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Original article

Patterns of parasitism by tracheal mites (*Locustacarus buchneri*) in natural bumble bee populations

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Abstract – Parasitic mites are among the most destructive enemies of social bees. However, aside from mites of honey bees, virtually nothing is known about the prevalence and effects of parasitic mites in natural bee populations. In this paper, we report on parasitism of bumble bees (*Bombus* spp.) by the tracheal mite *Locustacarus buchneri* Stammer in south-western Alberta, Canada. Parasitism of bumble bees by *L. buchneri* occurred at many sites and in several host species. However, *L. buchneri* appears to be relatively host-species specific as it was found primarily in bumble bee species belonging to the subgenus *Bombus* sensu stricto. Furthermore, bumble bees containing tracheal mites had significantly reduced lifespans in the laboratory. Implications of parasitism on bumble bee life history are discussed.

Bombus* / *Locustacarus buchneri* / parasitism / Podapolipidae / *Psithyrus

1. INTRODUCTION

Social bees are host to a variety of parasitic organisms (e.g. entomopathogenic fungi, mites, nematodes, parasitoids, protozoa, viruses) that may adversely affect their survival and reproductive success (Schmid-Hempel, 1998). Of these, parasitic mites are among the most destructive. For example, tracheal mites (e.g. *Acarapis woodi* Rennie) of honey bees (*Apis mellifera* Linnaeus) have been studied extensively (reviewed in Sammataro et al., 2000) and are known to affect host physiology (Harrison et al., 2001) and cause substantial colony loss (Otis and Scott-Dupree, 1992). Although other social bees, such as bumble bees (*Bombus* spp.), also harbour parasitic mites, relatively little is known about enemies of non-*Apis* bees.

Locustacarus buchneri Stammer (Acari: Podapolipidae) is a widespread parasitic mite of bumble bees and is known to affect host condition and behaviour adversely (Husband and Shina, 1970). Female *L. buchneri* overwinter in the trachea of hibernating bumble bee queens and lay eggs shortly after their host emerges in the spring. Hatching larviform female and male *L. buchneri* mate inside the host bee, and females transfer to the tracheae of other bumble bees in the nest to lay eggs. The lifecycle of *L. buchneri* may repeat several times before the infected bumble bee colony begins to produce sexuals in the fall, but only mites infecting young queen bees will survive to the following spring (Husband and Shina, 1970). Although *L. buchneri* is typically found in less than 10% of field-caught bumble bees (reviewed in MacFarlane et al., 1995), some species experience prevalences over 20% (Goldblatt and Fell, 1984). Large numbers of *L. buchneri* may accumulate in workers and cause their hosts to become lethargic and cease foraging (Husband and Shina, 1970). Here, we report on the occurrence and negative effects of *L. buchneri* in

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natural bumble bee populations in south-western Alberta, Canada.

2. MATERIALS AND METHODS

2.1. Study sites in Alberta

2.1.1. Main study site

At our main study site near Barrier Lake, in south-western Alberta, Canada, we collected 17 species of true bumble bees (*Bombus* Latr.) and 3 species of socially-parasitic bumble bees (*Psithyrus* Lepeletier) during the summers of 1997 (workers only, n = 244), 1998 (queens, workers and males, n = 1140), 1999 (queens, workers and males, n = 1349) and 2000 (workers and males, n = 716). Bumble bees were collected approximately every seven days at Barrier Lake during August 1997 and May-August 1998, and every 2–3 days during July-August 1999 and 2000.

2.1.2. Additional study sites

During July-August 2000, we also sampled bumble bee workers (n = 503) and males (n = 217) at 7 sites across south-western Alberta (collectively referred to as the 'survey sites'): Claresholm, Coleman, Drumheller, Innisfail, Fortress Mountain, Sibbald Flats, and along highway 40 North (hereafter referred to as the 'Trunk Road' site). The survey sites were chosen as representative subalpine, grassland and parkland locations (according to ecoregions of Alberta defined by Strong, 1992). Each of the survey sites was sampled once, except for Sibbald Flats, which was sampled three times. Finally, bumble bee workers (n = 277) and males (n = 92) were sampled in Calgary (University of Calgary campus and Heritage Park) on 5 dates during July-August, 1998.

