The parasite’s long arm: a tapeworm parasite induces behavioural changes in uninfected group members of its social host

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Parasites can induce alterations in host phenotypes in order to enhance their own survival and transmission. Parasites of social insects might not only benefit from altering their individual hosts, but also from inducing changes in uninfected group members. *Temnothorax nylanderi* ant workers infected with the tapeworm *Anomotaenia brevis* are known to be chemically distinct from nest-mates and do not contribute to colony fitness, but are tolerated in their colonies and well cared for. Here, we investigated how tapeworm-infected workers affect colony aggression by manipulating their presence in ant colonies and analysing whether their absence or presence resulted in behavioural alterations in their nest-mates. We report a parasite-induced shift in colony aggression, shown by lower aggression of uninfected nest-mates from parasitized colonies towards conspecifics, potentially explaining the tolerance towards infected ants. We also demonstrate that tapeworm-infected workers showed a reduced flight response and higher survival, while their presence caused a decrease in survival of uninfected nest-mates. This anomalous behaviour of infected ants, coupled with their increased survival, could facilitate the parasites’ transmission to its definitive hosts, woodpeckers. We conclude that parasites exploiting individuals that are part of a society not only induce phenotypic changes within their individual hosts, but in uninfected group members as well.

1. Introduction

Parasites have developed a number of fascinating strategies to infect, thrive and reproduce within their hosts [1]. Among these strategies is the manipulation of host appearance and behaviour, where the altered host traits may be regarded as the parasites’ extended phenotype [2]. Host manipulation is frequently observed in parasites possessing complex life cycles reliant upon trophic transmission [1]. The most severe parasite-induced alterations are exhibited by intermediate hosts, whose aberrant phenotypes can contribute to parasites’ transmission into subsequent hosts, furthering the parasites’ life cycle [3–6]. Many manipulative parasites use group-living organisms such as social insects as hosts [7]. Indeed, some of the most prominent examples of host manipulation have been observed in social insects infected with endoparasites. For instance, *Formica* and *Camponotus* ants infected with the lancet liver fluke attach themselves to the tips of grass blades, where they are more likely to be ingested by grazing mammals, the parasite’s definitive hosts [8]. Intermediate ant hosts infected with the nematode *Myrmeconema neotropicum* linger in rainforest canopies, lifting their red, berry-like abdomen to draw the attention of nearby avian hosts [9].

While our understanding of such parasite-induced alterations in individually infected hosts is rapidly growing (e.g. proximate mechanisms [10]), it is less well understood how the altered phenotypes of infected hosts affect other social group members. For instance, parasite infections in social insects...
change their hosts’ chemical signature (e.g. [11–14]), which may in turn affect social communication, and thus the functioning of societies. Such parasite-induced changes in cuticular hydrocarbon profiles [11–14] may enable group members to recognize infected individuals, and to either provide enhanced care towards infected members to reduce the risk of pathogen spread [15,16] or to expel them from the colony if their maintenance is costly [17,18]. Social insects use cuticular hydrocarbons generally as recognition cues to discriminate nest-mates from non-nest-mates [19,20]. They detect differences based on the quantitative variations of cuticular hydrocarbons [21]. Usually, individuals within a colony share a colony-specific odour, which results from the frequent exchange of recognition cues among group members (reviewed in [22]). The presence of infected individuals with altered chemical profiles may lead to a more diverse chemical signature within colonies, increasing the likelihood of odour overlap with other conspecific colonies, which share the same cuticular hydrocarbons but in different quantities (reviewed in [22]). Consequently, group members of infected workers may be impaired in their nest-mate recognition, thus affecting colonies’ defence against intruders.

