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ORIGINAL ARTICLE

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Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees

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Abstract Parasites can affect host behavior in subtle but ecologically important ways. In the laboratory, we conducted experiments to determine whether parasitic infection by the intestinal protozoan *Crithidia bombi* or the tracheal mite *Locustacarus buchneri* alters the foraging behavior of the bumble bee *Bombus impatiens*. Using an array of equally rewarding yellow and blue artificial flowers, we measured the foraging rate (flowers visited per minute, flower handling time, and flight time between flowers) and flower constancy (tendency to sequentially visit flowers of the same type) of bees with varying intensities of infection. Bumble bee workers infected with tracheal mites foraged as rapidly as uninfected workers, but were considerably more constant to a single flower type (yellow or blue). In contrast, workers infected with intestinal protozoa showed similar levels of flower constancy, but visited 12% fewer flowers per minute on average than uninfected bees. By altering the foraging behavior of bees, such parasites may influence interactions between plants and pollinators, as well as the reproductive output of bumble bee colonies. Our study is the first to investigate the effects of parasitic protozoa and tracheal mites on the foraging behavior of bumble bees, and provides the first report of *Crithidia bombi* in commercial bumble bees in North America.

Keywords Behavior · Bombus · Crithidia bombi · Foraging · Locustacarus buchneri · Parasites

Introduction

Although the capacity of parasites to negatively affect their hosts is typically gauged in terms of parasite-induced mortality, parasites may also alter host behavior in subtle ways (reviewed by Moore 2002). If such changes involve host foraging behavior, parasitism may compromise the host's ability to exploit resources needed for survival and reproduction. For example, sublethal nematode parasites that infect ungulates can indirectly reduce host fitness by adversely affecting host foraging efficiency (Gunn and Irvine 2003). Sublethal parasitism may therefore influence both the foraging decisions of hosts (Gunn and Irvine 2003) and the dynamics of host populations (Feore et al. 1997; Ives and Murray 1997). Here, we examine the effects of two common parasites on the behavior of foraging bumble bees.

Bumble bees (Hymenoptera, Apidae) are a model system for investigations of animal foraging (Heinrich 1979; Goulson 2003) and host-parasite interactions (Schmid-Hempel 2001). While foraging, workers are attacked by a variety of parasites, including tracheal mites and intestinal protozoa (Schmid-Hempel 1998). Indeed, the tracheal mite *Locustacarus buchneri* Stammer (Podapolipidae) can be prevalent in both wild bumble bee populations (up to 50% of bees infected depending on time of year and host species, Otterstatter and Whidden 2004) and among commercial colonies (20% of colonies infected on average, Goka et al. 2000). Similar frequencies of infection are known for the intestinal protozoan *Crithidia bombi* Lipa and Triggiani (Trypanosomatidae) in natural bumble bee populations (10–30% of bees infected on average, Schmid-Hempel 1998). Nevertheless, *C. bombi* and *L. buchneri* are usually considered relatively benign parasites (Schmid-Hempel 1998), perhaps because they do not appear to affect the survival of host colonies (Husband and Sinha 1970), or affect host fitness only during times of stress (Brown et al. 2000; Brown et al. 2003). However, the effects of these parasites on bee foraging are poorly known.

Parasitic infections may diminish the reproductive output of bumble bee colonies by affecting the foraging behavior of workers. Bumble bee colonies depend on the resources (pollen and nectar) that workers collect (Sutcliffe and Plowright 1988). Parasites that reduce the efficiency of a colony's worker force may therefore diminish colony

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growth and reproduction (Muller and Schmid-Hempel 1992a; Muller and Schmid-Hempel 1992b). Although the effects of parasites on bee foraging may be subtle, they nonetheless can alter ecologically important aspects of host behavior. For example, the tendency of workers to sequentially visit plants of the same species (flower constancy, Chittka et al. 1999; Goulson 1999), and their choice of plant species in general, is known to differ among bumble bees infected and uninfected with parasitoid larvae (Schmid-Hempel and Schmid-Hempel 1990; Schmid-Hempel and Stauffer 1998). Similarly, infection by *C. bombi* appears to make bees less likely to collect pollen (Shykoff and Schmid-Hempel 1991), and infection by *L. buchneri* causes bees to become lethargic and eventually cease foraging (Husband and Sinha 1970). In this way, parasite-induced changes in bee foraging may also affect the success of plant species that depend on bees for pollination. Here, we used laboratory experiments to determine the influence of infection by *L. buchneri* and *C. bombi* on the foraging rate (i.e., flowers visited per minute, flower handling time, and flight time between flowers) and flower constancy of bumble bee workers as they foraged on arrays of artificial flowers.