2.2. Collecting bumble bees

In total, we collected 4834 foraging bumble bees. Subsequent to capture, each bee was stored individually for live transfer to the laboratory. Bees collected during 2000 were held at room temperature in the laboratory for two hours to consume their nectar reserves and then weighed to ± 0.1 mg. For each bee, we recorded the species, and whether it was a queen, worker or male. Bees were housed individually in seven-dram vials, provided with sugar water ad libitum (60:40, distilled water:sugar), and checked daily for dead individuals. After a bee died, the residual lifespan (number of days alive after capture) was recorded. The right forewing was removed and measured (proximal end of median plate to distal end of radial cell) as an indicator of bee body size (Harder, 1982). Dead bees were dissected under a stereomicroscope to determine whether or not internal mites were present. All internal mites were *Locustacarus buchneri* (R.W. Husband, pers. comm.).

2.3. Statistical analyses

2.3.1. Prevalence

We used logistic regression (McCullagh and Nelder, 1989) to assess the effects of sampling location, host species, host type (queen, worker or male), host mass, and year on the proportion of bees parasitized by tracheal mites (prevalence).

2.3.2. Prevalence – mass relationship

To compare the mass of bumble bees parasitized and unparasitized by tracheal mites, we used ANOVA (Sokal and Rohlf, 1995) and treated parasitized (yes/no), bee sex (worker/male), and collecting location as categorical explanatory variables. Only *B. moderatus*, *B. occidentalis*, and *B. terricola* were included in this analysis as mite prevalence was very low (< 4%) among most other species. Because parasitism by tracheal mites was very rare among bumble bees at Red Deer, Fortress Mountain, and Coleman (< 2.5%), we excluded these sites from analyses comparing the mass of parasitized and unparasitized bumble bees. We also compared the mean wing length of parasitized and unparasitized *B. occidentalis* workers and males using t-tests (Sokal and Rohlf, 1995).

2.3.3. Lifespan – parasitism relationship

We compared the survival after capture between parasitized and unparasitized bumble bees using nonparametric methods (Wilcoxon test, Proc LIFETEST, SAS Institute, 1998) because the probability of death was not constant for parasitized bees (Lee, 1980). Only *B. occidentalis* was used to compare the survival of parasitized and unparasitized bees as tracheal mites were relatively rare among most other bumble bee species.

3. RESULTS

3.1. Prevalence relationship with location and year

Across south-western Alberta, we found the tracheal mite *L. buchneri* infecting bumble

Table I. Percentages of bumble bee queens, workers, and males in south-western Alberta containing tracheal mites.

Location	Year	Queens (n)	Workers (n)	Males (n)	Total (n)
Barrier Lake	1997	-	3.3 (244)	-	3.3 (244)
	1998	2.3 (350)	3.8 (739)	2.0 (51)	3.2 (1140)
	1999	0.0 (28)	2.8 (1193)	0.8 (128)	2.5 (1349)
	2000	-	5.6 (585)	1.5 (131)	4.9 (716)
Total		**2.1 (378)**	**3.7 (2761)**	**1.3 (310)**	**3.3 (3449)**
Calgary	1998	-	13.4 (277)	15.2 (92)	13.8 (369)
Survey sites					
Claresholm	2000	-	4.3 (46)	37.5 (32)	17.9 (78)
Coleman	2000	-	0.0 (28)	0.0 (56)	0.0 (84)
Drumheller	2000	-	0.0 (61)	14.3 (21)	3.7 (82)
Fortress Mt.	2000	-	0.0 (34)	0.0 (5)	0.0 (39)
Red Deer	2000	-	0.0 (58)	8.7 (23)	2.5 (81)
Sibbald Flats	2000	-	3.3 (183)	9.1 (11)	3.6 (194)
Trunk Road	2000	-	0.0 (41)	6.3 (48)	3.4 (89)
Total		**-**	**6.2 (728)**	**12.2 (288)**	**7.9 (1016)**