An interesting model to investigate parasite-induced changes on the individual and collective level is the interaction between the common endoparasitic tapeworm _Anomotaenia brevis_ and its intermediate host, the ant _Temnothorax nylanderi_ (formerly _Leptothorax nylanderi_ [23–25]). Ants become infected as larvae, after they are fed with bird faeces containing tapeworm eggs [25]. The parasitic tapeworm penetrates the ant’s gut wall and transforms into a cysticercoid within the haemocoel (see the electronic supplementary material, video). In this stage, the parasite cannot be transmitted between adult ants. It completes its life cycle when ants are preyed upon by the definitive hosts, woodpeckers [25]. Most tapeworm-infected ants are easily identified by their smaller size and their yellow cuticle (figure 1), which contrasts with the regular brown coloration of _T. nylanderi_ ants. Moreover, they exhibit a quantitatively different cuticular hydrocarbon profile [25], which may affect their group members’ nest-mate recognition. Workers can be infected with several cysticercoids, and chemical as well as morphological alterations become more pronounced with increasing parasite load [25,26]. On the behavioural level, infected workers are inactive and remain inside the nest, where they rarely engage in social tasks such as brood care [26].

The aims of this study were threefold. First, by simulating nest attacks, we tested whether infected workers were less likely to evacuate their nest when attacked are likely to be eaten by woodpeckers. The potential lack of a flight response is thus thought to promote the transmission of the parasite to its definitive host. Second, we investigated whether worker survival is related either to the infection status (i.e. infected with _A. brevis_ or not) or the presence of infected workers within a colony. A previous study showed that uninfected workers provide better care for infected than for uninfected nest-mates [26], which may come at the expense of their own survival. As infected workers are tolerated in their colony and well cared for [26], we finally investigated whether colony aggression, an important collective trait involved in nest-mate recognition and nest defence, is affected by the presence of infected workers. Specifically, we evaluated the aggressive responses of ant colonies that were either naturally parasitized (i.e. with infected workers) or unparasitized (i.e. without infected workers). We then repeated the aggression tests following experimental manipulation of colony parasitism status (i.e. the absence or the presence of infected workers). If infected workers may lead to a broader colony odour, we predicted parasitized colonies to be less aggressive, in particular towards conspecifics.

2. Material and methods

(a) Ant collection and maintenance

From April to June 2013, we collected 221 ant colonies in an oak forest near Mainz, Germany (50°00’00.3’’N, 8°08’46.4’’E). Colonies of _T. nylanderi_ consist of several dozen monomorphic workers and a single queen, which reside in preformed natural cavities (e.g. acorns, sticks) in the leaf litter of deciduous forests throughout Europe (e.g. [27]). Parasite pressure in the local population is high, as approximately 30% of the colonies contain one or more tapeworm-infected individuals [26]. Ant colonies were transferred in their natural nest structures into ziploc bags, transported to the laboratory and relocated to artificial observation nests composed of a piece of Plexiglas with a pre-cut rectangular cavity (50 × 10 × 3 mm; 3 mm wide entrance) sandwiched between two microscope glass slides. These nests were placed in 100 × 100 × 30 mm boxes with a plaster floor. Colonies were fed weekly with honey, crickets and water. Unless otherwise stated, colonies were kept at 18°C: 14°C in a 12 L: 12 D cycle.

(b) Parasitism by _Anomotaenia brevis_

After collection, we counted the number of brood and adult ants per colony, differentiating between workers of the common brown and yellow phenotype. Parasitized colonies from this...
collection (n = 59, 26.7%) harboured 1–32 infected workers, yielding intra-colonial parasitism rates of 2–54% (15.1 ± 11.9%, mean ± s.d.). In a previous study [26], we confirmed that workers of the yellow phenotype are invariably infected with tapeworm cysticercoids; however, 2% of the workers exhibiting the brown phenotype in parasitized colonies can carry A. brevis cysticercoids as well.

(c) Nest disturbance

To assess whether infected workers were indeed less likely to escape following nest disturbance, potentially promoting predation of the parasite by the definitive host, we cracked the surface of 40 undamaged acorns containing T. nylanderi colonies and shook them for 10 s. We recorded the number of infected and uninfected workers observed escaping the nest within a 90 s timeframe and calculated the proportion of escaped workers based on the colony counts obtained the next day. Of these 40 colonies, 16 contained 1–32 infected ants. Fourteen colonies (six parasitized and eight unparasitized) were later used in the aggression experiments.

