

Research article

Low parasite loads accompany the invading population of the bumblebee, *Bombus terrestris* in Tasmania

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Abstract. In its native Europe, the bumblebee, *Bombus terrestris* (L.) has co-evolved with a large array of parasites whose numbers are negatively linked to the genetic diversity of the colony. In Tasmania *B. terrestris* was first detected in 1992 and has since spread over much of the state. In order to understand the bee's invasive success and as part of a wider study into the genetic diversity of bumblebees across Tasmania, we screened bees for co-invasions of ectoparasitic and endoparasitic mites, nematodes and micro-organisms, and searched their nests for brood parasites. The only bee parasite detected was the relatively benign acarid mite *Kuzinia laevis* (Dujardin) whose numbers per bee did not vary according to region. Nests supported no brood parasites, but did contain the pollen-feeding life stages of *K. laevis*. Upon summer-autumn collected drones and queens, mites were present on over 80% of bees, averaged ca. 350–400 per bee and were more abundant on younger bees. Nest searching spring queens had similar mite numbers to those collected in summer-autumn but mite numbers dropped significantly once spring queens began foraging for pollen. The average number of mites per queen bee was over 30 fold greater than that reported in Europe. Mite incidence and mite numbers were significantly lower on worker bees than drones or queens, being present on just 51% of bees and averaging 38 mites per bee. Our reported incidence of worker bee parasitism by this mite is 5–50 times higher than reported in Europe. That only one parasite species co-invaded Tasmania supports the notion that a small number of queens founded the Tasmanian population. However, it is clearly evident that both the bee in the absence of parasites, and the mite have been extraordinarily successful invaders.

Keywords: Founder population, introduction, genetic diversity, mites, *Kuzinia*.

Introduction

The success of invasive species is often attributed to escape from biotic forces, especially from parasites and diseases, which may regulate populations in their native environment (see Keane and Crawley, 2002). Conversely, the failure of deliberate invasions of biocontrol agents is often attributed to low genetic diversity (Hopper et al., 1993). The large earth bumblebee, *Bombus terrestris* (L.) (Hymenoptera: Apidae), was first detected in Hobart in 1992 (Semmens et al., 1993) and first spread throughout southern Tasmania and in more recent years throughout most of the state (Hergstrom et al., 2005). It is hypothesised to have arrived to Tasmania via New Zealand (Semmens et al., 1993). If this introduction was accidental, the number of founding queens for this population is likely to be one; if illegally, a few queens may have founded the population. Either way, Tasmanian bumblebees represent a highly inbred – yet successful – population. Indeed, we show elsewhere that the Tasmanian population of *B. terrestris* is genetically impoverished as compared to their counterparts in New Zealand and Europe (Schmid-Hempel et al., in prep.).

Given such a low number of establishing queens, and hence low genetic diversity, bumblebees in Tasmania have been extremely invasive. Within eight years following introduction, high densities of bees could be found along the south-eastern coast, and in the west-coast towns of Queenstown and Strahan about 200 km from Hobart.

Why have these bees been so prolific when genetic diversity is a key factor affecting the establishment of many species, such as biocontrol agents, in foreign habitats (e.g., Simberloff, 1989; Hopper and Roush, 1993)? One hypothesis is that Tasmanian bumblebees due to their introduction in small numbers may accidentally be relatively free of parasites, and without this constraint, their low genetic diversity has not been a disadvantage.