bees at seven of nine sites and occurring, on average, in less than 5% of *Bombus* at all sites except Claresholm (18%) and Calgary (14%) (Tab. I). Intense sampling at our main study site (Barrier Lake) over four years revealed consistently low seasonal averages in the prevalence of *L. buchneri* among *Bombus* queens (0–2.3%), workers (2.8–5.6%), and males (0.8–2.0%) (Tab. I). Despite this, some bumble bee species (*B. moderatus*, *B. occidentalis*, *B. terricola*) consistently experienced prevalences of up to 40–50% during mid-summer (Fig. 1). Approximately 5% (1/18) of the socially parasitic bumble bee (*Psithyrus*) queens at Barrier Lake contained mites during 1999, but none (0/39) were parasitized during 1998. Because of small sample sizes, *Psithyrus* are not included in the following analyses.

3.2. Prevalence relationship with host species, sex and size

The prevalence of *L. buchneri* differed among bumble bee species both at Barrier Lake (data pooled, 1997–2000) (G = 294.6, df = 7, P < 0.001) and among the survey sites (sites pooled) (G = 70.8, df = 8, P < 0.001) (Tab. II). At all sites, *L. buchneri* occurred most frequently in *B. occidentalis* (average prevalence across all sites = 20%, n = 498) and, to a lesser extent, in *B. terricola* (9%, n = 147) and *B. moderatus* (7%, n = 91) (Tab. II). Although *B. moderatus*, *B. occidentalis*, and *B. terricola* together comprised only 18% (736/4096) of all bees analyzed, they accounted for approximately 83% (119/143) of all bees parasitized by *L. buchneri*. Among other bumble bee species, the prevalence of *L. buchneri* was very low (< 4%), except for *B. rufocinctus*, which experienced about the same prevalence as *B. terricola* (Tab. II). Of the nine most abundant bumble bee species collected at Barrier Lake, *L. buchneri* was found in spring queens or males of only three species, but in workers of seven species (Tab. II).

The prevalence of *L. buchneri* differed significantly between bumble bee workers and males, but not according to bee size. After accounting for significant differences in the prevalence of *L. buchneri* among years (Barrier Lake, G = 8.8, df = 2, P < 0.05) and among sites (survey sites, G = 17.3, df = 4, P < 0.001), prevalence was significantly higher among

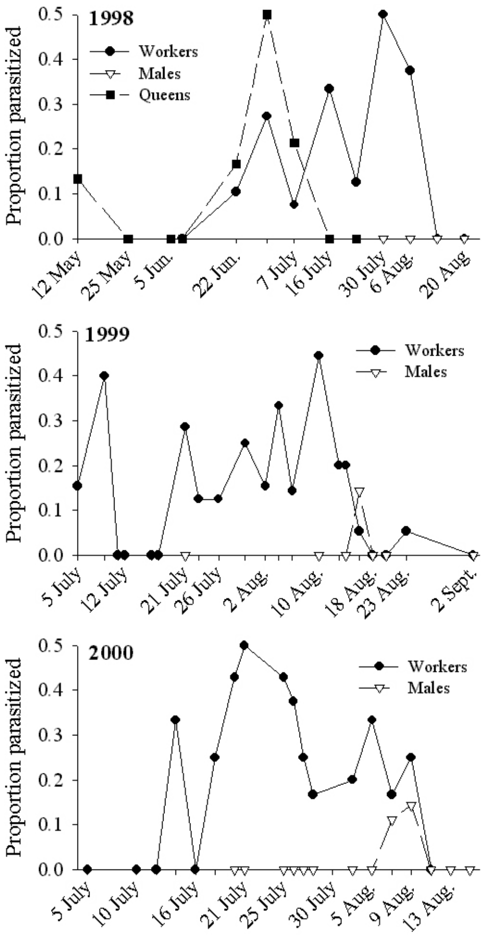

Figure 1. Seasonal prevalence of the tracheal mite, *L. buchneri*, among three commonly parasitized bumble bee species, *B. moderatus*, *B. occidentalis*, *B. terricola* (data pooled), at Barrier Lake, Kananaskis, during 1998–2000.