(d) Experimental design

For the aggression experiments, we selected 114 colonies, 38 of which contained workers infected with A. brevis (range: 1–27 infected workers; parasitism rate: 15.4 ± 10.3%, mean ± s.d.). As the presence of the queen can influence workers’ aggression [28], we chose only colonies with a resident queen. Colony sizes (range: 20–140 workers; 58.3 ± 28.2, mean ± s.d.) did not differ between parasitized and unparasitized colonies (Wilcoxon test: W = 22219, p = 0.920). The effect of infected nest-mates on colony aggression (§2e) was assessed before and after manipulation of the colonies’ parasitism status.

We manipulated the parasitism status of colonies by adding or removing workers using a blocked experimental design (figure 1). We first allocated colonies into one of 19 blocks, with each block consisting of two parasitized and four unparasitized colonies that were subjected to the aggression tests on the same day. Colonies assigned to the same block were comparable in worker number, and the two parasitized colonies exhibited similar parasitism rates. Within blocks, unparasitized and parasitized colonies were assigned to six treatments. Treatments included (I) parasitized—control, (II) unparasitized—control, (III) parasitized—unparasitized by removing infected workers and (IV) unparasitized—parasitized by adding infected workers. To control for the removal or addition of workers, we further included (V) unparasitized—unparasitized by removing uninfected workers and (VI) unparasitized—unparasitized by adding uninfected workers.

The manipulation of colony composition is possible in T. nylanderi as colony take-over and merging occur commonly in the field [29]. Nonetheless, steps were taken to reduce the likelihood of rejection of transferred non-nest-mates: workers and their recipient colony were anaesthetized with CO_2_ nests were gently shaken after worker addition to promote the passive exchange of cuticular hydrocarbons; and colonies were cooled to 8°C for one week during which expelled workers were reintroduced. Control colonies (treatments I and II) and colonies from which workers were removed (treatments III and V) were likewise subjected to anaesthetization and cooling.

Manipulation failed in three colonies receiving infected workers as all transferred workers were found dead. These were excluded from further analyses. Because we could not determine worker acceptance in colonies that received (indistinguishable) uninfected workers, we repeated the addition of infected (n = 20) and uninfected workers (n = 20) with 40 other colonies using metal-wire-marked ants. These experiments showed that 76.88% of the infected and 60.38% of the uninfected workers were accepted. Hence, infected workers tended to be more—though not significantly—readily accepted (quasi-binomial generalized linear model: F = 2.77, d.f. = 1, p = 0.108).

(e) Behavioural experiments: colony-level aggression

Pre-manipulation aggression was assessed 17.8 ± 11.9 (mean ± s.d.) days after collection and post-manipulation aggression 30 days after manipulation. Colony aggression in this species is consistent [30], thus we expected any change in aggression to be the result of manipulating the parasitism status of the colony.

Every colony was confronted with four non-nest-mate opponents from the same study site: (i) an infected worker from a parasitized T. nylanderi colony; (ii) an uninfected worker from a parasitized T. nylanderi colony; (iii) an uninfected worker from an unparasitized T. nylanderi colony; and (iv) an uninfected T. affinis worker. Ants often show higher aggression towards ants of a different, but related species [31] as they are more easily recognized as alien by their qualitatively different chemical profile. To exclude variance generated by the opponents’ behaviour [32], and because aggression against live and dead opponents is correlated in Temnothorax ants [30,33], we used a single, freshly defeated worker for each test. The opponent was carefully positioned inside the nest, next to the ant cluster and the nest entrance was sealed. For 5 min, we recorded the behaviour of each ant interacting with the opponent at 20–30 s intervals (i.e. within the first minute every 20 s, after that every 30 s), yielding 11 observations per aggression test per colony. We differentiated between ants that behaved aggressively (i.e. mandible spreading, dragging, holding, biting and very rarely stinging) or non-aggressively (i.e. grooming and antennating), as well as between uninfected and infected workers (i.e. in parasitized colonies) interacting with the opponent. We calculated the proportion of aggressive and non-aggressive interactions based on the total number of aggressive and non-aggressive interactions for each test.