Methods

Bumble bees

We used five colonies of *Bombus impatiens* Cresson (obtained from a commercial rearing company in North America), each with 30–50 workers, for all experiments. We determined through dissection and fecal screening that all five colonies were infected with either the protozoan *Crithidia bombi* (identified following Lipa and Triggiani 1980), the tracheal mite *Locustacarus buchneri* (identified following Husband and Sinha 1970), or both, upon their arrival from the commercial supplier. We provided colonies with a constant supply of pollen and supplemented them with nectar. Prior to the experiment, we connected each colony to a screened flight cage (1.5 m long × 1.05 m wide × 1 m high) using a wire mesh tube with plastic gates. Each bee was given a unique mark using colored correction fluid.

Foraging array

Artificial flowers were designed to simulate natural open-tube flowers (Laverty 1994; Gegear and Laverty 1998). We constructed each flower by removing the cap from a 1.5 ml Eppendorf centrifuge tube (blue or yellow) and then fastening a circular (3 cm diameter) acetate 'corolla' (blue or yellow to match tube) around the entrance of the tube. To properly access each flower, bees had to land on the corolla and crawl down to the bottom of the tube to obtain the reward. Our experimental array was based on that of Gegear and Thomson (2004), and consisted of 60 flowers (30 blue and 30 yellow) arranged in 12 rows of 5 (alternating two rows of yellow, two rows of blue). Within rows, flowers were separated by 10 cm, and the distance between adjacent rows was 5 cm. Alternating rows were offset by 5 cm so that the nearest neighbor distance was 7.1 cm. In this way, from non-edge rows, bees had an equal choice of both flower colors at nearest- and second nearest-neighbor distances. Although all nearest-neighbor flowers were the same color on the short edges of the array (yellow on one edge, blue on the other), bees were never observed to spend a disproportionate amount of time on these flowers. The design of our array minimizes any trade off between flower constancy and foraging rate as bees that prefer one flower type (e.g. yellow) do not have to fly over flowers of the alternate type (blue) to remain constant. Each flower was filled with 2 µl of 30% sucrose solution and refilled using a Hamilton microdispenser (Reno, Nevada).

We first trained bees to visit flowers of each color by allowing them several hours of foraging on monotypic arrays of each color. In this way, bees acquired skill at handling flowers and associated each color with reward prior to testing. Training and testing flowers provided the same concentrations of sucrose. Immediately prior to testing a bee, we allowed it to forage for three trips each on pure blue and pure yellow arrays (color order alternated among bees). This procedure controlled for the possibility that bees had not retained from training either the handling technique of the flowers or the color-reward association. We then presented the bee with a mixed array of both colors containing equal rewards, and videotaped the first 70 flowers visited (corresponding to about two full foraging trips). During this time, we prevented other bees from accessing the foraging arena by blocking the wire mesh tube that connected the colony to the flight cage. During testing, we refilled drained flowers so that bees always encountered the same number of rewarding flowers while foraging. Re-filling occurred as the test bee entered a subsequent flower to make certain that individuals were not disturbed in any way while foraging. Flowers were replaced between test bees.

Although our objective was to determine the effects of *C. bombi* and *L. buchneri* on bee foraging, it is also possible that host foraging behavior may influence the probability of exposure to these parasites (e.g. Durrer and Schmid-Hempel 1994), thereby confounding our study. We therefore allowed colonies access to the foraging arena for a maximum of 7 days, which is equal to the typical latency period (duration between exposure and infectiousness) for *C. bombi* infections under our laboratory conditions, and only half the latency period for *L. buchneri* infections (Husband and Sinha 1970). This design ensured that infected workers acquired parasites inside the colony prior to the beginning of our experiment (not during training), and that observed differences in foraging behavior among workers were the result, not the cause, of infection.

