

Termites and mites – adaptive behavioural responses to infestation?

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Summary

Rapid adaptation to their hosts' defence systems usually allows parasites to keep the upper hand in the co-evolutionary arms race between hosts and parasites. However, although morphological and physiological adaptations are generally far slower in hosts than in their parasites, the former can rapidly respond to a parasite challenge by dispersal-related, adaptive changes in their behaviour. We investigated whether the drywood termite *Cryptotermes secundus* altered its behaviour in response to an infestation with parasitic, astigmatic mites. The frequency of the vital, dispersal-related behaviours allogrooming and proctodeal trophallaxis did not differ between colonies or between individuals with mites compared to without mites. However, activity levels were lower in mite-infested colonies and individuals spent more time resting and feeding when mites were present in the colony, irrespective of whether they were infested themselves or not. This behavioural pattern shown by individuals from infested mite-colonies is known to be associated with a development of *C. secundus* workers into winged dispersing sexuals. As dispersing individuals were less likely to have mites, this behavioural response to the mites' infestation might be an adaptive response to escape the deteriorating nest conditions.

Keywords: co-evolution, termite, mite, adaptive, parasite, behaviour.

Introduction

In the co-evolutionary arms race between hosts and parasites, both opponents repeatedly undergo adaptive changes to outwit or manipulate their antagonist to their own advantage. Generally parasites are seen to have the edge on their

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hosts because they can more rapidly evolve new counter-adaptations to their hosts' defences due to their shorter generation time and generally higher population size (Tobby, 1982; Rice, 1983; Seger & Hamilton, 1988). However, a rapid response by the immune system or behavioural changes also allow a host to immediately and adaptively respond to an ectoparasitic challenge (Buechler et al., 1992; Boecking et al., 1993; Rosengaus et al., 1998, 1999; Moret & Schmid-Hempel, 2000; Lamberty et al., 2001; Traniello et al., 2002). For social insects in particular, behavioural changes are an important means to ward off parasites. Individuals in a colony cannot only directly respond to parasites (Buechler et al., 1992; Danka & Villa, 1998), but they can also induce their nestmates to mount other defensive behaviours such as allogrooming (Boecking et al., 1993; Spivak & Reuter, 1998; Rosengaus et al., 1999). However, behavioural changes also result when parasites manipulate their hosts in order to facilitate their own transmission (Schmid-Hempel, 1998). This needs to be considered when testing for adaptive responses of the host. Furthermore, the behaviours must have fitness-relevance for either host or parasite in order to be considered as adaptive changes (Poulin, 1995).

In our study, we investigated the effect of an as yet undescribed parasitic, astigmatic mite on the behaviour of the drywood termite *Cryptotermes secundus* (Kalotermitidae). *C. secundus* belongs to the one-piece-life-type termites (OP-termites) (Abe, 1987), which spend their entire lives in a single piece of wood (except for the brief dispersal period) that serves both as food source and as shelter (Lenz, 1994). Such a lifestyle is associated with flexible development in which the immature workers are totipotent to explore all caste options. This means that *C. secundus* workers can either stay in the natal colony with a chance to inherit the breeding position when the reproductives die (replacement reproductive) or they can switch towards becoming a winged sexual (alate) that founds a new colony (primary reproductive), or they can develop into soldiers (Korb & Katrantzis, 2004). Proctodeal trophallaxis (= anal feeding) and allogrooming influence the development of individuals into reproductives (hereafter 'dispersal-related' behaviours). The most active food providers are more likely to develop into dispersing sexuals that found a new nest, and allogrooming (active and passive) seems to be essential during the sexual development as it provides the necessary information about the developmental status via cuticular hydrocarbons (Korb & Schmidinger, 2004; unpubl. data). Such a link to sexual development could

not be ascertained for the other behaviours which were mainly activity related and which are called 'activity-related behaviours' hereafter (Korb & Schmidinger, 2004).