In their native European habitat (Shykoff and Schmid-Hempel, 1991a; Durrer and Schmid-Hempel, 1995) as well as in the established populations in New Zealand (Macfarlane et al., 1995) *B. terrestris* are host to an impressive diversity of parasitic organisms. Several species of mite (*Garmaniella* spp., *Hypoaspis* spp., *Kuzinia laevis*, *Parasitellus* spp., and *Scutacarus acarorum* (Goeze)) live in the nests of bumblebees where they feed on pollen stores, debris, and nest microfauna (Chmielewski, 1971; Schmid-Hempel, 1998). These mites have phoretic life stages that can be found on the exterior of the bees (Schwarz et al., 1996); for example, *Kuzinia laevis* disperses as a non-feeding deutonymph. *Locustacarus buchneri* (Stammer) is an extraordinary mite that lives within the tracheae of adult bees (Husband and Sinha, 1970). The parasitic wasp *Melittobia acasta* (Walker) can quickly overcome bumblebee colonies (De Wael et al., 1995); parasitic conopid flies attack bees as they forage (Schmid-Hempel and Schmid-Hempel, 1988); nematodes live within and eventually kill queens soon after emerging from diapause; wax moths invade and destroy nests; and the protozoan *Nosema bombi* Fantham and Porter can kill numerous bees (Fantham and Porter, 1914), as can the trypanosome *Crithidia bombi* Lipa and Triggiani (Brown et al., 2000), which additionally is responsible for high rates of failure in colony founding by spring queens (Brown et al., 2003).

Some of these parasites, such as the external mites, appear benign. However, mites such as the tracheal mite *Lucastacarus buchneri* can have important effects on its host, *Bombus impatiens*, with infections being associated with increased flower constancy. Lower foraging rates were observed with infections by the trypanosome, *Crithidia bombi* (Otterstatter et al., 2005). The insect parasitoids, nematodes, and internal microparasites can kill individuals and, in some cases, significantly damage or even kill colonies (e.g. Müller and Schmid-Hempel, 1993a; Schmid-Hempel and Loosli, 1998; Brown et al., 2003). In *Bombus terrestris*, the number of parasites in a colony is closely linked with the genetic diversity of the colony (Shykoff and Schmid-Hempel, 1991b; Liersch and Schmid-Hempel, 1998; Schmid-Hempel and Loosli, 1998; Baer and Schmid-Hempel, 1999). On a landscape scale, we would therefore expect that parasites would cause considerable damage to a genetically homogenous population, such as that in Tasmania. However, should Tasmanian bumblebee colonies be free of parasites, then they could be further used to understand the interplay between parasites and genetic diversity. In this

paper we test whether *B. terrestris* in Tasmania is indeed free of or at least has only a few parasites. We identify any parasites found to be associated with the Tasmanian bumblebee population and report their level of infestation across different bumblebee castes and geographic regions of Tasmania. In addition we examined whether parasite load was correlated with possible host fitness parameters including bee body size, bee age (measured by wing wear) and foraging activity (measured by pollen load). All parameters may influence both the probability of parasite encounter and successful parasite infection as has been demonstrated for this and other host-parasite systems (for body size: Müller et al., 1996; Salkeld and Schwarzkopf, 2005, for age: Imhoof and Schmid-Hempel, 1998; Müller and Schmid-Hempel, 1993a; Schmid-Hempel and Schmid-Hempel, 1996; Blaser and Schmid-Hempel, 2005, for foraging activity: König and Schmid-Hempel, 1995).

Methods

Capturing bees

Summer-Autumn

We captured bumblebees between January and April 2000. To gain an overview of parasite prevalence we split the known distribution of *B. terrestris* in Tasmania into five geographic regions: Southern, West Coast, Derwent Valley, Northern, and Eastern (Fig. 1). In each of these regions, five locations were sampled, but bumblebees were absent or in insufficient numbers in some locations. Locations with sufficient bumblebees were: Southern (Huonville, Pelterata, Geeveston, Southport, Cockle Ck); West Coast (Strahan, Queenstown); Derwent Valley (Hobart, New Norfolk, Ouse, Blue Gum Knob, Maydena); Northern (Oatlands); Eastern (Sorell, Orford). Within each of these locations, where possible, we captured bumblebees at 5 sites that were at least 1 km apart. Worker bumblebees are thought not to forage further than 1 km from their nests (Dramstad, 1996; Osborne et al., 1999), even though there are reports of ranges up to almost 2 km with a rapidly decreasing density as distance from the nest increases (Walther-Hellwig and Frankl, 2000). Although foraging distance does overlap with our sampling intervals in space, genetic studies have shown that there is only a small chance of catching individuals from the same nest in any situation such as ours, where presumably many nests are present in a given area (Chapman et al., 2003). We therefore feel that our procedure is not biased towards kinships in the samples – certainly not more than sampling any other insect population. At each site, we captured at least 5 bees. Because the primary aim of this study was to investigate the parasite load of workers – the class of individuals responsible for colony growth, at least three workers were captured from each site. However, drones and queens were also captured. Bumblebees were placed into labelled tubes, which were in turn placed into a cooled container. Bees were returned to the laboratory and placed into a fridge at about 7 °C; after cooling, the bees were placed into labelled cryotubes and frozen in liquid nitrogen.

