Original article

Incidence and effects of four parasites in natural populations of bumble bees in Switzerland

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Summary — Field caught bumble bee (*Bombus* Latreille and *Psithyrus* Lepeletier) workers, males and queens were examined for the presence of 4 parasites. High prevalence of parasitization by conopid flies (20.2%) and the trypanosome *Crithidia bombi* (35.7%), moderate to low prevalence by the microsporidian *Nosema bombi* (9.0%) and the mite *Bombacarus buchneri* (3.6%) were found. Infestations by the 4 parasites were independent of one another but significant differences were found for bumble bee species and sex. Workers parasitized by *C bombi* were significantly less likely to forage for pollen and had developed ovaries in significantly more cases than did uninfested workers. Spring queens of *B terrestris* and *B lucorum* had lower prevalence of infestation by *C bombi* than was found in workers the previous summer.

***Bombus* / *Psithyrus* / parasitism / *Crithidia* / *Nosema* / *Bombacarus* / Conopidae**

INTRODUCTION

Bumble bees (*Bombus* Latreille and *Psithyrus* Lepeletier), economically and ecologically important pollinators of many temperate plant species (Heinrich, 1979), harbour a number of parasites and parasitoids (Alford, 1975). Field collections in northwestern Switzerland reveal high prevalence of conopid fly eggs and larvae (Diptera, Conopidae) (Schmid-Hempel and Schmid-Hempel, 1988, 1989; Schmid-Hempel *et al*, 1990). Nest-seeking spring queens often contain *Sphaerularia bombi* (Nematoda, Tylenchoidea, Allantonematidae) and occasionally *Syntretus splendid-us* (Hymenoptera, Braconidae) infestations (Schmid-Hempel *et al*, 1990). Other bumble bee parasites include the tracheal mite, *Bombacarus buchneri* (Acarina, Podapolipodidae) (Stammer, 1951), and the protozoans *Nosema bombi* (Microsporidia, Nosematidae) (Showers *et al*, 1967; de Jonghe, 1986; Fisher and Pomeroy, 1989) and *Crithidia bombi* (Trypanosomatidae, Zoomastigophorea) (Lipa and Triggiani, 1980; Gorbunov, 1987).

Parasites can have negative effects on the individual and the colony. Bumble bees infested with conopids have shorter lifespans than uninfested ones (Schmid-Hempel and Schmid-Hempel, 1988), re-

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sulting in lower return per unit investment for the colony and reduced worker populations. Parasitized workers prefer different flowers than do unparasitized workers, which may alter their effectiveness as pollinators and competitors (Schmid-Hempel and Schmid-Hempel, 1990). Queens infested with the braconid *S splendidus* or the nematode *S bombi* fail to found nests. Little is known about the effects of protozoa on bumble bees. In honey bees, *N apis* causes higher winter losses (Jeffree and Allen, 1956) and reduced honey yields in infested colonies, infested queens are more often superseded (Farrar, 1947), and infested workers show reduced hoarding behaviour (Rinderer and Elliott, 1977). Bumble bees cross-infected with *N apis* show reduced activity (Showers *et al*, 1967), though Fisher and Pomeroy (1989) found no effect of *N bombi* on either colony performance or queen success. *Crithidia* spp are pathogens of other insects (Clark *et al*, 1964), but little is known about their effects on bees (Fyg, 1954; Langridge and Mcghee, 1967). Because parasites could affect bumble bee population dynamics, behaviour and ecology, more information is needed on parasites in natural bumble bee populations.

To date, few data are available on the distribution, abundance, and ecological effects of parasites in natural populations of their hosts. Here we report the results of field surveys in northwestern Switzerland, conducted to assess the distribution, abundance and impact of a number of parasites in natural populations of bumble bees.

MATERIALS AND METHODS

Eight samples, each of ≈ 50 bumble bees, were collected at 2 field sites in the vicinity of Basel, Switzerland in early and late July and August, 1988. In the laboratory, bees were checked for presence of pollen in the corbiculae, freeze-killed, dissected, and examined for the presence of various parasites. Each individual was scored for the presence of the 2 protozoans, *Crithidia bombi* and *Nosema bombi*, eggs or larvae of conopid flies and tracheal mites, *Bombacarus buchneri*. In addition the state of development of the ovaries was scored. Fisher's exact tests (for 2 x 2 contingency tables) or G log-likelihood tests (for higher order tables) were used to test whether infestation prevalence was independent of site, host species and sex, if presence of the various parasites was independent of one another and to determine the relationship between infestation, host foraging behaviour (pollen foraging or not) and host ovarian development (Zar, 1984; SAS Institute, 1985). All probability levels reported are two-tailed.