The undescribed astigmatic mite could not be identified further (Eberhard Wurst, pers. com.). The life cycle of these astigmatic mites is typically composed of egg, larva, protonymph, deutonymph, tritonymph and adult (Walter & Proctor, 1999). All of these developmental stages were found in the termites' nests. Deutonymphs of the astigmatic mites were found attached to the living termites' mouthparts or various other bodyparts, often resulting in the death of infested individuals (Fuchs, 2004). Therefore we used these deutonymphs to assess the degree of infestation of both individuals and colonies. Deutonymphs are not directly transmitted between individuals, so that no transfer occurs during interactive behaviours within the colony. The spread to a new termite is only possible during other developmental stages, e.g., as protonymph or as adult. This provides ideal test conditions as the interactive behaviour among individuals within a colony is not confounded by the mites interest to spread within the colony. Rather deutonymphs are stages that spread to new colonies which provide abundant food conditions and allow the development into adults (Walter & Proctor, 1999).

To test whether the mites have an effect on the termites' behaviour and whether the termites respond through behavioural adaptations, we compared the occurrence of the dispersal-related interactive behaviours, allogrooming and proctodeal trophallaxis, and the activity-related behaviours in colonies of *C. secundus* with and without mites. Feeding and resting behaviour was also recorded as hosts frequently increase their food-intake or decrease their energy-expenditure in response to the parasites' drain of resources (Poulin, 1995; Christie et al., 1996; Moret & Schmid-Hempel, 2000). In addition, to investigate whether the direct presence of a mite on a termite or the mere presence of mites in a colony alone induce behavioural changes in *C. secundus*, we compared the behaviours of (1) individuals with and without mites in colonies with mites and (2) individuals without mites in colonies with mites and in colonies without mites. We further asked whether dispersing individuals have less mites than individuals staying in the colony. This would be expected, if developing into winged sexuals is an adaptive response by the termites to escape the infection with mites.

Material and methods

Species collection and maintenance

Colonies of *Cryptotermes secundus* Hill (Kalotermitidae) were collected from dead *Ceriops tagal* trees (Perr.) (Rhizophoraceae) from a mangrove area near Palmerston-Channel Island in Darwin Harbour (Northern Territory, Australia; 12°30'S, 131°0'E) (for more details see Korb & Lenz, 2004). Complete colonies with an unaltered colony composition were set up in *Pinus radiata* wood blocks and were directly transferred to the laboratory in Regensburg (Germany) (with permission of Environment Australia: permit no. PWS P20011508) where they were kept in a climate chamber under conditions of 28°C, 70% relative humidity and artificial light from 8 am to 8 pm. Wood block size was adjusted to colony size to provide abundant food conditions (Korb & Lenz, 2004). These conditions do not affect behaviour, development, growth or caste composition of the colonies (Korb & Katrantzis, 2004; Korb & Lenz, 2004; Lenz, 1994).

Experimental set-up

A total of 31 colonies, 19 with mites from 2002 and 12 without mites from 2003, entered the experiment. Colony size ranged from four to 138 individuals (mean \pm SE = 62 ± 7 individuals). As the collection process is very labour intensive, it was necessary to include all colonies to have a large enough sample size. This also meant that both monogamous (with one pair of reproductives) and polygamous (with two or more pairs of reproductives) colonies were used. The total number of observed individuals was 837 (median: 30 individuals/colony), with 478 originating from colonies with mites and 359 from colonies without mites. After the splitting of the wood blocks, focal individuals beyond the third instar were arbitrarily chosen from each colony. Prior to the behavioural observations, mites were counted on all focal individuals with the help of a dissecting microscope (Wild, magnification 80 \times). Focal individuals were individually marked with two dots of enamel paint (Revell, Germany), one on the head and the thorax. Vanishing or lost markings were reapplied when necessary. All individuals (marked and unmarked) of one colony were transferred in a new block of *P. radiata* for the behavioural observations. A hole, adjusted to colony size, which had been drilled in the wood block and which was covered with a sealed glass plate,

served as observation chamber (see also: Korb & Schmidinger, 2004). All colonies were provided with wet filter paper and some wood chips, and were left undisturbed to adjust to the new environment for at least twelve hours prior to the observations.