Spring

In spring, that is September and October 2000, we also captured 50 queens from numerous locations within Hobart. These queens were returned to the laboratory, killed, and dissected for the purpose of detecting parasitic nematodes (*Sphaerularia bombi*). We also recorded whether these queen bees were foraging or nest-searching because the nematode alters its host's behaviour by causing it to search for nests continually (Lundberg and Svensson, 1975). We did not sample outside of Hobart because the highest chance of detecting these parasites would

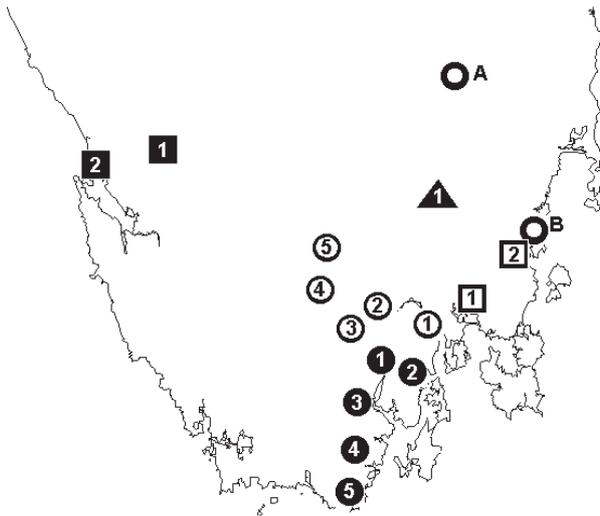


Figure 1. Collection locations of bumblebees in Tasmania. Open circles (Derwent Valley region): 1=Hobart; 2=New Norfolk; 3=Blue Gum Knob; 4=Maydena; 5=Ouse. Filled circles (southern region): 1=Huonville; 2=Pelverata; 3=Geeveston; 4=Southport; 5=Cockle Ck. Filled squares (western region): 1=Queenstown; 2=Strahan. Open squares (eastern region): 1=Sorell; 2=Orford. Triangle (northern region): 1=Oatlands. Locations A (Campbell Town) and B (Triabunna) represent well-searched places where bumblebees were not found.

be closest to their point of entry into Tasmania because of their limited dispersal capacities (Macfarlane and Griffin, 1990).

Examination for parasites

The length of each bee was measured with digital callipers by pressing them down against a hard object, and measuring the bee from the front of the clypeus to the tip of the abdomen. As an indication of the age of the bees, whether or not the wings showed signs of wear (tattering) was recorded as was whether the bee was carrying pollen on its hind tibia. In the case of wing wear we hereafter refer to bees without wing wear as young and bees with wing wear as older bees. The exterior was then examined for mites, and the number of mites estimated; exact counts were impossible as mites were extremely abundant and the amount of time bees were allowed to defrost had to be minimised. These estimates amounted to an average absolute % difference to actual counts of $7.4 \pm 1\%$ SE ($n=20$).

For queens and workers, the head and mesosoma was removed and returned to liquid nitrogen storage; drones were treated similarly, but not all were bisected. The bee metasomata were initially sterilised, externally, by placing molten wax on the anterior and posterior orifices (to protect the haemocoel from the sterilising solutions), dipping in 95% ethanol for 2 sec, soaking in 5.25% sodium hypochlorite for 3.5 min, soaking in 10% sodium thiosulfate for 3.5 min, then washing three times in sterile distilled water. The bee was then dissected, and a sample of haemolymph, midgut tissue, and hindgut tissue removed. Samples of haemolymph were smeared on glass slides and stained with a standard Gram-stain method; samples of midgut and hindgut were treated similarly, but treated with a Giemsa-stain method. During preparation of the slides, the remainder of the abdomen was examined for tracheal mites, nematodes and parasitoid larvae. Prepared slides were examined at $\times 1000$ under phase contrast for micro-organisms.