In spring 1989, foraging and nest-searching queens of *Bombus terrestris* L and *Bombus lucorum* L were collected. The queens were placed in the laboratory in wooden boxes containing nest material (upholsterer's cotton), and given sugar/honey solution and pollen (for methods on bumble bee rearing, see Plowright and Jay, 1966). Fresh faeces were obtained from all queens whenever possible and examined for *N bombi* spores and cells of *C bombi* at 400 X magnification. Queens which died or failed to commence egg-laying within 3 wk were examined for parasites, and the 3 largest terminal oocytes were measured using an eyepiece micrometer in a dissecting microscope. Tests of association as above were performed to investigate whether nest-founding success was independent of infestation by *N bombi* or *C bombi*. Average length of the 3 largest oocytes was compared between individuals infected or uninfected with *N bombi* and *C bombi* using a *t*-test. In addition, prevalence of infestation by *N bombi* and *C bombi* in spring queens was compared with that in workers from the summer before using a G log-likelihood test.

RESULTS

A total of 446 bumble bees (313 workers and 133 males) were investigated for parasites in July and August 1988. Representatives of 9 species were found, the commonest being *B pascuorum* Scop, *B lapidarius* L, *B terrestris* and *B lucorum*.

Workers of the last 2 species are difficult to distinguish from one another so they are combined in the analyses, as are the remaining rare species in all except for the analysis of tracheal mite infestation by species. The 2 field sites were consistent in patterns of parasite prevalence, so sites were also combined in the following analyses.

Altogether 20.2% of the bumble bees were infested with conopids, 35.7% with *C bombi*, 9.0% with *N bombi* and 3.6% with *Bombacarus buchneri*. Parasitization differed by host species for all parasites and by host sex for conopids, *C bombi*, *N bombi* (table I). Conopid parasitization was more common than expected in *B pascuorum* (G = 18.1, df = 3, P < 0.0001). *B lapidarius* and combined *B terrestris/lucorum* showed higher than expected prevalence of *C bombi* infestation (G = 134.251, df = 3, P < 0.0001). Combined *B terrestris/lucorum* had higher than expected *N bombi* infestation (G = 30.463, df = 3, P <

Table I. Parasitization of bumble bee species in northwestern Switzerland in the summer of 1988. The table shows the total number of individuals of each species and sex examined, and the number and percent of those which contained parasites. The parasites represented here include conopoid flies (*Sicus* sp and *Physocephala* sp), the trypanosome *Crithidia bombi,* the microsporidian *Nosema bombi,* and the tracheal mite *Bombacarus buchneri.* Some bees contained more than one parasite species.

Species sex	Total examined	No of individuals parasitized with (%)			
		Conopoids	C bombi	N bombi	B buchneri
B terrestris/lucorum					
Workers	61	14 (22.9)	49 (80.3)	9 (14.8)	0
Males	24	4 (16.7)	13 (54.2)	12 (50.0)	0
B pascuorum					
Workers	132	40 (30.3)	11 (8.3)	3 (2.3)	8 (6.1)
Males	35	3 (8.6)	0	3 (8.6)	2 (5.7)
B lapidarius					
Workers	81	22 (27.2)	43 (53.1)	0	0
Males	26	2 (7.7)	4 (15.4)	4 (15.4)	0
B pratorum					
Workers	12	1 (8.3)	7 (58.3)	0	6 (50.0)
Males	6	0	1 (16.7)	0	0
B hortorum					
Workers	11	2 (18.2)	4 (36.4)	6 (54.5)	0
Males	10	2 (20.0)	5 (50.0)	1 (10.0)	0
B hypnorum					
Workers	8	0	8 (100)	1 (12.5)	0
Males	8	0	4 (50.0)	1 (12.5)	0
B humilis and *B sylvarum*					
Workers	6	0	2 (33.3)	0	0
Males	0	0	0	0	0
Psithyrus spp					
Females	2	0	0	0	0
Males	24	0	8 (33.3)	0	0
Total	446	90 (20.2)	159 (35.7)	40 (9.0)	16 (3.6)