Tests against the four opponents were carried out consecutively over 4 days (with a 24 h time interval between tests) in a randomized order to control for potential carry-over effects. Experiments were conducted blindly where possible (note that infected workers were apparent due to their yellow coloration). Nests were reopened following each aggression test, and opponents were removed and subsequently inspected for cysticercoids. Dissections confirmed that all opponents of the yellow phenotype contained cysticercoids (min.–max.: 1–56). Only 1.6% of the 684 opponents of the regular phenotype (i.e. brownish coloured T. nylanderi, n = 9; reddish coloured T. affinis, n = 2) carried cysticercoids. The associated aggression tests were excluded from further analyses.

(f) Worker survival

The consequences of tapeworm infection on worker survival were assessed by counting the workers on the day of manipulation and then by recounting them when the first new workers began to eclose from the pupae. We only included naturally parasitized and unparasitized colonies (i.e. treatments I and II), because these had suffered from parasitism for a longer time span. Although counting times varied (103 ± 32 days, mean ± s.d.) due to differences in brood development between colonies, time intervals did not differ between parasitized and unparasitized colonies (Wilcoxon test: W = 1703.5, p = 0.780, n_{Wilcoxon} = 38). Moreover, the survival of infected and uninfected workers from the same colony was assessed on the same day.

(g) Statistical analyses

To assess whether or not worker types (i.e. infected and uninfected workers from parasitized colonies, uninfected workers from unparasitized colonies) differed in their response to nest disturbance, we...
analyses were performed in R v. 2.15.2 [37]. To evaluate whether natural or experimental parasitism by A. brevis affected the aggressive responses of colonies, we used quasi-binomial GLMMs (glmPQL) with logit-link function. The proportion of aggressive interactions (i.e. aggressive versus non-aggressive) served as the dependent variable, worker type as the fixed predictor and colony identity served as a random factor. We used penalized quasi-likelihood parameter estimation to account for overdispersion (i.e. glmPQL function implemented in the MASS package [34]).

If the analyses of pre-manipulation aggression, we fitted the natural parasitism status of colonies, the opponent type and their interaction as fixed predictors. The time interval between collection and the first aggression trial as well as the colony size served as covariates in the initial model, but only the former was retained in our final model (time interval: Wald, $\chi^2 = 6.30$, $p = 0.012$; colony size: Wald, $\chi^2 = 0.44$, $p = 0.510$). For the analyses of post-manipulation aggression, we included the natural and current parasitism status, the opponent type and their interactions as fixed predictors. The type of manipulation (i.e. worker removal/addition/no numerical change) was fitted as a cofactor to account for the change in colony size due to the manipulation. Additionally, we evaluated the association between the aggression towards infected opponents and their parasite load (i.e. number of cysticercoids of A. brevis). Here, the proportion of aggressive interactions towards infected opponents was used as the dependent variable, the number of cysticercoids as a continuous variable and the time interval between collection and testing as a covariate. In all three analyses of colony aggression, colony identity nested in block identity was entered as a random factor. For model selection, we used a backwards-stepwise procedure ($\alpha = 0.05$) based on the Wald $\chi^2$-test [35]. To rule out that differences in the aggressive responses between parasitized and unparasitized colonies were due to the lethargic behaviour of infected workers, we repeated the analyses excluding the interactions of infected workers. We only report the latter results, as infected workers performed only 1.75% of all observed interactions, and their exclusion did not yield qualitatively different outcomes.