Bumblebee nest survey

The contents of bumblebee nests were examined from colonies in natural and artificial nests. These colonies were used in another study by one of us (RB) and as such were only occasionally destroyed while producing workers. However, when the colony began to die, or a dead colony was retrieved from the field, the contents of the nest were thoroughly examined and brood dissected or reared at room temperature. Dead and live arthropods were collected into 80% ethanol, and identified with the aid of dissecting and slide microscopes, where appropriate.

Statistical analysis

Analysis of variance was first used to test for differences in parasite prevalence between castes of bees. Due to significant differences being evident between castes, castes were analysed separately using hierarchical analysis of variance upon the square root transformed level of parasitism per bee and testing for region (except for queens where replication was too low), bee size, bee age (wing wear) and foraging activity (pollen load-except for drones). Only bees that had records for all three characters (ie. size, age or foraging activity) were used in the final analysis. Location within region was not tested for in the analyses due to insufficient sample sizes to warrant this level of partitioning. The independently collected sample of spring queens was also analysed as above though in this case queen size, foraging activity (pollen load) and nest searching were tested.

Results

Summer-Autumn

We captured a total of 511 bees (47 queens, 181 drones, 283 workers) from 15 sites scattered across 5 regions (Fig. 1). Bumblebees were absent at Campbell Town and Triabunna (A and B on Fig. 1 respectively). We examined a total of 200 bees (30 queens, 20 drones, 150 workers) for internal parasites and found only gut bacteria associated with $>90\%$ of bees but no nematodes, protozoa, or endoparasitic insect larvae.

External parasites were represented by only one species, the phoretic deutonymphs of the mite *Kuzinia laevis* (Acari: Astigmata). There were significant differences between castes in the number of mites present on bees ($F_{2,508} = 124.82$, $P < 0.0001$). Mites were extraordinarily abundant on drones (355 ± 31 per bee, range: 0–2000; 87% with mites, $n=181$) and queens (411 ± 84 per bee, range 0–2400; 81% with mites, $n=47$), but were relatively uncommon on workers (38 ± 9 per bee, range 0–1400; 51% with mites, $n=283$).

Young drones – as classified by wing wear – had on average 3 times more mites upon them (513 ± 49 per bee, $n=97$) than older drones (171 ± 27 per bee, $n=84$) (Fig. 2; $F_{1,179} = 37.04$, $P < 0.0001$). Neither drone size ($F_{1,130} = 0.05$, $P = 0.81$) nor geographic region ($F_{4,130} = 0.48$, $P = 0.75$) significantly influenced mite numbers (Table 1). At the Hobart site where collections of drones were made over a longer period than other sites, that is over 39 days, time since the first collection day had no significant influence on mite numbers ($F_{1,33} = 0.84$, $P = 0.37$).

Table 1. Average number of mites (*K. laevis*) found on individual hosts of *B. terrestris* in summer-autumn according to caste and sampling location (c.f. Fig. 1) (Mean ± S.E.; sample size in parentheses).

Region	Derwent	South	East	North	West
Workers:					
With pollen	14 ± 5 (43)	12 ± 5 (75)	31 ± 20 (5)	15 ± 6 (10)	10 ± 4 (33)
Without pollen	81 ± 48 (33)	73 ± 26 (54)	83 ± 83 (3)	1 ± 1 (6)	82 ± 58 (21)
Queens:					
Wing intact	729 ± 145 (13)	339 ± 106 (7)	450 ± 104 (3)	–	2200 (1)
Wing damage	28 ± 19 (6)	79 ± 26 (9)	163 ± 93 (4)	–	600 ± 600 (4)
Drones:					
Wing intact	567 ± 68 (52)	402 ± 84 (28)	207 ± 71 (6)	365 ± 145 (2)	789 ± 201 (9)
Wing damage	157 ± 25 (51)	202 ± 61 (18)	198 ± 44 (11)	–	137 ± 85 (4)