Behavioural observations

Each marked individual was observed for 15 minutes according to a standard protocol developed for this species (Korb & Schmidinger, 2004). All focal individuals within one colony were observed within two days to guarantee comparability among individuals and minimise disturbance from repeated re-marking of individuals losing their colour. Nevertheless, we covered a reasonable period in developmental terms as all observations were expanded over a period of three months with a total observation time of 210 hours (colonies with mites: 120 hours; colonies without mites: 90 hours). For the interactive behaviours we distinguished whether an individual actively performed a behaviour or whether it was the passive recipient of a behaviour that had been initiated by another individual. The frequencies of the following interactive behaviours were recorded:

- proctodeal trophallaxis: anal feeding of nestmates (note: if an individual passed on food to a nestmate, it acts as active donor; in the reverse case, it is termed the passive recipient)
- allogrooming: an individual moves its mouthparts over the body of a nestmate (note: often recipients of allogrooming froze in an elevated posture to make lateral and ventral bodyparts more easily accessible for allogrooming)
- butting: rapid forward and backward movement along the longitudinal body axis thereby hitting another individual with the head
- antennation: individuals contact each other with the antennae
- bout rate: sum of the frequencies of all interactive behaviours; this measure was used as an indicator of the overall level of activity of the interactive behaviours

We also recorded the following non-interactive behaviours which were used to further determine the general level of activity:

- resting and feeding: an individual remains in one spot and does not move; as feeding (= movement of mouthparts and food up-take) is hard

to distinguish from resting, the two behaviours were combined in one category

- moving and building: an individual moves or is involved in ‘nest construction’ (= deposition and handling of faecal material or transport of faecal pellets or wood chips)

Other behaviours (selfgrooming, selftrophallaxis, stomodeal trophallaxis, and carcass feeding) were observed too rarely to be analysed.

Mite counts on dispersing and staying individuals

To test whether the mites manipulated the behaviour of the termites in their own interest or whether the behaviour was an adaptive response by the termites, we re-examined the studied colonies during the following dispersal season and recorded the presence of mites on dispersing individuals (alates) and individuals remaining in the colony (workers) in all colonies with a dissecting microscope (Wild, magnification 80×).

Statistical analysis

SPSS 11.5 was used for all statistical analysis. As the assumptions to perform a multivariate ANOVA, multivariate normality and equality of variances, were not met by our data, we used univariate analysis. The samples within a colony were not independent. Therefore gamy (monogamous or polygamous) and colony size were used as an additional factor and covariate, respectively, in a general linear model to account for colony specific effects and block ‘colony’ as a variable. Gamy was included because according to the ‘diversity against parasite hypothesis’ (Tobby, 1982; Hamilton, 1987), polygamous colonies with a higher genetic diversity are expected to be more successful in the defence against parasites than monogamous colonies (Fuchs, 2004). So ANCOVAS were performed with mite (factor levels: with mites/without mites) and gamy (factor levels: monogamous/polygamous) as fixed factors and colony size as covariate to compare the frequencies of the observed behaviours. If colony size was significant in the ANCOVA, Pearson correlation (r_P) was used to ascertain the direction of the correlation. All possible interactions were analysed; if interactions or terms were not significant, they were removed and the model was rerun. p -values were corrected for multiple comparisons using step-up FDR (Benjamini & Hochberg, 1995; García, 2004). To analyse the mite counts

on dispersing and staying individuals, we performed a binary logistic regression (mite/no mite) using colony size as a continuous predictor variable and dispersing vs staying as a categorical predictor variable. All tests were two-tailed. Differences in sample size for the various behaviours stem from missing values. For non-significant results of a mite effect the effect size index f for an ANOVA design (Cohen, 1988) was calculated using the computer program Gpower (Erdfelder et al., 1996; available at <http://www.psych.uni-duesseldorf.de/aap/projects/gpower/index.html>). Additionally, partial η^2 scores were provided as implemented in SPSS to show the effect size of non-significant mite effects relative to other effects (i.e. gamy and colony size). If not noted otherwise, means \pm SE are given.