workers than males at Barrier Lake ($G = 7.7$, df = 1, $P < 0.01$), but the reverse was true among the survey sites ($G = 29.6$, df = 1, $P < 0.001$; Tab. I). However, the prevalence of *L. buchneri* did not differ significantly between queens, workers or males ($G = 4.51$, df = 2, $P > 0.10$) when considering only those years with data for all bumble bee castes and sexes. Prevalence of *L. buchneri* did not vary with bumble bee mass ($G = 0.9$, df = 1, $P = 0.34$) after accounting for differences in prevalence between workers and males and among sites. Similarly, using wing length as an estimate of body size showed no differences in the size of parasitized and unparasitized *B. occidentalis* (the most commonly infested species) (mean ± SE wing length (mm), parasitized vs. unparasitized: workers, 220.8 ± 2.94 vs. 222.8 ± 1.75, $t = -0.59$, df = 135, $P > 0.50$; males, 256.8 ± 3.36 vs. 258.3 ± 1.85, $t = -0.38$, df = 57, $P > 0.70$).

3.3. Effect of parasitism on host lifespan

Bumble bees containing *L. buchneri* typically lived shorter lifespans after capture than unparasitized bees. The mean lifespan after capture of male bees containing *L. buchneri* was significantly shorter than that of unparasitized males (mean ± SE lifespan: unparasitized: 11.69 ± 0.85 days, $n = 70$, range, 0–32 days; parasitized: 7.00 ± 1.44 days, $n = 13$, range, 1–21 days; Wilcoxon $\chi^2 = 7.85$, df = 1, $P = 0.005$). Although workers containing *L. buchneri* also survived, on average, for shorter periods than unparasitized workers, the difference only approached significance (unparasitized: 7.57 ± 0.44 days, $n = 277$, range, 0–36 days; parasitized: 5.98 ± 0.69 days, $n = 80$, range, 0.5–31 days; Wilcoxon $\chi^2 = 3.29$, df = 1, $P = 0.07$).

4. DISCUSSION

Although the parasitic mite *Locustacarus buchneri* is known to attack at least 25 bumble bee species across the Holarctic region (Husband, 1969; Husband and Husband, 1997), it typically occurs in only a small fraction of the host species available at a site. In south-western Alberta, we found *L. buchneri* parasitized, on average, 20% of *B. occidentalis* (with seasonal peaks between 40–50%), whereas prevalences were very low (<4%) among most other bumble bee species. Further, these differences in mite prevalence among bumble bee species were inexplicable in terms of bee size. Similar patterns have also been found in the eastern United States, where *L. buchneri* parasitized primarily *B. vagans* (mean prevalence = 21%) and *B. bimaculatus* (23%) queens, but infected <1% of queens of eight other species (Goldblatt and Fell, 1984). Further, in Switzerland *L. buchneri* was found in only two of eight bumble bee species sampled (Shykoff and Schmid-Hempel, 1991) and only three of 13 species collected across North

Table II. Percentages of bumble bees of different species containing tracheal mites at Barrier Lake during 1997–2000 (data pooled across years) and among 7 sites sampled in south-western Alberta during 2000 (data pooled across sites). Only species where total n > 10 are shown.