Quantifying parasite intensity

After completing 70 flower visits, the bee was immediately placed in a clean plastic vial and freeze-killed at −20°C. For each worker, the hind gut was removed and 4 µl of feces was transferred to a clean glass slide. Feces samples were

air dried, fixed with absolute methanol for 2 minutes, and stained with 10% Giemsa stain for 2 h. For each slide, we counted the number of *C. bombi* cells (400 × magnification, using an ocular counting grid of 10 mm × 10 mm) at five randomly chosen fields of view and averaged these counts for an estimate of *C. bombi* intensity. We also dissected each worker and assessed the intensity of tracheal mite infection by counting the number of gravid *L. buchneri* females, larviform males and females, and eggs present in the host's tracheal tubes. All estimates of mite load were highly correlated with one another and we present only the number of gravid female *L. buchneri* per bee as our measure of mite intensity. *Crithidia bombi* and *L. buchneri* counts were made blind with respect to a bee's foraging performance. Finally, we measured the length of the radial cell on the right forewing of each bee as an estimate of body size.

Data analysis

For each bee, we selected a sequence of ten consecutive flower visits from the latter half of the 70 recorded visits that was free of revisits, falls, and any unusual behavior. These sequences were chosen so as to capture the maximum foraging performance of each bee. From these sequences, we measured the average time spent on flowers (handling time), time from initial contact with a flower until the bee's forward motion into the tube ceased (access time), time spent motionless at the bottom of tube (ingestion time), time spent flying between flowers (flight time), and the number of flowers visited per minute (foraging rate). All measurements were taken with a digital stopwatch, by an observer who was blind to the infection status of the bees.

We quantified the flower constancy of bees, i.e., the tendency to sequentially visit one flower type while bypassing other equally rewarding flower types, using the following measure: Constancy Index, $CI=(c-e)/((c+e)-(2ce))$, where c is the observed proportion of moves a bee made between flowers of the same color, and e is the expected proportion of moves between flowers of the same color based on the overall frequency of visits to each color across all bees tested. Thus, CI represents the degree to which an individual bee moved between flowers of the same color, controlling for any overall color preference. Possible values range from –1 (complete inconstancy) to 0 (random foraging) to +1 (complete constancy). For values of 1 and −1, this index does not reflect a bee's color preference (e.g. bees that are completely constant to blue flowers would get the same score as those completely constant to yellow flowers). This measure has been used elsewhere to quantify the flower constancy of individual bees (Gegear and Thomson 2004).

We used multiple linear regression to determine the effects of *C. bombi* or *L. buchneri* intensity, bee size, bee age, and colony of origin on the time bees spent handling flowers, flying between flowers, and the number of flowers bees visited per minute. Although these three measures of foraging efficiency each provide useful information, they are not entirely independent; the flower handling time and flight time of a bee directly determine the number of flowers that bee visits per minute. We log transformed handling time and flight time to satisfy the assumption of normally distributed residuals, and in all cases the residuals satisfied the assumption of equal variance (Sokal and Rohlf 1995). For those foragers that we marked at the time of eclosion (and therefore of a known age), it was possible to test for age effects on foraging. However, among uninfected bees age did not correlate with handling time ($r=-0.084$, $P=0.818$, $n=10$) or flight time ($r=-0.002$, $P=0.997$, $n=10$), and was therefore excluded from further analyses. We used G-tests of independence (Sokal and Rohlf 1995) to compare the proportions of infected and uninfected bees that visited flowers of only one color (i.e., were 100% flower constant). We compared all other behaviors (e.g. flower rejections, grooming) between infected and uninfected bees using *t*-tests (Sokal and Rohlf 1995). All analyses were performed in SAS (SAS Institute 1999).