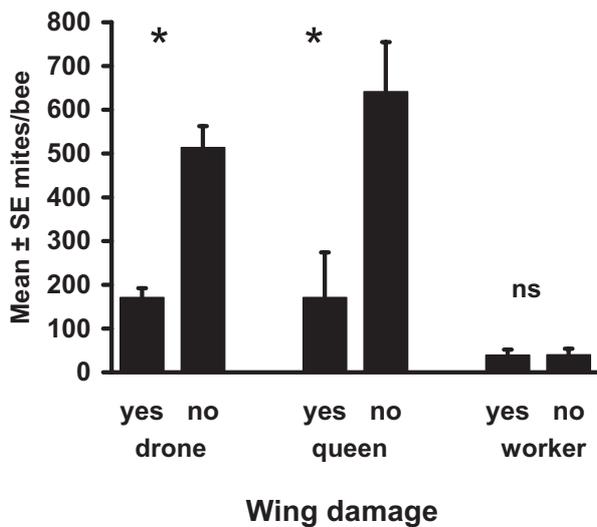


Figure 2. Mean ± s.e. *Kuzinia laevis* on bumblebee castes in summer-autumn with (yes, old bees) and without (no, young bees) wing damage. * = significant difference at $P < 0.05$, ns = not significant. Sample sizes from left to right: 84, 97, 23, 24, 166 and 79.

Young queens had on average nearly 4 times more mites upon them (641 ± 113 per bee, $n = 24$) than older queens (171 ± 104 per bee, $n = 23$) (Fig. 2; $F_{1,45} = 22.39$, $P < 0.0001$). Neither queen size ($F_{1,39} = 2.72$, $P = 0.11$) nor whether a queen was carrying a pollen load (Fig. 3; $F_{1,39} = 0.57$, $P = 0.46$) significantly influenced mite numbers.

For worker bees and unlike drones and queens, we found that there was no significant difference in mite infection levels with age: young workers (40 ± 14 per bee, $n = 79$) and older workers (39 ± 13 per bee, $n = 166$) (Fig. 2; $F_{1,241} = 0.96$, $P = 0.33$). However, workers carrying a pollen load (14 ± 3 per bee, $n = 147$) had significantly fewer mites upon them than those without a pollen load

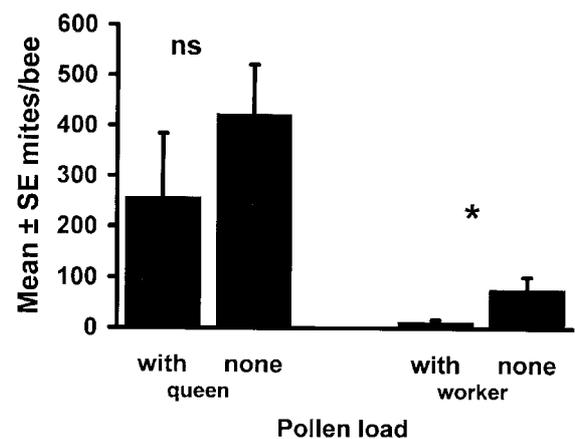


Figure 3. Mean ± s.e. *Kuzinia laevis* on bumblebee queens and workers in summer-autumn with and without (none) pollen loads on their hind tibia. * = significant difference at $P < 0.05$, ns = not significant. Sample sizes from left to right: 4, 39, 147 and 98.

(78 ± 24 per bee, $n = 98$) (Fig. 3; $F_{1,242} = 9.66$, $P = 0.002$). Worker size did affect mite numbers ($F_{1,242} = 5.15$, $P = 0.02$) with mite numbers increasing with increasing worker size ($r^2 = 0.14$, $P = 0.03$, $n = 245$). There was no significant difference in mite numbers found on workers across the five geographic regions (Table 1, $F_{4,238} = 0.73$, $P = 0.57$).