Results

Comparison of colonies with and without mites

Comparing colonies with and without mites, we found no significant interactions between variables ($p > 0.05$). Gamy never had an influence on the frequency of any behaviour, while colony size was positively correlated with the active and passive bout rate (active: $r_p = 0.672$, $N = 31$, $p < 0.001$; passive: $r_p = 0.668$, $N = 31$, $p < 0.001$), the frequency of passive antennation ($r_p = 0.665$, $N = 31$, $p < 0.001$), and the frequency of active butting ($r_p = 0.41$, $N = 31$, $p = 0.022$).

Including these colony specific variables, the active bout rate (ANCOVA: $F_{1,23} = 6.87$, $p = 0.015$), active and passive antennation (active: $F_{1,23} = 11.59$, $p = 0.002$; passive: $F_{1,23} = 8.64$, $p = 0.007$) (Figure 1a, b), and the time spent moving and building ($F_{1,23} = 12.30$, $p = 0.002$) were higher in colonies without mites, whereas in colonies with mites individuals spent more time resting and feeding ($F_{1,23} = 7.11$, $p = 0.014$) (Figure 2a). Thus, in colonies with mites individuals were less active. By contrast, the frequency of the dispersal-related interactive behaviours allogrooming and proctodeal trophallaxis did not differ between colonies with mites compared to colonies without mites ($p > 0.05$) (Figure 3a,b).

For active interactions the effect size f was 0.16 and 0.24 for proctodeal trophallaxis and allogrooming, respectively. For passive interactions the corresponding values were 0.29 and 0.28. The partial η^2 showed that the presence of mites accounted for less than 0.1% and 3% of the total variability