To assess the differences in worker survival, we used a binomial GLMM with logit-link function [36], fitting the proportion of workers that survived (i.e. surviving versus non-surviving workers) as the dependent variable, worker type as the fixed predictor and colony identity as a random factor. All statistical analyses were performed in R v. 2.15.2 [37].

3. Results

(a) Nest disturbance

Worker types (i.e. infected or uninfected) differed in their response to nest disturbance (GLMM; Wald, $\chi^2 = 17.89$, $p < 0.001$). Only five out of 155 infected (3.2%) ants escaped, whereas 634 out of the 1075 uninfected workers (58.9%) from parasitized colonies and 677 out of the 1410 workers (48.0%) from unparasitized colonies fled. Thus, infected workers less frequently evacuated their nests compared with uninfected workers from parasitized ($t_{15} = -4.08$, $p = 0.001$) or unparasitized colonies ($t_{14} = -3.34$, $p = 0.005$). There was no difference between the latter two worker types ($t_{14} = 0.82$, $p = 0.425$).

(b) Aggression before manipulation

Naturally parasitized colonies were less aggressive than unparasitized colonies (GLMM; Wald, $\chi^2 = 9.80$, $p = 0.002$; figure 2a), although this effect also depended on the opponent type (parasitism status x opponent type: Wald, $\chi^2 = 9.70$, $p = 0.021$; figure 2b). Parasitized colonies were less aggressive towards non-nest-mate conspecifics than unparasitized colonies, regardless of whether the opponent was an infected worker ($t_{22} = -2.90$, $p = 0.005$), an uninfected worker from a parasitized colony ($t_{22} = -2.96$, $p = 0.004$) or an uninfected worker from an unparasitized colony ($t_{22} = -2.77$, $p = 0.007$; figure 2b).

Conversely, parasitized and unparasitized colonies responded with similar high aggression towards T. affinis workers ($t_{22} = 0.05$, $p = 0.963$). Colonies were more aggressive towards infected than towards uninfected opponents (from parasitized colonies: $t_{328} = 1.94$, $p = 0.053$; from unparasitized colonies: $t_{328} = 2.48$, $p = 0.014$), although this higher aggression was independent of the parasite load (i.e. the number of cysticercoids within infected ants; Wald, $\chi^2 = 0.02$, $p = 0.877$). There was no difference in aggression towards uninfected workers from parasitized and unparasitized colonies ($t_{328} = 0.55$, $p = 0.583$). Colonies responded most aggressively towards T. affinis workers compared with infected T. nylanderi workers ($t_{328} = 5.48$, $p < 0.0001$), uninfected T. nylanderi workers from parasitized colonies ($t_{328} = 7.21$, $p < 0.0001$) and T. nylanderi workers from unparasitized colonies ($t_{328} = 7.64$, $p < 0.0001$).

(c) Aggression after manipulation

Post-manipulation aggression was lower in currently parasitized (treatments I and IV) than in unparasitized colonies (treatments II, III, V and VI; GLMM: current parasitism status: Wald, $\chi^2 = 10.40$, $p = 0.001$; figure 2a). Colony aggression varied with the opponent type (Wald, $\chi^2 = 12.30$, $p = 0.006$), but there was no interaction between current parasitism status and opponent type (Wald, $\chi^2 = 3.56$, $p = 0.313$). Colonies were more aggressive towards heterospecific opponents than towards infected workers ($t_{319} = -3.38$, $p < 0.001$), uninfected workers from parasitized colonies ($t_{319} = -1.91$, $p = 0.057$) and uninfected workers from unparasitized colonies ($t_{319} = -2.52$, $p = 0.012$). Post-manipulation aggression did not differ between the three conspecific opponents (all $p > 0.1$).