Results

Parasite prevalence and intensity

Of our four colonies infected by *C. bombi*, two contained both infected and uninfected workers (18 of 29 foragers used in the experiment were infected; range of *C. bombi* intensity among infected individuals = 0.5–45.2 cells), and were therefore useful for assessing within-colony effects of parasitic protozoa on host foraging. In contrast, among the remaining two colonies infected by *C. bombi*, virtually all workers (27/29) possessed a uniform, low-level, infection (intensity < 5 for all bees) that did not provide sufficient variation for analyses. All workers tested ($n=10$, 10, 9) in our three *L. buchneri*-infected colonies contained tracheal mites (mean intensity = 3.6 gravid female mites per bee, range = 1–12) so within-colony comparisons of mite-infected and uninfected bees were not possible. We instead relied primarily on between-colony comparisons to analyze the effects of *L. buchneri* on the constancy and foraging rate of bees. To determine whether mite-infected bees ($n=29$) were generally less efficient foragers, we compared their foraging rate against that of bees uninfected by either *L. buchneri* or *C. bombi* ($n=11$, from two colonies).

Effects of parasites on the flower constancy of bees

Bumble-bee workers infected with the tracheal mite *L. buchneri* were more constant to a single flower type (blue or yellow) than bees not infected by *L. buchneri*. The frequency distributions of our constancy index for bees infected and uninfected by *L. buchneri* reveal a significantly greater bias towards constancy among infected bees (Fig. 1; Kolmogorov-Smirnov two-sample test, $P=0.011$). Indeed, across all five colonies, 69% (20/29) of mite-infected foragers visited flowers of only one color, whereas only 34% (10/29) of uninfected foragers were entirely constant. There

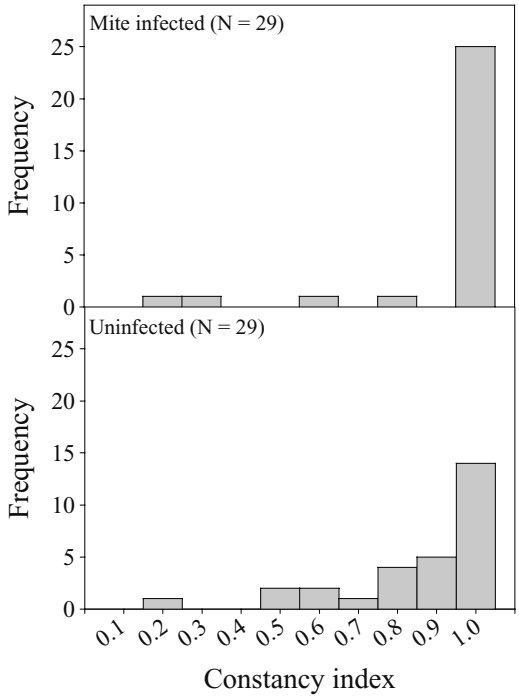

Fig. 1 Frequency histograms of flower constancy index (see Methods) for workers infected and uninfected by the tracheal mite *L. buchneri*

was no evidence that mite infection influenced the flower-color preference of bees, as color choice was independent of mite-infection status among bees that were entirely constant (G=0.09, P=0.76). Constancy did not correlate with bee size (Spearman's r=0.19, P=0.14, n=58) or bee age (Spearman's r=0.07, P=0.71, n=33).

Although many of our bees (36/58) in the above analysis of constancy were also infected with the intestinal protozoan *Crithidia bombi*, there was no evidence that infection by this parasite influenced flower constancy. The proportion of workers that were entirely constant to one flower type was independent of *C. bombi* infection status (infected: 18/36; uninfected: 12/22; G=0.30, P=0.58), and our constancy index did not vary with *C. bombi* intensity ($F_{1,27}$=0.65, P=0.43). Workers simultaneously infected with *L. buchneri* and *C. bombi* displayed the same high level of constancy (13/18 visited only a single flower color) as bees infected with only *L. buchneri* (20/29 visited only a single flower color), suggesting that these parasites did not interact in their effects on the foraging behavior of bumble bees.

Effects of parasites on the foraging rate of bees

We did not find strong effects of tracheal mites on the foraging rate of bumble bees. Flower-handling time (access or ingestion time), flight time between flowers, and the number of flowers visited per minute did not vary with the number of mites per bee (Table 1). Although mite-infected workers were somewhat slower, on average, at handling flowers compared to uninfected workers (mean ± SE handling time (sec.): 4.36±0.17, n=29 vs. 3.74±0.15 s, n=11; t=1.94, P=0.061), this difference should be treated cautiously as the effects of mites and colony of origin cannot be fully separated in this analysis (mite-infected and uninfected bees originated from different colonies).