0.0001). The mite *B buchneri* was only found in *B pascuorum* and *B pratorum* L (G = 39.295, df = 8, *P* < 0.0001). Parasitization by conopids and *C bombi* was higher for workers than males in all species but *B hortorum* L. While 25.2% of workers contained conopid larvae or eggs, only 8.3% of males were parasitized by conopids (Fisher's exact test, *P* < 0.0001). *C bombi* was found in 39.6% of workers *vs* 26.3% of males (Fisher's exact test, *P* = 0.009), and *N bombi* in 6.1% of workers *vs* 15.8% of males (Fisher's exact test, *P* = 0.002). This pattern of parasitization between sexes was consistent over species, *ie* in all species workers were more often infested than expected with conopids and *C bombi*, and less often than expected with *N bombi*. No sex difference was observed for infestations of *B buchneri*.

The distribution of infestation was independent among the 4 parasites *ie*, parasitization by one did not make the host more or less likely to be infested by another. A weak positive association such that double infestations were somewhat more common than expected was observed between *C bombi* and *N bombi* (Fisher's exact test, *P* = 0.057).

No relationship could be determined between infestation with conopids, *N bombi*, or *Bombacarus buchneri* and either pollen collecting or ovarian development. Workers infested with *C bombi*, however, were less likely to carry pollen in their corbiculae than uninfested workers (48.4% infested workers *vs* 72.6% of uninfested workers carrying pollen, all species combined, Fisher's exact test, *P* < 0.0001). They were also more likely to have developed ovaries (14.5% infested workers *vs* 4.3% uninfested workers with developed ovaries, all species combined, Fisher's exact test, *P* = 0.003).

In spring 1989, 208 queens, 101 *B terrestris* and 107 *B lucorum*, were caught in the area of Basel. Prevalence of infestation with *C bombi* differed in the 2 species (47.5% for *B terrestris* and 29.9% for *B lucorum*, Fisher's exact test, *P* = 0.01), while only a tendency was found with *N bombi* (prevalence 13.5% for *B terrestris* and 5.6% for *B lucorum* (Fisher's exact test, *P* = 0.058).

Nest-founding success in the laboratory was independent of infestation with either parasite in both species. Infestation, however, had a negative effect on oocyte size in queens which failed to build nests in the laboratory. Queens of *B lucorum* infested with *N bombi* had smaller oocytes than uninfested queens (0.3 mm, *n* = 6 *vs* 1.1 mm, *n* = 96, *t* = 3.269, df = 100, *P* = 0.0015). No difference was found for *B terrestris*. *C bombi* had a comparable effect on *B terrestris* (infested 1.0 mm, *n* = 38, uninfested 1.3 mm, *n* = 42, *t* = 2.05, df = 78, *P* = 0.04) but not on *B lucorum*.

We compared the infestation rates by *C bombi* and *N bombi* of spring queens with the infestation rates of *B terrestris* and *B lucorum* workers from the summer before in an attempt to address the question of whether parasitization affects hibernation success. We used the prevalence values for infestation of previous summer workers to generate expected values. The distribution of infestation differed markedly between summer workers and spring queens (combined species G = 175.52, df = 1, *P* < 0.0001, *B terrestris* G = 53.86, df = 1, *P* < 0.0001, *B lucorum* G = 133.15, df = 1, *P* < 0.0001). Uninfested individuals were much more common than expected in the spring queen sample and *C bombi* infestations were rarer than expected (table II). The weak positive association between *C bombi* and *N bombi* reported for summer workers was not evident in spring queens. No significant difference was found between infestation rates of *N bombi* for summer workers and spring queens.

Table II. Comparison of infestation by protozoan parasites N bombi and C bombi in summer workers and spring queens. Numbers in parentheses represent expected values generated from the observed frequencies of parasitization in workers the previous summer.