Species	Barrier Lake				Survey sites		
	Queens (n)	Workers (n)	Males (n)	Total (n)	Workers (n)	Males (n)	Total (n)
B. bifarius	0.0 (24)	0.2 (808)	0.0 (36)	0.2 (868)	0.0 (141)	0.0 (31)	0.0 (172)
B. californicus	0.0 (24)	1.8 (325)	3.7 (27)	1.9 (376)	-	-	-
B. flavifrons	0.0 (137)	0.1 (797)	0.0 (105)	0.1(1039)	5.7 (35)	0.0 (18)	3.8 (53)
B. frigidus	0.0 (58)	0.0 (129)	0.0 (6)	0.0 (193)	0.0 (22)	0.0 (17)	0.0 (39)
B. huntii	-	-	-	-	0.0 (46)	0.0 (7)	0.0 (53)
B. melanopygus	0.0 (16)	4.5 (89)	-	3.8 (105)	0.0 (29)	0.0 (23)	0.0 (52)
B. mixtus	0.0 (14)	0.0 (45)	-	0.0 (59)		-	-
B. moderatus	0.0 (3)	7.9 (38)	0.0 (36)	3.9 (77)	0.0 (3)	27.3 (11)	21.4 (14)
B. occidentalis	17.6 (34)	21.7 (351)	4.1 (73)	18.6 (458)	23.8 (21)	52.6 (19)	37.5 (40)
B. rufocinctus	-	-	-	-	0.0 (48)	17.6 (34)	7.3 (82)
B. terricola	11.1 (9)	10.8 (93)	0.0 (12)	9.6 (114)	0.0 (18)	13.3 (15)	6.1 (33)
B. vagans	-	-	-	-	0.0 (24)	0.0 (5)	0.0 (29)

America (reviewed in MacFarlane et al., 1995). Although it is unclear why *L. buchneri* parasitizes certain bumble bee species more frequently than others, our results do not support MacFarlane et al.'s (1995) suggestion that *L. buchneri* occurs most commonly in early emerging bumble bee species that form above-ground nests; our most commonly parasitized species, *B. occidentalis*, although emerging early, typically forms underground nests (Hobbs, 1968), and the earliest emerging species in our study area that nests above ground, *B. mixtus*, was free of internal mites. We also did not find evidence to support Goldblatt and Fell's (1984) suggestion that *B. vagans* is a preferred host of *L. buchneri*. Interestingly, we found the highest prevalences of *L. buchneri* typically occurred among bumble bee species in the subgenus *Bombus* Latr. sensu stricto (*B. moderatus*, *B. occidentalis*, *B. terricola*). Life-history similarities shared by these closely related species, such as nesting ecology, floral visitation, phenology, and overwintering habits may increase their susceptibility to, or suitability for, *L. buchneri*. Associations between such life-history traits in bumble bees and susceptibility/suitability for tracheal mites warrants further investigation.

Bumble bee colonies infected with *L. buchneri* may pose a threat to uninfected colonies if mites are able to move between nests. Indeed, concerns have been raised about the potential for *L. buchneri* to spread from imported, commercial bumble bee species to native species (Goka et al., 2000, 2001). Although we found *L. buchneri* in spring queens of only two species at Barrier Lake, by mid-summer, workers of virtually all (7/9) bumble bee species we collected at this site contained mites. Such a pattern may suggest that *L. buchneri* is able to spread between bumble bee colonies and species during the summer. Larviform-female *L. buchneri* may be able to disperse to new colonies via 'drifting' workers (i.e. workers that enter a foreign colony rather than their own, e.g. Free, 1958; Jay and Warr, 1984; Williams, 1997) or via inquiline species that move between bumble bee nests, such as queens of the socially parasitic *Psithyrus* (Husband and Shina, 1970; Schmid-Hempel, 1998). However, this latter explanation seems unlikely as only 1/57 *Psithyrus* queens we collected at Barrier Lake contained *L. buchneri*. Alternatively, *L. buchneri* may transfer between host species at flowers, as is known for other mites of bumble bees (Schwarz and Huck, 1997).

Although *L. buchneri* is thought to have relatively benign effects on natural bumble bee colonies (Alford, 1975; MacFarlane et al., 1995; but see Schmid-Hempel, 2001), at high levels of infestation these mites may damage the trachea of bumble bees and cause their hosts to become lethargic and cease foraging (Husband and Shina, 1970; Alford, 1975). In this study, only foraging bumble bees were collected, and therefore the prevalence and impact of *L. buchneri* on non-foraging 'house' bees is unknown. Nevertheless, field-caught workers and males parasitized by tracheal mites lived shorter lifespans in the lab than bees that were unparasitized. It cannot be ruled out, however, that differences in the survival of parasitized and unparasitized bees may be due to parasitized bees being older and therefore living shorter periods after capture, and not because of the presence of tracheal mites. Given that *L. buchneri* can be very common among certain bumble bee species, and that it has the potential to negatively affect host survival, these parasitic mites clearly warrant further attention.