Spring

We found no nematodes in foraging or nest-searching bees that had over-wintered as adults. In New Zealand overall levels of nematode infection of spring queens average 9.7% (range 4.2 to 12.3%) (MacFarlane and Griffin, 1990). Assuming Tasmanian levels of nematode

parasitism are similar to the New Zealand average, the probability of sampling 50 individuals without any positive case is $p < 0.006$, such an outcome is not contained within the 95% C.I. (lower $p = 0.015$, normal approximation) of the corresponding binomial distribution, and hence is significantly different from New Zealand. Put another way, with an error of 5% we may have missed an overall infection prevalence of maximally $x = 0.058$ when no cases are found and the sample size is $n = 50$. Spring queens had high loads of the mite *K. laevis*, as had young summer-autumn collected queens collected in the previous season. There was no significant difference in mite loads between queens that were collected when searching for a nest (654 ± 67 per bee, $n = 20$) and those that were collected foraging on flowers (534 ± 65 per bee, $n = 27$) (Fig. 4; $F_{1,42} = 0.04$, $P = 0.84$). However, unlike summer-autumn queens (but like summer-autumn workers) the spring queen bees that were carrying pollen had significantly lower mite loads (13 ± 7 per bee, $n = 4$) than those without pollen loads (foraging: 624 ± 58 , $n = 23$; foraging and searching pooled: 624 ± 45 per bee, $n = 43$) ($F_{1,42} = 39.14$, $P < 0.0001$). Queen size also had no significant effect on mite load ($F_{1,42} = 0.17$, $P = 0.68$). Although spring queen collections were made over 46 days the number of days that had elapsed since the first collection day had no significant influence on mite numbers ($F_{1,42} = 0.06$, $df = 1,42$, $P = 0.80$).

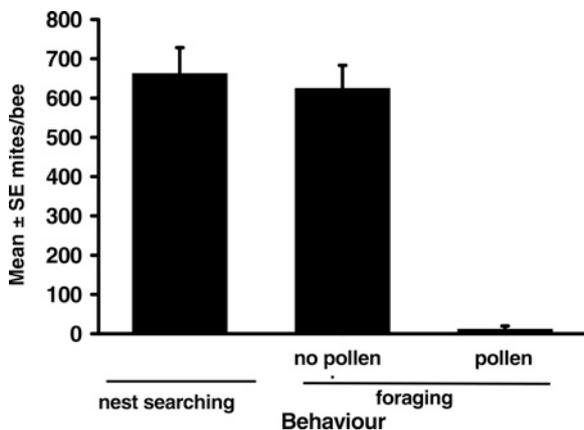


Figure 4. Mean \pm s.e. *Kuzinia laevis* on bumblebee queens captured in Hobart during spring. Queens were classified as nest searching, foraging (no pollen load on hind tibia (no pollen)), or foraging (with pollen load on hind tibia (pollen)). Sample sizes from left to right: 20, 23 and 4.

Bumblebee nest survey

We searched 17 nests and found no evidence of brood parasitism, wax moths, or any other bumblebee parasite with the exception of the free-living life stages of *K. laevis*. These mites were always present in active nests, and in some cases were infesting the pollen stores in uncountable thousands (up to a conservative estimate of 1 million in 3 nests). Other common invertebrates associated with

the nest were booklice (*Liposcelis* sp), ants of several genera (especially *Technomyrmex albipes* (F. Smith) [pale-footed house ant], *Linepithema humile* (Mayr) [Argentine ant], and an *Anonychomyrma* sp.), tenebrionid larvae, and *Forficula auricularia* L. (European earwigs).

