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Original article

A contribution to the knowledge of *Nosema* infections in bumble bees, *Bombus* spp.

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Abstract – Experimental infections of adult and larval workers and adult males of *Bombus terrestris* with the microsporidium *Nosema bombi* showed all stages and both sexes to be susceptible. On average 19–29 % of infections were successful and no significant differences among these host categories were found. Different sources of *Nosema* spores differed in their success in infecting different host colonies, suggesting genotype–genotype interactions at the level of colonies and parasite sources. In a second experiment, *N. bombi* obtained from *B. terrestris* were found to be infective for workers of *B. lapidarius* and *B. hypnorum*, although less so in these foreign hosts. On the other hand, case mortality was significantly higher in foreign hosts than in *B. terrestris*. Infection and high spore loads correlated with early death of the host. In addition, a factorial analysis showed that variation among-colonies-within-species explained more of the variation in infection success than the factor species per se. © Inra/DIB/AGIB/Elsevier, Paris

parasite / brood / host specificity / *Bombus* / *Nosema bombi*

1. INTRODUCTION

Microsporidia are an important group of protozoan parasites, especially of insects, where they often infect epithelial cells or the fat body [6, 40]. More recently, infections by microsporidia in humans have become more important, owing to the increase in the number of patients with immunodeficiency [7, 8]. In social insects, microsporidia have been reported from all major groups, i.e. the termites, wasps, ants and bees [33]. In particular, *Nosema apis* Z. infecting the honey bee, *Apis mellifera* L., has been studied in some detail because of the economic importance of its host [3].

Bumble bees, *Bombus* spp., are eusocial bees with an annual life cycle and are of increasing economic interest as pollinators of crop. In addition, the importance of their

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diseases, for example caused by *Nosema bombi* Fantham & Porter, has been recognized since early in this century [16]. In fact, *Nosema* has been reported for a number of *Bombus* species [26, 33]. So far, all infections in bumble bees have been attributed to *N. bombi* Fantham & Porter, although it is unclear whether all infections are in fact by the same parasite. Typically, identification is by light microscopy and inspection of spores, a procedure that is not always reliable [25]. Some authors have even considered *N. bombi* to be the same species as *N. apis* [38, 40], and suggested that these two parasites are cross-infective for the two hosts [15, 23, 35]. But later and more recent work has clearly demonstrated that these two parasites are different and that reports of successful cross-infections are ambiguous [14, 27, 41]. Here, we follow the currently accepted nomenclature of using *N. bombi* for all of our sources.

In the field, prevalences of infection range widely. For example, up to 55 % of workers and 8–50 % of males in European populations of various species were found to be infected by *N. bombi* [13, 36]. According to Betts [4], all hibernated spring queens of *B. lapidarius* collected in England were found to be infected. Severe infestations of autumn queens of *B. terrestris* collected in Denmark were found by Skou et al. [37]. In New Zealand, where bumble bees have been imported in the last century, 76 % of all nests ($n = 76$) and 10 % of queens ($n = 275$) of *B. terrestris* were found to be infected [26].

The effects of *N. bombi* on its host are quite variable. According to our own observations, infected workers often become sluggish, die early and the affected colonies may eventually perish. MacFarlane et al. [26] suggest that *Nosema* infection paralyses the abdomen of the queen and completely prevents mating. A similar observation was also made by DeJonghe [11]. On the other hand, no difference in body mass of 12 severely infected queens as compared to 1 275 non-infected ones was found by MacFarlane et al. [26]. In fact, not all colonies and individuals are affected in the same way and the effects are not universally detrimental. Several authors have found few or no externally visible effects of experimental infections [17, 27] or even found increased production of sexuals in naturally infected colonies [22]. Similarly, overwintered queens that have become infected in their maternal colony often manage to found a colony, to raise brood and to complete an apparently normal life cycle (pers. obs.).