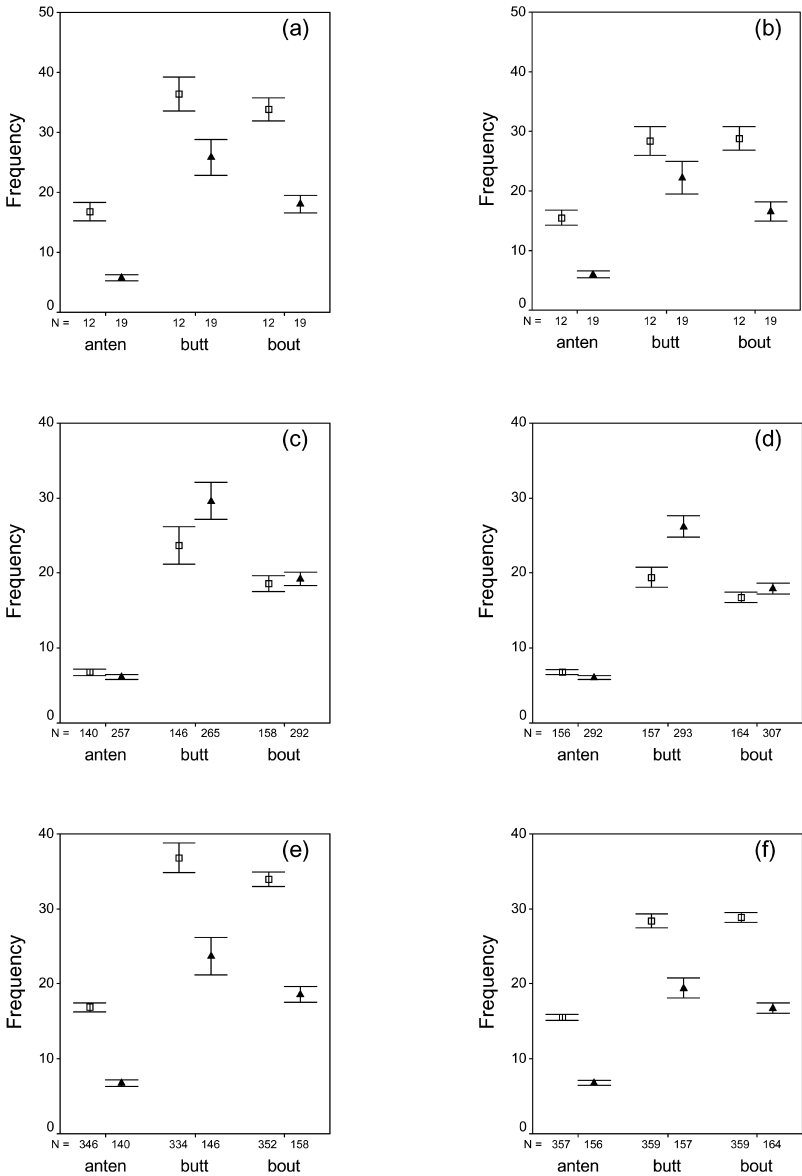


Figure 1. Frequencies of the interactive activity-related behaviours antennation (anten), butting (butt), and bout rate (bout) in relation to the presence of mites (open squares: no mites; filled triangles: with mites). Comparison of: (a) active and (b) passive behaviours in colonies with and without mites; (c) active and (d) passive behaviours of individuals with and without mites in colonies with mites; and (e) active and (f) passive behaviours of individuals without mites in colonies with and in colonies without mites. Means \pm 1 SE are given.

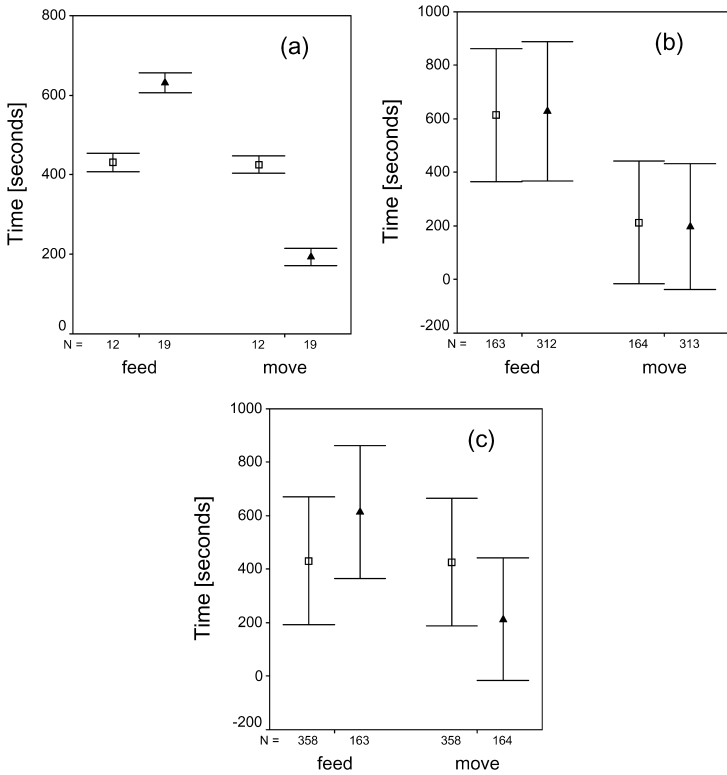


Figure 2. Time spent on resting and feeding (feed) respectively moving and building (move) in (a) colonies with and without mites, (b) individuals with and without mites in colonies with mites, and (c) individuals without mites in colonies with and in colonies without mites. Means \pm 1 SE are given. Open squares: without mites; filled triangles: with mites.

in active proctodeal trophallaxis and allogrooming, respectively. The corresponding values for passive proctodeal trophallaxis and allogrooming were 4% and 3%.

Colonies with mites: Comparison of individuals with and without mites

In colonies with mites, the active and passive bout rates were again positively correlated with colony size (active: $r_P = 0.248$, $N = 471$, $p < 0.001$; passive: $r_P = 0.177$, $N = 450$, $p < 0.001$), and so was passive antennation ($r_P = 0.332$, $N = 448$, $p < 0.001$). The two-way and three-way interactions showed significant results for the passive bout rate (colony size \times gamy: $F_{1,463} = 12.68$, $p < 0.001$; colony size \times mites: $F_{1,463} = 10.75$, $p = 0.001$;