In contrast, bumble-bee workers infected with the intestinal protozoan *C. bombi* foraged more slowly than uninfected bees. The number of flowers visited per minute declined with increasing levels of *C. bombi* infection

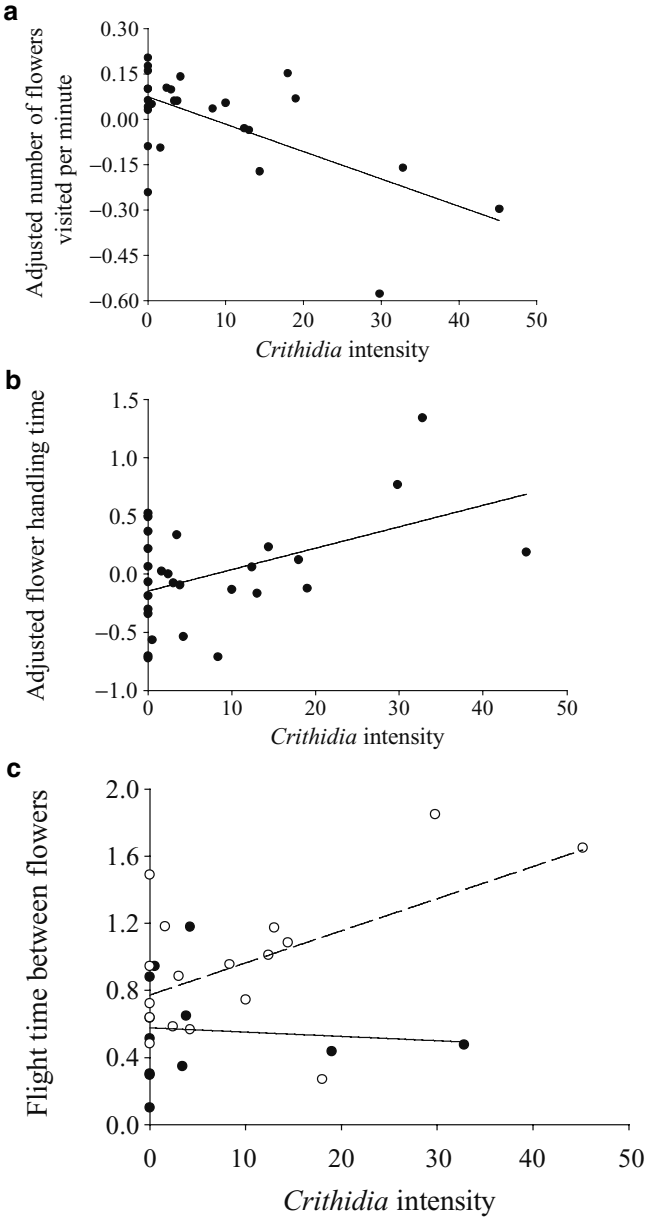

Fig. 2 Relation between the intensity of infection by the intestinal protozoan *C. bombi* and **a** number of flowers bees visited per minute, **b** flower handling time, and **c** flight time between flowers. In panel **c**, *open circles* and *dashed line* represent bees smaller than the average size of all bees tested, and *filled circles* and *solid line* represent bees larger than the average size. Measures of foraging rate in panels a and b have been adjusted for the effects of bumble bee size and colony of origin

Table 1 ANCOVA statistics comparing the foraging performance of bees with the intensity of infection by *C. bombi* and *L. buchneri*

Dependent variable	*C. bombi* infection			*L. buchneri* infection		
Explanatory variable	*F*	*df*	*P*	*F*	*df*	*P*
Handling time						
Parasite intensity	7.42	1, 24	**0.012**	0.82	1, 23	0.370
Bee size	6.23	1, 24	**0.020**	0.25	1, 23	0.620
Colony	8.19	1, 24	**0.009**	0.16	2, 23	0.860
Flight time						
Parasite intensity	16.01	1, 21	**<0.001**	0.49	1, 23	0.490
Bee size	2.34	1, 21	0.140	0.45	1, 23	0.510
Colony	0.00	1, 21	0.970	6.84	2, 23	**0.005**
Intensity × size	14.08	1, 21	**0.001**	–	–	–
Foraging rate						
Parasite intensity	17.46	1, 23	<**0.001**	1.35	1, 23	0.260
Bee size	0.47	1, 23	0.500	0.08	1, 23	0.790
Colony	0.28	1, 23	0.601	0.63	2, 23	0.540