Given the biology of *N. bombi*, infection of hibernating queens should be the most important or even only route of vertical transmission between the annual generations. *Nosema* spores are susceptible to UV-light and desiccation [5], conditions likely to be encountered outside the host. Spores of *N. apis* can persist for 1–2 years or more in honey stores of honey bees [29], but such a long-lasting reservoir is not available in bumble bees. Transovarial (vertical) transmission is known to occur in other *Nosema* species [28] but so far has not been reported from *N. bombi* and seems unlikely from detailed investigations of reproductive structures [27]. Within the colony, *N. bombi* spreads by ingestion of spores shed by infected workers [14]. However, colonies also contract novel infections from outside, as previously uninfected colonies in the field may suddenly contain infected workers [22]. Perhaps, such horizontal transmission between colonies occurs via spores deposited on flowers as has been shown for the trypanosome *C. bombi* in the same hosts [12], or by increased drifting rates of infected workers as is known for honey bees infected by the *Varroa* mite [32]. But apart from a few studies on the phenology of the parasite within its host [27, 41], not much is known of the general biology and ecology of *N. bombi*, despite the potential importance of microsporidia in general and of this parasite in an economically interesting host in particular. Here, we report the results of two infection experiments with *N. bombi* and

three species of bumble bees. The aim of our study is to broaden our knowledge of an important microsporidian parasite and, at the same time, to elucidate its ecology by investigating whether this parasite can cross-infect to other *Bombus* species and to what extent the effect of infection varies among colonies within and between host species.

2. MATERIALS AND METHODS

Spores of *N. bombi* were identified by light microscopy [27]. Results from pilot experiments based on 95 workers and males suggested an overall modest infection success when spore suspensions are fed to workers. Furthermore, spores often appeared in the host's faeces only 2–3 weeks post-infection. Guided by these previous observations, we evaluated infection success ('infected' versus 'not infected') 21 days post-infection. In the second experiment, we also scored spore loads in the freshly dead workers if they had died before these 21 days. We used an arbitrary scale for infection intensity, i.e. spore concentration in the host, as follows: 0 = no spores found (not infected), 1 = low infection (up to 100 spores·μL^{-1}), 2 = moderate infection (up to 1 000·μL^{-1}), 3 = heavy infection (up to 10 000·μL^{-1}), 4 = very heavy infection (more than 10 000·μL^{-1}); grades 1–3 were considered to be infected. To measure spore concentration, the abdomen of the test worker was homogenized in 0.5 mL water. Subsamples were then taken and counted in a haemocytometer (Neubauer chamber) under the microscope. All experimentally infected workers were kept individually in small wooden boxes with sugar water (diluted Apinvert®) ad libitum and under controlled conditions (28 °C, 60–80 % R.H.). If not indicated otherwise, values are given as means and S.E. All analyses were performed with SPSS6.1 and two-tailed probabilities are reported.

2.1. Experiment 1: infection with two sources (A, B) of spores

Spores of *Nosema* were prepared as follows. One worker each was taken from two infected colonies of *B. terrestris* L. (labelled as sources A, B). These colonies were laboratory-raised from queens caught around Zürich, Switzerland, in spring 1995. The abdomen was homogenized in water, spore load counted and diluted to a suspension of 12 000 spores·μL^{-1}. The same volume of sugar water (Apinvert®) was then added. Finally, a standard inoculum of 10 µL (i.e. 60 000 spores; similar to ref. [27]) was prepared. We considered these two solutions as representing different sources of *Nosema*, probably containing a different set of 'strains'. This assumption was later justified by the results. Workers from three non-infected colonies of *B. terrestris* (K162, K166, K226), raised from the same stock of queens, were chosen at random to receive the inocula. Each was offered the standard of 10 µL after starvation for 3 h; in each case, the entire dose was quickly imbibed. For the infection of larvae, a similarly sized piece of brood was cut out from the same colonies and the number of larvae in it estimated. With a standard of 10 µL·$larva^{-1}$, a dose for the entire piece of brood was calculated. This amount of spore suspension was then applied with a fine brush to the entire clump. All larvae were 1–5 days old when infected. We also added three non-infected nurse workers to the brood clump for the daily routine of brood care. These were removed as soon as the larvae pupated and before the first worker hatched. To evaluate infection success, we checked the workers (that had hatched from these larvae) on day 21 post-emergence.