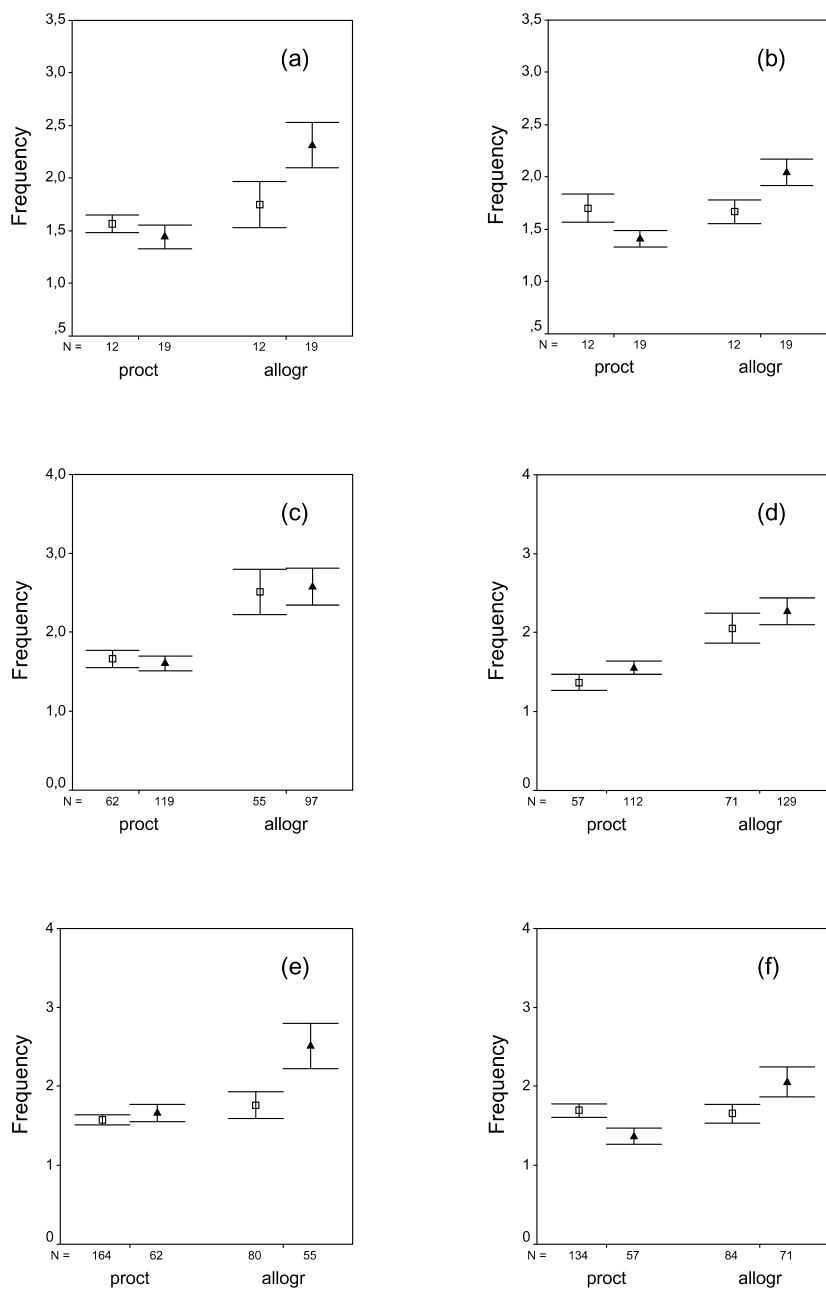


Figure 3.

colony size x gamy x mites: $F_{1,463} = 7.49$, $p = 0.006$), passive antennation (colony size x gamy: $F_{1,440} = 5.12$, $p = 0.024$). These interactions result from the following correlations among factors and the covariate 'colony size': First, the likelihood that an individual had mites increased with colony size (logistic regression: regression coefficient $\beta = 0.627 \pm 0.097$; Wald $\chi^2 = 42.01$, $p < 0.0001$). Second, in polygamous colonies, which were larger than monogamous colonies ($t_{29} = 2.94$, $p = 0.006$), the frequency of both the passive bout rate ($F_{1,463} = 16.05$, $p < 0.0001$) and passive antennation ($F_{1,440} = 7.17$, $p = 0.008$) were higher than in monogamous colonies. So there was an association between polygamy and larger colony sizes and between monogamy and smaller colony sizes. As both the likelihood to have mites and the frequency of passive bout rate and passive antennation correlated with colony size the interactions emerged. So what seemed to be a mite effect on behaviour was actually a colony size effect. Correspondingly, colony size differences account for the only significant mite effects found for the interactive activity-related behaviours, namely significantly higher frequencies of passive antennation ($F_{1,440} = 8.26$, $p = 0.0004$) and passive bout rate ($F_{1,463} = 8.24$, $p < 0.0001$) for individuals with mites compared to individuals without mites (Figure 1c,d).

