 5. Mean size (±S.E; in mm) of morphometric traits for *C. domesticus*.

width increased significantly with the number of antennal segments (linear mixed models: always $p \leq 0.003$). For soldiers, there was also a significant positive correlation between head height and the number of antennal segments (linear mixed models: $F_{1,31} = 6.3$, $p = 0.018$), while all other correlations between morphometric traits and the number of antennal segments were non significant (linear mixed models: always $p \geq 0.13$).

In both species, for none of the investigated traits the variance differed significantly between sexes (Levene's test: *C. secundus:* always $p \geq 0.14$; *C. domesticus:* always $p \geq 0.08$).

Behaviour

For both *C. secundus* and *C. domesticus*, none of the analysed factors (sex and caste) was significant for non-interactive behaviours (linear mixed models: always $p \geq 0.20$). Similarly, when the observed individuals were actors of an interactive behaviour, none of the factors had a significant effect (linear mixed models: always $p \geq 0.13$).

In *C. secundus*, when passive behaviours were considered, males were significantly less groomed than females (linear mixed models: $F_{1,25} = 8.78$, $p = 0.007$). As shown in Figure 6, this difference between sexes is particularly clear for imagos (i.e., soldiers and reproductives), whereas false workers of both sexes tended to have similar durations for allogrooming. None of the other passive behaviours, trophallaxis, jerking, and antennation, differed between sexes or castes (linear mixed models: always $p \geq 0.17$).

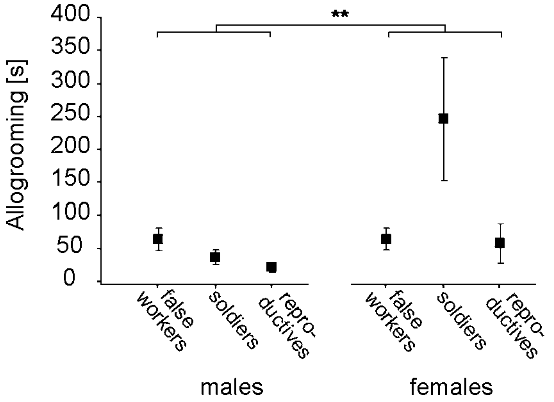


Figure 6. Mean duration (±S.E; in seconds) of passive grooming for *C. secundus*. **: $p = 0.007$.

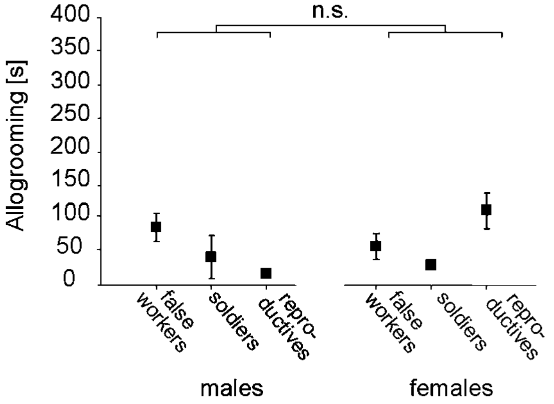


Figure 7. Mean duration (±S.E; in seconds) of passive grooming for *C. domesticus*. n.s.: non significant.

Contrary to *C. secundus*, in *C. domesticus* there was no significant difference between males and females for allogrooming in any caste (linear mixed models: $F_{1,34} = 0.40$, $p = 0.532$; Fig. 7). However, males received significantly fewer trophallaxis than females (linear mixed models: $F_{1,7} = 8.11$, $p = 0.025$; Fig. 8). Male false workers received fewer trophallaxis than any other caste of any sex (soldiers did not receive any trophallaxis during the observation period) (linear mixed models: $F_{2,7} = 8.87$, $p = 0.021$). The number of jerks an individual received declined significantly from reproductives via soldiers to false workers (linear mixed models: $F_{2,55} = 19.81$, $p < 0.001$). However, sexes did not differ significantly in the number of 'jerks' received (linear mixed models: $F_{1,55} = 1.06$, $p = 0.307$). Passive antennation did not differ between castes or sexes (linear mixed models: $p \geq 0.13$).