2.2. Experiment 2: infection of different hosts species

In this experiment, the abdomen of one worker of an infected colony of *B. terrestris*, laboratory-raised from a queen caught around Zürich, Switzerland (no. 198), in spring 1996, was homogenized in 0.5 mL of water and spores standardized to 12 000·μL^{-1}. An equal volume of sugar water (Apinvert®) was then added. All bees were infected with the standard inoculum of 10 µL (i.e. 60 000 spores) gained from this source and offered after 3 h of starvation. Workers of healthy colonies of *B. terrestris*, *B. lapidarius* L. and *B. hypnorum* L., laboratory-raised from queens caught in the same area around Zürich at the same time, served as experimental hosts. All workers were infected at age 1–4 days. Whether or not an infection had occurred, together with the assessment of infection intensity (grades 0–4), was evaluated either 21 days post-infection or in freshly dead workers for those that had died earlier. In addition, the number of surviving or dead animals up to 21 days was used to calculate case mortality rates (percentage dead before 21 days).

Table I. Numbers of infected (spores present) and non-infected (healthy; no spores present) individuals 21 days after inoculation with spores of *N. bombi*. Cases are pooled from infections by source A or B.

		Colony K162		Colony K166		Colony K226		Totals	
		Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected
Workers	Larvae	12	9	11	1	4	0	27	10
	Adults	8	2	6	5	10	1	24	8
Males*	Larvae	2	4	0	3	9	0	11	7

* No male adults could be tested.

3. RESULTS

3.1. Experiment 1: infection with two sources (A, B) of spores

A total of 87 individual hosts could be analysed (*table I*). Only 25 (28.7 %) of those actually had spores of *Nosema* 21 days post-infection. Thus, the average infection success was rather low. Infection success ('infected' versus 'not infected') in worker larvae as compared to adult workers showed no difference ($\chi^2 = 0.036$, $P = 0.84$). Although male larvae were more frequently infected (38.9 %, N = 18) than worker larvae (27.0 %, N = 37), the difference was also not significant ($\chi^2 = 0.798$, $P = 0.37$). Many infected larvae died during pupation or shortly afterwards and showed strong deformations.

On the other hand, there was a clear difference between colonies (colony K162: 40.5 % infected, N = 37; K166: 34.6 %, N = 26; K226: 4.2 %, N = 24) ($\chi^2 = 10.03$, $P = 0.007$) in infection success of workers, irrespective of adult or larval stage. Similarly, a strong effect for source of infection was found (average success with source A: 17.6 % of workers, N = 51; with source B: 44.4 %, N = 36) ($\chi^2 = 7.40$, $P = 0.007$). The same pattern emerged when, instead of using the dichotomous infected/non-infected classification, infection intensities (scale 0–4) were used (difference between sources A versus B, U-test: z = 2.66, $P = 0.008$; difference among colonies: Kruskal-Wallis H = 10.79, df = 2, $P = 0.005$). For two of the colonies (K162, K166) we had enough data to test for a host versus parasite interaction effect with a factorial analysis. Both the analysis with infection intensities (0–4) and infection success (yes/no) showed a clearly visible, but only marginally significant, interaction effect (*figure 1*).

3.2. Experiment 2: infection of different hosts species

In this second experiment, spores of *N. bombi* were extracted from the host *B. terrestris*. A total of 327 workers from 28 colonies of three species (*B. terrestris, B. lapidarius, B. hypnorum*) could be inoculated with this source, of which 305 could be reliably scored for infection. A total of 60 workers (19.7 %) contained spores 21 days post-infection or at the time of their death if before this census day, while 245 remained free of infection (*table II*). When the data were analysed per individual worker irrespective of colony, a clear difference among species was found for both, the success of infection (infected/non-infected) ($c^2 = 8.89$, df = 2, $P = 0.012$) and the intensity of infection per worker (scale 0–4: H = 8.59, df = 2, $P = 0.014$). A species dif-