For the other behaviours the interactions were not significant ($p > 0.05$). The duration of neither resting and feeding nor moving and building differed significantly between individuals with mites compared to individuals without mites (Figure 2b), nor did the frequency of the dispersal-related behaviours proctodeal trophallaxis and allogrooming (all $p > 0.05$) (Figure 3c,d). For active interactions the effect size f was 0.02 and 0.002 for proctodeal trophallaxis and allogrooming, respectively. For passive interactions the corresponding values were 0.15 and 0.02. The partial η^2 showed that the presence of mites never accounted for more than 0.3% of the variability in the dispersal-related behaviours.

Figure 3. Frequencies of the interactive dispersal-related behaviours proctodeal trophallaxis (proct) and allogrooming (allogr) in relation to the presence of mites (open squares: no mites; filled triangles: with mites). Comparison of: (a) active and (b) passive behaviours in colonies with and without mites; (c) active and (d) passive behaviours of individuals with and without mites in colonies with mites; and (e) active and (f) passive behaviours of individuals without mites in colonies with and in colonies without mites. Means ± 1 SE are given.

Individuals without mites: Comparison of colonies with and without mites

The comparison of individuals without mites from colonies with mites and from colonies without mites yielded in principle the same pattern as the comparison of colonies: no significant interactions among the variables were found. Passive bout rate and passive antennation were positively correlated with colony size (active: $r_P = 0.377$, $N = 523$, $p < 0.001$; passive: $r_P = 0.402$, $N = 513$, $p < 0.001$). Including these colony specific variables, the frequencies of active and passive antennation (active: $F_{1,460} = 7.03$, $p = 0.008$; passive: $F_{1,505} = 7.56$, $p = 0.006$) were higher for individuals from colonies without mites (Figure 1e, f), and individuals without mites from colonies with mites spent more time on resting and feeding ($F_{1,513} = 14.85$, $p < 0.001$) and less time on running and building ($F_{1,516} = 19.77$, $p < 0.001$) than individuals without mites from colonies without mites (Figure 2c). Again, the frequency of the dispersal-related behaviours proctodeal trophallaxis and allogrooming did not differ ($p > 0.05$) (Figure 3e, f). For active interactions the effect size f was 0.04 and 0.12 for proctodeal trophallaxis and allogrooming, respectively. For passive interactions the corresponding values were 0.18 and 0.10. The partial η^2 showed that the presence of mites never accounted for more than 1% of the variability in the dispersal-related behaviours.

Mite counts on dispersing and staying individuals

Dispersing individuals of *C. secundus* were less likely to have mites (20.4%, 209 out of 1026 individuals) than individuals staying in the colony (31.3%, 2293 out of 7327 individuals). This was significant even when accounting for colony size as confounding factor (binary logistic regression: disperse: regression coefficient $\beta = 0.363 \pm 0.084$; Wald $\chi^2 = 18.71$, $p < 0.0001$; colony size: regression coefficient $\beta = -0.002 \pm 0.0001$; Wald $\chi^2 = 177.77$, $p < 0.0001$).

Discussion

We found a conspicuous pattern in the behavioural changes in relation to the presence of mites (Table 1). Activity-related behaviours, such as feeding and resting or moving and building, differed both between infested and

Table 1. Overview of the behavioural changes associated with mite infestation. Behaviours that were displayed: more frequently in colonies with mites: +; less frequently in colonies with mites: -; showed no significant difference: ns. () indicates that the change was caused by an interaction with colony size. C.: colony; Ind.: individual; a: active; p: passive; feed: feeding & resting; move: moving & building; proct: proctodeal; allogr: allogrooming; anten: antennation; butt: butting; bout: bout rate.