N bombi	C bombi	
	Uninfested	Infested
B terrestris		
Uninfested	42	41
	(17.3)	(64.5)
Infested	8	5
	(1.6)	(12.6)
G = 53.86, df = 1, P < 0.0001		
B lucorum		
Uninfested	70	31
	(19.3)	(71.9)
Infested	5	1
	(1.8)	(14.0)
G = 133.15, df = 1, P < 0.0001		

DISCUSSION

We here report the distribution and abundance of 4 different parasites of bumble bees found in natural populations in central Europe (table I). Conopid prevalence was consistent with previous reports (Cumber, 1949a; Macfarlane and Pengelly, 1974; Pouvreau, 1974; Schmid-Hempel and Schmid-Hempel, 1988; Schmid-Hempel et al, 1990). In addition, high prevalence of the trypanosome C bombi was observed, particularly in workers, and moderate prevalence of the microsporidian N bombi, particularly in males. Differences in conopid parasitization by species and sex are known (eg, Schmid-Hempel and Schmid-Hempel, 1988; Schmid-Hempel et al, 1990) and may be due to species differences in degree of overlap between conopid and bumble bee abundances, and

sex specific behaviours. As yet we have no explanation for species differences in infestation rates for C bombi and N bombi.

Sex-related differences in infestation are opposite for these 2 parasites, with higher prevalence of C bombi in workers and of N bombi in males. This suggests that patterns of transmission or susceptibility for these 2 protozoan parasites differ. Laboratory investigations of C bombi and B terrestris show that parasite transmission occurs readily within nests and artificially established groups of worker bumble bees (Shykoff, unpublished data; Shykoff and Schmid-Hempel, 1991a, b). Low infestation rates in males may result from males spending less time within the nest than do workers, leaving permanently within 4 d of eclosion (Alford, 1975). Also they do not participate in brood care, which may expose workers to infection through contact with contaminated nest material.

The factors which reduce risk of C bombi transmission to males should have the same effect on N bombi, but we found higher rates of N bombi infestation in males than in workers. If, however, N bombi reduces the activity of infested bees as shown by Showers et al (1967) for bumble bees cross-infected with N apis, then parasitized invididuals may be less likely to forage than unparasitized individuals. Thus field samples would show higher infestation prevalence for males which, in contrast to workers, must leave the nest.

Evidence for pathogenic effects of Crithidia bombi is scanty. We found fewer infested workers than uninfested workers bearing pollen, and more infested workers than uninfested workers with developed ovaries. Ovarian development is a function of age (Röseler, 1987) and dominance rank (van Doorn, 1989) in bumble bees. Observations on C bombi infested nests of B terrestris have shown that older workers are more likely to be infested (Shykoff and

Schmid-Hempel, 1991b). Bumble bee foragers caught in the field represent a mixture of different aged individuals (Heinrich, 1979), therefore the relationship between developed ovaries and infestation with *C bombi* may result from a correlation of both of these factors with age. Age related patterns of infestation cannot explain the difference in pollen foraging, however, because division of labour in bumble bees does not appear to be age determined. Bumble bees can be effective pollinators without pollen foraging, but since workers infested with *C bombi* tended not to gather pollen, they may frequent different plant species or visit flowers differently (Galen and Plowright, 1985) than uninfested workers. Further work is planned to investigate whether parasitization with *C bombi* thus alters competitive interactions within bumble bee communities.

Infestations of *C bombi* and *N bombi* were found in spring queens of both *B terrestris* and *B lucorum* but the prevalence of *C bombi* infestations was significantly lower than that found in workers the previous summer (table II). To investigate the dynamics of this host parasite system one should ideally compare prevalence values for young queens in summer before they enter hibernation and spring queens emerging from hibernation. Young bumble bee queens in this region are seldom seen, presumably leaving the parental nest only for the mating flight and to find an overwintering site. This enables them largely to avoid parasitization by conopids which are abundant when colonies make reproductives (Schmid-Hempel *et al*, 1990). Since samples of young queens were not sufficient for meaningful comparisons, we considered that infestation rates for workers should be representative of infestation rates for queens produced at the same time. Young queens remain in the nest for 5 d on average before their mating flight (Alford, 1975) and feed heavily on

honey and pollen stores to build up fat bodies (Cumber, 1949b). After mating they often return to the parental nest (Cumber, 1953), and stay there until leaving to find a suitable hibernation site. While in the nest they participate in some brood care and are thus exposed to the same risks of transmission as are the workers. Therefore, the significant lower prevalence of *C bombi* infestation in spring queens than previous summer workers could indicate either that this parasite reduces hibernation sucess or that some overwintering queens are able to overcome their infestations.