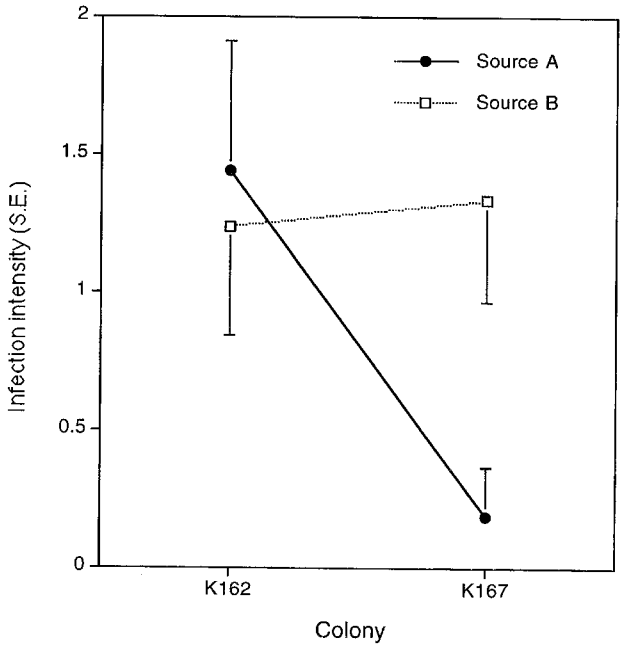

Figure 1. Intensity of infection (grades 0–4) as a function of source of infection (A, B) and host colony (K162, K166). ANOVA with ln-transformed intensity data (factor colony: $F_{1,59} = 1.06$, $P = 0.307$, factor strain: $F_{1,59} = 1.98$, $P = 0.165$, interaction: $F_{1,59} = 3.69$, $P = 0.060$; model $r^2 = 0.084$). A logit analysis with an infected/non-infected classification yielded the same result (interaction $z = 1.91$, $P = 0.056$). For clarity, only one error bar (S.E.) is shown; for sample sizes, see *table I*.

ference was also found for the average mortality rate per colony (*table II*; *figure 2*). However, the species differences in infection success and intensity disappeared when the average colony values instead of individual values were considered (*figure 2*).

Across all colonies and irrespective of species, the average infection intensity per worker was highly correlated with the prevalence of infection (percentage infected workers) in its colony (Spearman's $r_S = 0.99$, $P < 0.0001$, N = 28 colonies). Similarly, prevalence (arcsin-transformed: r = 0.399, $P = 0.036$) and infection intensity (sqrt-transformed: r = 0.424, $P = 0.024$) were positively correlated with case mortality rate in the colony. Interestingly, the average case mortality rate in colonies of the two foreign hosts (*B. lapidarius, B. hypnorum*) was significantly higher (37.1 ± 5.4 %, N = 16 colonies) than in colonies of the original host (*B. terrestris*: 16.4 ± 7.1 %, N = 12) (U-test: z = 2.727, $P = 0.006$, N = 28 colonies). In contrast, the average prevalence and infection intensity seemed higher on the original host, although not significantly so (*figure 2*; $P > 0.4$ in both cases).

The average infection intensity in bees that were infected at all and that had died before the census day 21 (mean = 1.344 ± 0.12, N = 32) was higher than in those that had survived to this day (mean = 1.107 ± 0.08, N = 28) although this difference was not significant (U-test: z = 1.588, N = 60, $P = 0.112$). On the other hand, we found that the survival of infected animals (survival 46.7 %, N = 60 bees) was significantly lower than that of non-infected animals, i.e.

Table II. Numbers of infected and non-infected (healthy) workers, and survival to 21 days (numbers alive and dead, respectively) after inoculation with *N. bombi* extracted from *B. terrestris*.

Colony	*B. terrestris*[1]			*B. lapidarius*[2]			*B. hypnorum*[3]		
	Healthy	Infected	Alive/ dead	Healthy	Infected	Alive/ dead	Healthy	Infected	Alive/ dead
K1	9	0	12/0	6	6	4/7	9	1	9/1
K2	10	1	10/1	12	0	10/3	11	1	9/3
K3	10	2	11/1	6	5	5/7	2	0	2/0
K4	11	0	9/3	11	0	7/4	10	0	8/2
K5	10	2	11/1	12	2	10/3	15	0	9/6
K6	8	3	11/1	3	9	9/3	9	2	5/6
K7	0	8	1/7	12	1	5/6			
K8	12	0	10/2	5	2	4/3			
K9	8	3	8/4	11	1	2/10			
K10	11	0	11/0	7	5	8/4			
K11	7	4	12/0						
K12	8	4	13/0						
Total*	104	27	119/20	85	29	64/50	56	4	42/18
(%)		20.6 %	14.4 %		25.4 %	43.9 %		6.7 %	30.0 %

* Percentage mortality for species. Test for homogeneity among colonies within species (infection; mortality).
[1] $\chi^2 = 46.55$, df = 11, $P < 0.0001$; $\chi^2 = 48.75$, df = 11, $P < 0.0001$.
[2] $\chi^2 = 33.46$, df = 9, $P < 0.001$; $\chi^2 = 17.96$, df = 9, $P = 0.036$.
[3] $\chi^2 = 4.50$, df = 5, $P = 0.48$; $\chi^2 = 7.25$, df = 5, $P = 0.203$.

where the inoculation did not lead to infection (survival 77.5 %, N = 240) ($\chi^2 = 22.32$, $P < 0.001$). Both findings suggest that heavy *Nosema* infections lead to premature host death.