		C. \pm mites	C. with mites: Ind. \pm mites	Ind. without mites: C. \pm mites
Non-interactive	feed	+	ns	+
	move	-	ns	-
Dispersal-related interactive	proct troph., a/p	ns/ns	ns/ns	ns/ns
	allogr, a/p	ns/ns	ns/ns	ns/ns
Activity-related interactive	anten, a/p	-/-	ns/(+)	-/-
	butt, a/p	ns/ns	ns/ns	ns/ns
	bout, a/p	-/ns	ns/(+)	ns/ns

uninfested colonies, and between uninfested individuals in colonies with and without mites. However, no differences were found for the dispersal-related behaviours allogrooming and proctodeal trophallaxis where the effect size was always small to medium, except for passive proctodeal trophallaxis (0.29) and allogrooming (0.28) at the colony level, and where the presence of mites never accounted for more than 4% of the variability in the dispersal-related behaviours (Table 1). The lack of changes in the dispersal-related behaviours is unlikely to be caused by too benign conditions as was found in other social insects (e.g., Brown et al., 2003) because then we also would not expect to find changes in activity-related behaviours. Thus, there is at least a difference in response. Under the same conditions activity-related behaviours were changed, but dispersal-related behaviours did not differ. This behavioural pattern might be a response to the deteriorating conditions in the nest to save energy by decreased moving and increased feeding, and promote an individual termite's progressive development towards a dispersing sexual as expected fitness returns from staying at the nest decreased. In *C. secundus*, individuals that perform most of the proctodeal feeding are those that develop progressively (Korb & Schmidinger, 2004). Thus, despite the general decrease in activity in mite-infested colonies, the termites seem to keep their proctodeal feeding activity constant which is essential for their progressive

development into winged sexuals (Korb & Schmidinger, 2004). Similarly, allogrooming is essential during sexual development as it seems to provide the necessary information about the reproductive and developmental status of individuals via cuticular hydrocarbons (unpubl. data). In line with this interpretation that the termites foster their development towards dispersing sexuals, former results revealed that mite-infested colonies show a premature development of dispersing sexuals with an increased likelihood to have winged sexuals compared to uninfested colonies (Fuchs, 2004). The following findings support that these behavioural responses are adaptive responses to the deteriorating nest conditions and not merely the passive side effect of an individual termite being infested with mites: (i) Even non-infested termites in colonies with mites showed these behavioural responses when compared with non-infested termites in colonies without mites (Table 1). (ii) There was no difference in the behavioural pattern between infested- and non-infested termites in colonies with mites when including colony size differences (Table 1). Furthermore, the development also cannot be a result of mites manipulating their host to promote their own vertical transmission to new colonies as dispersing individuals were less likely to have mites than individuals remaining in the colony.

Research on parasites in termites has so far mainly concentrated on bacteria and fungi (e.g., Kramm et al., 1982; Zoberi & Grace, 1990; Rosengaus et al., 1998; Traniello et al., 2002). These groups, however, seem to be of low importance for drywood termites which is probably related to their habit of nesting inside dry, non-decayed wood (Rosengaus et al., 2003). The impact of mites on social insects was studied, for example, in bees, where *Varroa jacobsoni* poses a major threat for apiculture (Schmid-Hempel, 1998; Duay, 2002; Harris et al., 2003). Among others, behavioural responses in infested honeybees include changes in the bees' hygienic behaviour to ward off mites (e.g., Spivak & Reuter, 1998; Arathi & Spivak, 2001; Stanimirovic et al., 2002). Contrary to this, we did not observe increased allogrooming frequencies in *C. secundus*, although infections of termites with fungus lead to more allogrooming (Rosengaus et al., 1999). This might be explained by the difficulty in removing mites compared fungal spores. The mites were so closely attached to the termites that even with forceps it was not possible to remove them. Thus, the only effective defence against mites might consist in uninfested termites leaving the nest as winged sexuals. This parallels the movement of whole colonies to a new nest site in other social insects (reviewed by

Schmid-Hempel, 1998) as well as social vertebrates (reviewed by Altizer et al., 2003), which is not an option for drywood termites that never leave their nest except for dispersal.

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