Non-significant interaction terms (e.g. Parasite intensity × Colony) were removed from each model and are not shown

(Table 1, Fig. 2a), and infected bees visited 12.4% fewer flowers per minute on average than uninfected bees (9.9 vs. 11.3; $t=-2.11$, $df=27$, $P=0.045$). Further analyses revealed that infected bees foraged more slowly primarily because they spent more time handling flowers, i.e., accessing and ingesting nectar. Flower-handling time increased significantly with the intensity of *C. bombi* infection (Table 1, Fig. 2b). Although infected bees took longer both to access and ingest nectar from flowers compared with uninfected bees, only the former comparison was significant (mean ± SE access time: 1.26±0.8 s vs. 1.04±0.4 s, $t=2.56$, $df=27$, $P=0.02$; mean ± SE ingestion time: 1.85±0.11 s vs. 1.64±0.06 s, $t=1.71$, $df=27$, $P=0.11$). In addition, the time bees spent flying between flowers increased with their level of *C. bombi* infection for small-bodied but not large-bodied bees (significant body size x parasitism interaction, Table 1; Fig. 2c). Our analyses of the effects of *C. bombi* on bee foraging rate did not include, and therefore were not influenced by, bees infected with tracheal mites.

Additional changes in the behavior of parasitized bees

Infection by protozoa, but not tracheal mites, was associated with changes in the behavior of bees as they foraged. During 70 flower visits, *C. bombi* -infected individuals rejected (landed on but did not probe) more flowers than uninfected bees (mean ± SE rejections, 29.2±3.2 vs. 18.9±2.4, respectively; $t=2.6$, $df=16$, $P=0.02$). Furthermore, we observed more instances of *C. bombi* -infected bees grooming on flowers (6.8±1.4 vs. 1.9±0.8, respectively; Mann-Whitney $U=6.96$, $P=0.008$), and falling from flowers during taking off and landing (4.0±1.0 vs. 1.0±0.4, respectively; Mann-Whitney $U=5.47$, $P=0.01$) compared to uninfected bees. None of these behaviors correlated with *L. buchneri* intensity ($P>0.25$ in all cases).

Discussion

Bumble bees are a model system for studies of both host-parasite interactions (Schmid-Hempel 2001) and animal foraging (Goulson 2003); however, these topics are rarely considered simultaneously, despite observations suggesting that parasites influence the foraging behavior of bees (Schmid-Hempel and Schmid-Hempel 1991; Schmid-Hempel and Stauffer 1998). Here, we demonstrate that two common parasites of bumble bees, the tracheal mite *Locustacarus buchneri* and the intestinal protozoan *Crithidia bombi*, have substantial but contrasting effects on the foraging rate and flower constancy of worker bees. When foraging on artificial flowers, workers infected with *L. buchneri* were considerably more flower constant, but no less efficient, than uninfected bees. Indeed, twice as many bees infected by *L. buchneri* foraged on only one flower type (blue or yellow) relative to uninfected bees. In contrast, although *C. bombi* had no observable effects on the flower constancy of bees, workers infected with this parasite were substantially slower at handling flowers and visited 12% fewer flowers per minute on average than uninfected bees. Although relatively few bees in this study were heavily infected with *C. bombi*, further work has demonstrated a consistent decline in flower handling time among workers with high intensities of *C. bombi* (Gegear et al. in press). Our data also show that bees infected with *L. buchneri* were slightly slower on average at handling flowers compared to uninfected bees, and it is possible that a larger sample size would reveal that tracheal mites also have a significant impact on bee foraging rate. In any

case, the observed behavioral differences likely reflect the effects of parasites, as we controlled for factors known to influence bee foraging behavior, including the size, age and foraging experience of workers, and the type and availability of flowers. Our study is the first to investigate the effects of parasitic protozoa or tracheal mites on the foraging behavior of bumble bees, and the first report of *C. bombi* infecting commercial bumble bees in North America.