Post-manipulation aggression was unrelated to the natural parasitism status of colonies (Wald, $\chi^2 = 1.78$, $p = 0.182$) or its interaction with experimental parasitism status (Wald, $\chi^2 = 0.25$, $p = 0.616$), opponent type (Wald, $\chi^2 = 6.55$, $p = 0.088$) or both (Wald, $\chi^2 = 7.23$, $p = 0.065$). Hence, the effect of the current parasitism status (treatments I and IV) on post-manipulation aggression did not differ between manipulated (treatments III and IV) and control colonies (treatments I, II, V and VI; separate GLMM assessing control versus experimental status x current parasitism status: Wald, $\chi^2 = 0.86$, $p = 0.354$). The addition or removal of workers had no influence on aggression (Wald, $\chi^2 = 0.10$, $p = 0.950$).

(d) Worker survival

Worker types differed in their survival (GLMM $\chi^2 = 48.28$, $p < 0.0001$). Remarkably, 97.2% of the 144 infected workers survived until pupal eclosion, compared with only 56.3% of the 839 uninfected workers from parasitized colonies and 69.5% of the 995 workers from unparasitized colonies. Hence, survival of tapeworm-infected workers was higher than that of their uninfected nest-mates ($z = 6.58$, $p < 0.0001$).
$p < 0.0001, n_{\text{colonies}} = 19$; figure 3) or of workers from unparasitized colonies ($z = 4.83, p < 0.0001, n_{\text{colonies}} = 38$). Uninfected workers from parasitized colonies showed lower survival than workers from unparasitized colonies ($z = -2.50, p = 0.012, n_{\text{colonies}} = 38$; figure 3).

4. Discussion

Compared with solitary species, group-living animals face a unique set of lifestyle-derived benefits and challenges. Upon infection with a parasite, infected individuals of a social group may benefit from the care provided by other group members. But social groups are also known to collectively defend themselves against exploitation by parasites [38] and competitors [22].

In this study, we investigated how the presence of infected ants affected their colony members, combining experiments on the individual (i.e. flight response, survival) and collective level (i.e. colony defence). We demonstrate that tapeworm-infected ants were less likely to flee in response to simulated nest attacks and exhibited a much higher survival while their uninfected nest-mates survived less well. Moreover, the chemical profile of tapeworm-infected non-nest-mates elicited more aggression in *Temnothorax* workers than uninfected non-nest-mates. However, the latter responded with lower aggression towards conspecific intruders when infected ants lived in their colony. This finding indicates that the action component of nest-mate recognition (i.e. behavioural response), but not the perception component (i.e. cue assessment), might be impaired.

Parasite-induced changes, whether in the individual host or the host’s colony, can be due to host defences; they can either be side-effects of infection or the result of active manipulation of host phenotype by the parasite [39]. While we did not directly assess the fitness consequences for *A. brevis* (we only simulated predator attacks), our findings suggest that the observed parasite-induced alterations in infected host individuals could benefit the parasite’s survival and transmission success. First, the reduced flight response of infected *T. nylanderi* workers in response to nest attacks would presumably increase the tapeworms’ transmission into the definitive avian host, which preys upon ant brood or beetle larvae. Causes of the lower escape rate might be,
in addition to the lower activity of infected workers [26], their smaller eye and body size, and shorter legs [25]. Second, the higher survival of infected ants would extend the parasite's time period for transmission, because predation events by woodpeckers might be rare. Interestingly, two studies support the suggestion that parasites can be responsible for the increased survival of their intermediate hosts. For instance, survival of female beetles increased upon infection with the rat tapeworm Hymenolepis diminuta [40]. Moreover, a recent transcriptome study on the T. nylanderi–A. brevis system reports a downregulation of muscle (functionality) genes and an upregulation of longevity-related genes in infected workers [41], which corresponds to their inactivity and may explain increased survival.