Discussion

Surveys of *B. terrestris* in its native European habitat demonstrate that the species is host to a number of protozoan parasites (such as the protozoans *Crithidia bombi*, *Nosema bombi*, and various gregarines), larvae of parasitic flies (conopids), nematodes, and mites (Table 2). In New Zealand *B. terrestris* is host to the internal parasites the protozoan *Nosema bombi*, the nematode *Sphaerularia bombi* and the mite *Locustacurus buchneri*, (MacFarlane et al., 1995), though comparative levels of infection are not precisely known. In Europe, the trypanosome *C. bombi* appears to be the most prevalent parasite to be found. Its major effect is to reduce colony-founding success (Brown et al., 2003), to increase worker mortality rates under adverse environmental conditions (Brown et al., 2000), and to delay worker-queen conflicts (Shykoff and Schmid-Hempel, 1991c). A similarly strong impact is due to parasitization by larvae of conopid flies, which translates into increased worker mortality rates and, under certain conditions, decreased colony performance (Müller and Schmid-Hempel, 1992, 1993b; Müller et al., 1996). The data reported here clearly show that Tasmanian populations have few if any of these parasites that are typical for the native European populations. In general terms, therefore, Tasmanian bumblebees are largely free of parasites with major effects.

The mite *K. laevis*, the only parasite we found of Tasmanian bumblebees and which does not occur otherwise on this island, is a common associate of bumblebees. However, on individual bees *K. laevis* is primarily a phoretic mite whose deutonymphs, the dispersal stage, are carried by the bumblebee host. Usually, the majority of the population is infested, a pattern that is in contrast to the distribution of many other parasite species that usually are found on or in the minority of individuals (Schmid-Hempel, 1998; Corbet and Morris, 1999). This persistent occurrence on many individuals of a population, also found in the presumably ancestral New Zealand population (Schmid Hempel et al., in prep), may explain why the founding population of *B. terrestris* apparently carried *K. laevis* but no other parasite. Phoretic stages of mites also regularly infect spring queens in European populations, (e.g. half of the spring queens of *B. terrestris*, *B. lucorum*, and *B. lapidarius* were infested with 1 to 20 individuals of *Parasitellus fucorum*, De Geer, Schwarz et al., 1996), whilst mite loads of field-collected workers during the season are much less intense (Table 2). Although the data in Table 2 were not collected with the aim to precisely assess mite loads, collectively, several

Table 2. Parasite prevalences in workers of European *B. terrestris*^a (Switzerland). Number of sampled workers in parentheses. Prevalence expressed as a fraction of one.

Study	Shykoff & Schmid-Hempel (1991) ^a	Durrer (1996)	Durrer (1996)	various ^c	Baer & Schmid-Hempel (1999)	Baer & Schmid-Hempel (2001)
Study year	1990–1991	1990	1991	1988–1993	1997	1998
Site	NW Switzerland	Jura mountains	Jura mountains	NW Switzerland	Lowlands	Lowlands
Type ^b	F	F	F	F	E	E
Crithidia	0.80 (61)	0.18 (385)	0.83 (293)	0.11 (902)	0.60 (355)	0.62 (1199)
Nosema	0.15 (61)	0.01 (384)	0.16 (293)	0.01 (902)	0.02 (355)	0.05 (1199)
Apicystis Gregarines ^c	–	0.01 (384)	0.01 (293)	0.01 (902)	0.08 (355)	0.02 (1199)
Nematodes	–	0.01 (384)	–	–	–	–
External mites	0 (61)	0.07 (541)	0.07 (293)	0.10 (902)	0.01 (355)	0.01 (1199)
Tracheal mites	0 (61)	0.02 (384)	0.02 (293)	0.01 (902)	0 (355)	–
Conopids ^d	0.23 (61)	0.44 (544)	0.07 (293)	0.36 (902)	0.01 (355)	0.01 (1199)

^a Note: Parasite screening in each study was done for slightly differing purposes. Hence, the data allow only a rough comparative overview over study sites and years.

^b F = Field collections of workers; E = Workers from experimental colonies in the field.

^c *Apicystis (Mattesia) bombi* was the most common gregarine.

^d Because of parasite-induced changes in behaviour (Müller & Schmid-Hempel 1993b), conopid larvae are prevalent in workers captured in the field but are much rarer in workers collected inside the nest.

^e P. Schmid-Hempel & R. Schmid-Hempel, unpubl. data.

independent studies suggest that European populations of *B. terrestris* (e.g. Skou et al., 1963; Chmielewski, 1971; Schwarz et al., 1996) as well as bumblebee populations elsewhere (Goldblatt, 1984; Macfarlane et al., 1995) generally have low mite loads as compared to Tasmanian populations.