We used bees naturally infected within the nest to determine whether realistic levels of infection alter host foraging. Nevertheless, we cannot rule out the possibility that bees with poor foraging ability may have been more susceptible to *C. bombi*, rather than infection itself being the cause of poor foraging. However, bees with low levels of infection often foraged as rapidly as uninfected bees, suggesting that infection was not simply confined to poor foragers. Furthermore, the rate at which bees foraged declined with increasing levels of infection by *C. bombi*, suggesting that the differences we observed in foraging were related to the effects of parasitism, not the cause. Nevertheless, further studies in which bees are artificially infected are necessary to verify causality.

Parasites can affect the behavior of hosts in a variety of ways. Parasites may indirectly influence host decisions by imposing physiological stress, or purposefully alter host behavior to facilitate transmission (Stamp 1981; Holmes and Zohar 1990; Brodeur and McNeil 1992; Poulin et al. 1994; Moore 2002). Although we cannot discern which mechanism underlies the observed behavioral differences in our study, it is likely that the tracheal mite *L. buchneri*, which can block and damage a bee's respiratory tubes (Husband and Sinha 1970), has substantial pathological effects on foraging bees. This is supported by the observation that bumble bees with heavy infections of *L. buchneri* are lethargic and may cease foraging entirely (Husband and Sinha 1970). Physiological stress imposed on bees by tracheal mites can influence energetically expensive activities such as foraging behavior (Harrison et al. 2001), and may alter foraging decisions such as flower choice and constancy. Indeed, other parasites are known to alter the food choice of insect hosts (Karban and English-Loeb 1997), including the flower choice of bumble bees (Schmid-Hempel and Stauffer 1998). Physiological stress arising from parasitism may also explain why bees infected by *C. bombi* in our study had considerable difficulty with foraging behaviors that require substantial effort and motor control, such as landing on or taking off from flowers. These results support the previous suggestion that pathological effects arising from parasitism may explain differences in flower choice between parasitized and unparasitized bumble bees (Schmid-Hempel and Stauffer 1998). Another possibility is that the parasites in our study modify the behavior of bees to facilitate transmission. For *C. bombi*, transmission between bumble bee colonies occurs at flowers when infected bees shed parasite cells that are picked up by subsequent foragers (Durrer and Schmid-Hempel 1994). Horizontal transmission of *C. bombi* should therefore be facilitated if infected bees spend longer on flowers or visit more flowers. Indeed, we found that bees infected by *C. bombi* do spend longer on flowers, visit more flowers without probing for nectar, and frequently groom before leaving a flower. It is possible that these behaviors speed the spread of *C. bombi* between colonies in natural populations (e.g. Imhoof and Schmid-Hempel 1999). However, further work is needed to determine whether the behavior of parasitized bumble bees actually increases the probability of parasite transmission.

Parasite-induced changes in host foraging behavior can influence both host fitness and ecologically important interactions between species. Our results show that, even for relatively simple flowers, parasites can reduce the rate with which bumble bees access and ingest nectar. Parasitized bees may therefore perform quite poorly on morphologically complex flowers that require considerable skill to access nectar. Indeed, further work in our laboratory has shown that heavy infections by *C. bombi* impair the ability of bumble bees to learn and use complex artificial flowers (Gegear et al. in press). If parasites substantially reduce the rate with which bees handle flowers, infected workers may choose to forage on simpler flowers than those used by healthy workers. This is consistent with the observation that, in the field, bumble bees parasitized by conopid flies tend to forage on plant species that require less time to access nectar than those visited by unparasitized bees (Schmid-Hempel and Schmid-Hempel 1990). Because *C. bombi* often infects the majority of bees within a colony (Imhoof and Schmid-Hempel 1999), this parasite may reduce the efficiency of the entire worker force of a colony and, in turn, diminish the colony's reproductive success. Differences in the behavior of infected bees, including spending more time on flowers, visiting more flowers without probing for nectar, and grooming more often on flowers, may also influence their role as pollinators. It is conceivable that such behaviors could increase the amount of pollen that infected bees pick up or deposit on flowers during foraging. If so, parasites may have a previously unsuspected influence on the reproductive success of plants.

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