However, the higher survival of infected T. nylanderi workers might not be the result of active manipulation by the parasite but rather due to the compensatory behaviour of nest-mates. Indeed, a previous investigation has shown that A. brevis-infected workers receive ample social care, as they are more often fed and groomed than uninfected nest-mates [26]. Similarly, Acromyrmex leaf-cutting ants exposed to a parasitic fungus were more often groomed by their nest-mates [16], and hence had a better chance to survive the infection in the presence of group members [42]. Likewise, mange mite-infected wolves survived better in larger packs [43], presumably due to the compensatory behaviours of pack-mates. While these examples do indeed represent some of the benefits of group-living, our findings also reveal costs of this lifestyle. Uninfected T. nylanderi ants exhibited decreased survival compared not only with infected individuals, but also with uninfected workers within unparasitized colonies. This outcome is likely to be related to the additional strain on colony resources required to care for infected ants and compensate for missing workforce because the infected individuals do not engage in colony tasks.

Although the increased survival and reduced flight responses may enhance the likelihood that the parasite will complete its life cycle, it does not explain why infected workers that compromise their nest-mates’ survival are tolerated by host colonies. It is puzzling, as workers—both from parasitized and unparasitized colonies—were more aggressive towards infected ants, be it non-nest-mates or nest-mates [26]. This suggests that workers discriminated infected from uninfected ants due to the quantitative changes in their chemical profile [25], although aggression did not further increase with parasite load. However, we also found that the mere presence of infected ants—either naturally occurring or experimentally introduced—triggered a reduction in aggression of parasitized colonies towards conspecifics, but not towards heterospecific intruders.

On a proximate level, aggression in ants depends on their nestmates, but not towards heterospecific intruders. Among the many models describing nest-mate recognition, the adjustable threshold for recognition of conspecifics [44] assumes that aggression is only triggered when recognition cues perceived by the actor exceed or fall below a certain threshold (reviewed in [45]). This threshold can be adjusted, depending on the costs or benefits of errors, which are affected by the cue diversity in the nest. As shown in Myrmica ants [45], colonies harbouring more queens responded with lower aggression towards conspecifics as their cuticular hydrocarbon diversity increased due to genetic differences. In our study system, the presence of infected workers with their quantitatively different chemical profiles could similarly lead to a generally lowered aggression towards conspecifics. However, accidental or not, the induced changes could offer an explanation for the tolerance of infected workers within their colonies. For instance, integration into ant colonies is promoted by a uniform colony odour, which is achieved by an active exchange of recognition cues, either via trophallaxis or allogrooming [46]. Both behaviours are elevated in parasitized colonies [26] and may promote the tolerance of infected workers, related or not.

On an ultimate level, reduced aggression towards conspecific competitors is expected to impair a colony’s ability to defend its nest, which is a limiting resource among Temnothorax ants [28]. Similar costs of parasite presence were reported within the red invasive fire ants, which reduced their foraging activity in the presence of parasitoid phorid flies, potentially resulting in a competitive disadvantage [47]. In dense T. nylanderi populations, approximately 40% of all colonies are invaded by conspecifics searching for a new nest. This typically results in the death of the queen, but not the workers [28]. The competitive disadvantage of less aggressive, parasitized colonies could thus lead to the genetic death of the colony while the parasite’s individual host survives.

In conclusion, we demonstrate that the presence of tapeworm-infected individuals with drastically changed phenotypes induces behavioural alterations in uninfected group members, consequently affecting the entire social group. Additionally, our findings indicate that manipulative parasites may indirectly benefit from the social lifestyle of their hosts at the expense of other group members. This study highlights the great complexity and the impact of parasites on animal societies, and invites additional, more comprehensive exploration into the effect of parasitism in group-living hosts.

Ethics. We followed the guidelines of the Association for the Study of Animal Behaviour (2012), and legal and institutional rules. Permission for ant collection was obtained from the local forestry district.

Data accessibility. Data were uploaded to Dryad: http://dx.doi.org/10.5061/dryad.7ph0.

Authors’ contributions. S.B., E.J. and S.F. designed the study and wrote the manuscript. S.B. and F.H. collected the ant colonies and conducted the behavioural experiments. S.B. and E.J. analysed the data.

Competing interests. We declare we have no competing interests.

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