ACKNOWLEDGMENTS

Résumé — Présence et action de quatre parasites dans des populations naturelles de bourdons en Suisse. Nous avons étudié l'abondance et la distribution de 4 parasites naturels des bourdons (*Bombus* Latreille et *Psithyrus* Lepeletier). Sur 446 bourdons (313 ouvrières et 133 mâles) capturés sur des fleurs en juillet et août 1988, 20,2% étaient parasités par des conopidés (Diptera, Conopidae), 35,7% par *Crithidia bombi* (Zoomastigophorea, Trypanosomatina), 9,0% par *Nosema bombi* (Microsporidea, Microsporida) et 3,6% par *Bombacarus buchneri* (Acarina, Podapolipodidae). Le parasitisme a varié en fonction de l'espèce hôte pour tous les parasites et en fonction du sexe de l'hôte pour les conopidés, *C bombi* et *N bombi* (tableau I). Le parasitisme par les conopidés et *C bombi* était plus fort chez les ouvrières que chez les mâles, tandis que *N*

bombi était plus fréquemment rencontré chez les mâles que chez les ouvrières. La probabilité pour des ouvrières infestées par *C bombi* de porter des pelotes de pollen dans leurs corbicules était moindre que pour des ouvrières non infestées et celle d'avoir des ovaires développés, plus forte. En outre, les reines de printemps présentaient une prédominance plus faible de l'infestation par *C bombi* que les ouvrières de l'été précédent (tableau II). Les différences de parasitisme par les conopidés en fonction de l'espèce et du sexe peuvent être dues à des différences spécifiques dans le degré de recouvrement temporel des effectifs de bourdons et de conopidés et à des comportements sexuels spécifiques. La faible infestation des mâles par *C bombi* peut provenir du fait que ceux-ci passent moins de temps à l'intérieur des nids que les ouvrières et qu'ils ne participent pas aux soins au couvain. La différence de prédominance de *C bombi* entre les ouvrières d'été et les reines du printemps suivant peut indiquer que certaines reines infestées ne passent pas l'hiver et/ou que certaines sont capables de perdre leur parasitisme au cours de l'hiver.

Bombus / Psithyrus / parasitisme / Crithidia / Nosema / Bombacarus / Conopidae

Zusammenfassung — Vorkommen und Auswirkungen von vier Parasiten in natürlichen Hummel-Populationen der Schweiz. Wir haben Häufigkeit und Verteilung von vier natürlichen Parasiten von Hummeln untersucht. Von 446 Hummeln (313 Arbeiterinnen und 133 Männchen), die im Juli und August 1988 auf Blüten gefangen wurden, waren 20.2% von Conopiden (Diptera, Conopidae), 35.7% mit *Crithidia bombi* (Zoomastigophorea, Trypanosomatina), 9.0% mit *Nosema bombi* (Microsporea, Microsporidia) und 3.6% mit *Bombacarus buchneri* (Acarina, Podalipodidae) befallen. Für alle Parasiten war die Parasitierung je nach der Art des Wirtes verschieden, aber nur für Conopiden, *C bombi* und *N bombi* auch nach dem Geschlecht des Wirtes unterschiedlich (Tabelle I). Die Parasitierung durch Conopiden und *C bombi* war bei Arbeiterinnen höher als bei Männchen, für *N bombi* war es umgekehrt. Von *C bombi* befallene Arbeiterinnen trugen weniger häufig Pollen in ihren Körbchen und sie hatten öfter entwickelte Ovarien als unbefallene Arbeiterinnen. Außerdem zeigten Frühjahrsköniginnen einen weit geringeren Befallsgrad mit *C bombi* als Arbeiterinnen vom vorherigen Sommer (Tabelle II). Die Unterschiede im Befall der Arten und der beiden Geschlechter durch Conopiden könnte durch Artunterschiede bei der zeitlichen Überlappung der größten Häufigkeit von Conopiden und Hummeln und durch geschlechtsspezifisches Verhalten zu erklären sein. Der geringere Befall von *C bombi* bei Männchen könnte dadurch entstehen, daß sich Männchen weniger im Nest aufhalten und daß sie sich nicht an der Brutpflege beteiligen. Der Unterschied in der Befallshäufigkeit von *C bombi* bei Sommerarbeiterinnen und bei Königinnen im nächsten Frühjahr könnte dadurch entstehen, daß ein Teil der befallenen Königinnen den Winter nicht überlebt und/oder daß einige von ihnen in der Lage sind, die Infektion während des Winters wieder los zu werden.

Bombus / Psithyrus / Parasitismus / Crithidia / Nosema / Bombacarus / Conopidae

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