Discussion

The data presented in this study showed that the soldier sex ratio was biased in *C. secundus* (80 % of the soldiers were females), but not in *C. domesticus*. As the sex ratio of false workers was unbiased in both species, we can rule out an influence of false workers' sex ratio on those of soldiers. Similarly, a biased sexual sex ratio would indicate that one sex is more likely to develop into sexuals, thus potentially resulting in more soldiers of the opposite sex. This hypothesis can be rejected as the sex ratio of sexuals in *C. secundus* and last nymphal instars in *C. domesticus*

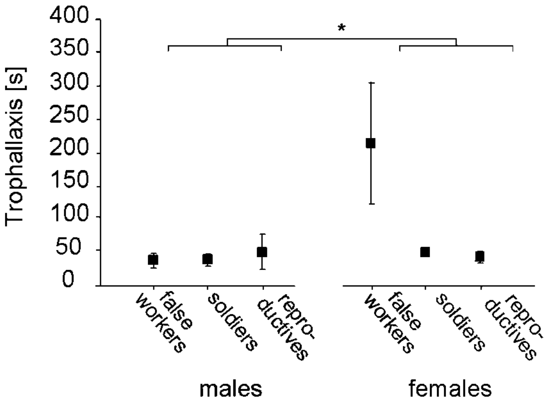


Figure 8. Mean duration (± S.E; in seconds) of passive trophallaxis for *C. domesticus.* *: $p = 0.025$.

did not deviate from 1 : 1. We thus exclude other castes' sex ratio as potential explanations for the biased sex ratio observed in *C. secundus* soldiers.

The morphometric analyses showed that there was no sexual size dimorphism in any of the castes investigated. Matsuura's hypothesis therefore would predict that there should be no bias in the soldiers' sex ratio. Our results are not consistent with this prediction as the sex ratio of *C. secundus* soldiers was strongly female biased. We thus reject Matsuura's hypothesis for our species. One might also suggest that it is the sex with the least size variation that might be favoured to become soldier, if tunnels are of consistent size. However, we also did not find any differences in size variation between the sexes.

These two potential explanations being discarded, we are left with the behavioural-predisposition hypothesis mentioned earlier. We could not find any behavioural differences between the sexes for 'active' behaviours. However, both sexes differed when the passive behaviours were considered. Males were less groomed in *C. secundus* and they received fewer proctodeal trophallaxis in *C. domesticus.* Moreover, in *C. secundus*, the behaviour towards imagos clearly accounted for most of this difference (Fig. 7) and it is most pronounced in soldiers. This could mean that female imagos, and especially the soldiers, are more attractive than males when it comes to grooming. Being attractive is very important for functioning effectively as a soldier. Soldiers regulate the number of soldiers present within a colony by inhibiting the differentiation of false workers into soldiers (Lefeuve and Bordereau, 1984; Henderson, 1998; Korb et al., 2003). The exact mechanisms how this is achieved are not fully understood, yet it seems to be mediated via short range substances, maybe transmitted via allogrooming (Korb et al., 2003). Thus, we speculate that *C. secundus* females are pre-adapted to function as soldiers because they are more attractive as adults than males. Hence they might be more efficient in preventing surplus soldier development which would be costly at the colony (soldiers need to be fed by colony members) and the individual level (soldiers are sterile). This hypothesis is corroborated by our findings for *C. domesticus.* Here, males and females did not differ in the degree of being allogroomed, and correspondingly, the sex ratio of soldiers did not deviate significantly from a 1 : 1 ratio. Whether our finding that *C. domesticus* males received less proctodeal trophallaxis than females has a similar significance that explains why 60 % of the soldiers are males, is even more speculative. Clearly, more studies are needed to test the behavioural pre-adaptation hypothesis for explaining sex ratio bias in termite soldiers. Subtle behavioural differences between both sexes might explain the intriguingly variable sexual caste dimorphism even between closely related termite taxa (Roisin, 2001). Differences in behaviour between sexes might result from selective pressure unrelated with soldier caste evolution and thus would result in species specific mechanisms for development into soldiers. The fact that the individuals taking the soldier's developmental pathway are passive during these key interactions indicates that caste determination does not necessarily rely on the individuals' 'decision', but more likely is the product of processes at the colony level. For the first time, we showed that sexes differed in behavioural terms in a lower wood-nesting termite. This should open the way to similar studies in other termite taxa and in *Cryptocercus* cockroaches, as it might reveal more tasks partitioning than previously thought and it raises questions concerning the selective pressures that acted on the evolution of castes in termites.

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