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Résumé – Caractéristiques du parasitisme par les acariens des trachées (*Locustacarus buchneri*) dans des populations naturelles de bourdons. Les acariens parasites, ennemis naturels importants des abeilles sociales, peuvent affecter négativement la physiologie et la survie de l'hôte. Pourtant, mis à part les acariens de l'Abeille domestique (*Apis mellifera* L.), on sait peu de chose concernant les acariens parasites des autres abeilles sociales. Nous avons étudié la présence de l'acarien parasite *Locustacarus buchneri* Stammer (Acari : Podapolipidae) et ses effets négatifs sur les bourdons (*Bombus* spp.) dans le sud-ouest de l'Alberta, Canada. Durant quatre années nous avons régulièrement récolté des bourdons sur le principal site d'étude et avons fait également des observations durant un été sur huit autres sites. Au laboratoire on a laissé les insectes terminer leur vie, puis on les a disséqués pour savoir si des acariens étaient ou non présents. Les bourdons étaient attaqués par les acariens dans la plupart des sites d'étude (Tab. II). Sur le site principal la proportion de bourdons parasités a même atteint 50 % chez certaines espèces (Fig. 1). Au laboratoire, les bourdons parasités ont eu une durée de vie plus courte que ceux qui ne l'étaient pas. Bien que l'on ignore pourquoi *L. buchneri* peut être spécifique de certaines espèces de bourdons, il justifie nettement notre attention étant donné sa prévalence et ss effets négatifs potentiels sur la survie de l'hôte.

Bombus* / *Locustacarus buchneri* / parasitisme / Podapolipidae / *Psithyrus

Zusammenfassung – Erscheinungsbilder des Parasitismus durch Tracheenmilben (*Locustacarus buchneri*) bei natürlichen Hummelpopulationen. Parasitische Milben sind bedeutende natürliche Feinde der sozialen Bienen, die die Physiologie und das Leben der Wirtstiere negativ beeinflussen. Aber mit Ausnahme von Milben der Honigbienen (*Apis mellifera* L.) ist wenig von parasitischen Milben der sozialen Bienen bekannt. Wir untersuchten das Vorkommen und die negativen Folgen des Parasitismus durch Milben (*Locustacarus buchneri* Stammer, Acari: Podapolipidae) bei Hummeln (*Bombus* spp.) in Südwest Alberta, Kanada. Wir sammelten während 4 Sommern regelmäßig in unserem Hauptversuchsgebiet, außerdem beobachteten wir in einem Sommer 9 zusätzliche Regionen. Im Labor wurden die Hummeln gut gepflegt bis sie starben. Danach wurden sie seziert und der Milbenbefall bestimmt. Wir fanden in fast allen Versuchsgebieten Hummeln mit parasitischen Milben. (Tab. I). Einige Hummelarten waren nur selten befallen, bestimmte Arten dagegen waren stark (Tab. II) befallen. In unserem Hauptversuchsgebiet erreichte die Proportion von befallenen Hummeln bei einigen Arten 50 % (Abb. 1). Im Labor hatten die mit Milben befallenen Hummeln typischerweise eine geringere Lebenserwartung als die nicht befallenen. Es ist unbekannt, warum spezifisch bestimmte Hummelarten befallen werden. Angesichts der Verbreitung der parasitischen Milben und ihres möglichen negativen Effekts auf die Lebensdauer der Hummeln sollten die Milben in Zukunft mehr Beachtung finden.

Bombus* / *Locustacarus buchneri* / Parasitismus / Podapolipidae / *Psithyrus

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