While deuteronymphs of *K. laevis* on queens, workers or males are phoretic the mite is considered a benign pollen-thief inside the bumblebee nest, having little or no measurable impact upon their hosts (Chmielewski, 1971, 1991). However, average mite numbers in Europe appear far less than those in Tasmania (Corbet and Morris, 1999). For example, the average number of *K. laevis* on Tasmanian queen bees is over 600 individuals, whereas queen bees from England have, on average, a conservative estimate of just 13 *K. laevis* (Corbet and Morris, 1999). Even if the Corbet and Morris (1999) estimate is low, mite load in the Tasmanian population is an order of magnitude greater than in their sample. This difference could have significant impacts on the success of nests, especially nest establishment.

As an example of the potential impacts of *K. laevis*, consider two queen bees: one with 10 mites, the other with 1000 mites. The pre-oviposition period of *K. laevis* is about 2.7 days, their egg-reproductive adult duration is about 20.3 days, oviposition period is 33.2 days, and their longevity is 65 days. Female *K. laevis* lay an average of 7.3

eggs per day and the sex ratio is 1:1 (Chmielewski, 1991, 1994). This means that a nest in Tasmania established on October 1 by the queen carrying 1000 mites will contain about 480,000 mites by November 1, and by December 1, the population of living females could potentially produce an astonishing 7.8 million eggs per day. This compares to about 78,000 mites per day on December 1 with the queen carrying just 10 mites. Clearly, initial mite populations are expected to be important for the eventual number of mites found in the colony and the queen. Furthermore, without known predators in Tasmania, only abiotic factors, competition and unknown parasites and predators of *Kuzinia* could keep their populations in check. Although *Kuzinia* may be more than a benign pollen thief when in extraordinary numbers, such as those found in some bumblebee nests, perhaps the major negative effect of mites is through the vectoring and activation of viral infections (Schmid-Hempel, 1998), in which case not the absolute infestation numbers but the number of vectoring events should be a more telling figure. Unfortunately, in this study, viruses could not be analysed and it thus remains unknown whether viral infections are present in Tasmania.

The patterns of *K. laevis* abundance on different castes of bees shows that drones and queens are far more attractive than workers (Fig. 2). The advantage of high numbers on queens seems obvious: by catching a ride on

queens, the mites will ensure they colonise a new nest. However, their equal abundance on males is more puzzling. Perhaps some mites transfer during bumblebee copulation, or move off males at a later time; otherwise, these mites will die (Huck et al., 1998). Their prevalence on young queens and drones (i.e. those with intact wings; Fig. 2) indicates that mites move onto bees soon after bees emerge from pupae. The gradual loss of mites may be caused by natural mortality, shedding during flight, or transferral to new nests or younger bees in the same nest. Bumblebees, unlike honey bees, do not allogroom but self-grooming may also result in some loss of mites. During spring, queens with pollen loads probably had few mites (Fig. 4) because they had established a nest with a pollen store, and the mites had disembarked.

The smaller number of mites on workers without pollen loads, compared with those carrying pollen, is difficult to explain (Fig. 3). The absence of differences in age classes, as indicated by wing tattering (Fig. 2), means that the explanation does not involve the age of the bee. However, beyond this we may not speculate further without more understanding of the behaviour and ecology of mites and bumblebees.

As we will report elsewhere (Schmid-Hempel et al., in prep.), Tasmanian populations of *B. terrestris* are genetically impoverished as compared to continental European populations and even when compared to the populations of Mediterranean islands or Madeira (Estoup et al., 1996) but similar to the isolated population of the Canary islands (Widmer et al., 1998). In this species, a decrease in genetic diversity – at least within colonies – leads to an increase in the parasite load with an associated loss of fitness (e.g. Baer and Schmid-Hempel, 1999). However, the loss of genetic diversity may not affect the Tasmanian population because most damaging parasites are absent in Tasmania, as a result of the same founder event by a small number of colonising hosts (Schmid-Hempel et al., in prep.). The particular situation in Tasmania therefore offers unique opportunities to study the unfolding of an invasion event in relation to co-evolving parasites.

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