Figure 2 shows that no species differences for infection success and intensity exist when the average values per colony are used instead of average values per worker. In fact, by looking at the data (*table II*), it is evident that variation at the level of the colony is more pronounced than variation at the species level. Consequently, we also compared infection intensities with a hierarchical factorial analysis (colony nested within species; a total of 28 colonies in three species; *table III*). When colony identity was explicitly taken into account in this way, a highly significant effect was found for variation among colonies while the species effect disappeared (*table III*).

4. DISCUSSION

The results of this study demonstrate that different sources of *Nosema bombi* vary considerably in their potential to infect a given colony (*figure 1*). This makes a genotype–genotype interaction between parasite 'strain' and host colony very likely. On the other hand, the results of cross-species infections with *N. bombi* from *B. terrestris* to different species showed that a certain degree of host specificity exists, since workers of *B. lapidarius* or *B. hypnorum* were less likely to become infected than those of the original host *B. terrestris* (*figure 2*, *table II*). Remarkably, the infection caused higher case mortality in the foreign than in the original host, while infection success showed the opposite tendency (*figure 2*). This suggests that populations of *N. bombi* in different host species may be differentiated from each other but are probably not different parasite species altogether. The result

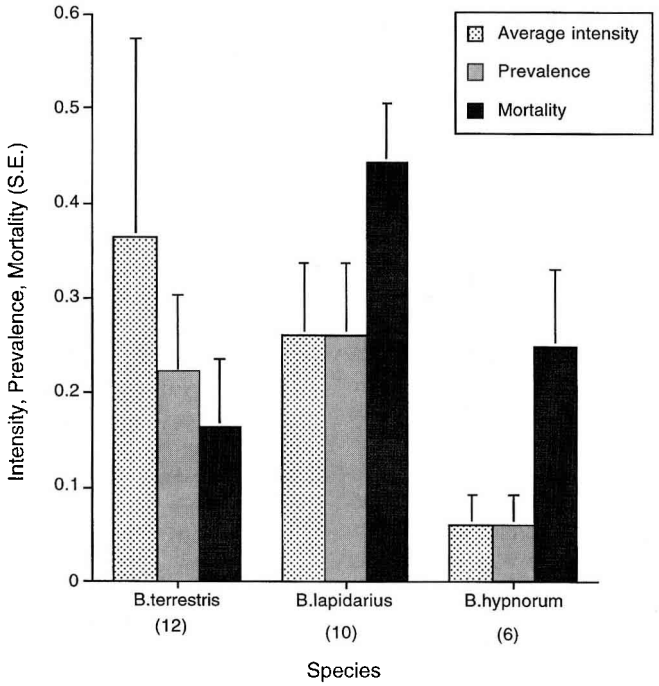

Figure 2. Results of the infection experiment with a *N. bombi* source from *B. terrestris*. The statistics for variation among species are: i) average infection intensity per colony: H = 3.061 df = 2, $P = 0.205$; ii) average prevalence per colony (percentage infected workers; ANOVA, arcsin-transformed data): $F_{2,25} = 1.30$, $P = 0.291$; evaluated per individual worker, these two measures are significantly different among species (see text; *table II*); iii) average case mortality rate per colony: (ANOVA, arcsin-transformed data): $F_{2,25} = 5.01$, $P = 0.015$. Small figures are sample sizes (number of colonies).

Table III. Hierarchical ANOVA for average infection intensity per colony nested within species.

Factor [1]	SS	df	MS	F	*P*
Colony (error 1)	10.41	25	0.42	10.99	< 0.0001
Residual error	10.49	277	0.04		
Species	0.37	2	0.19	0.45	0.643
(Error 1)	10.41	25	0.42		

[1] Values sqrt (0.4 + intensity) – transformed (after ref. [31]).

also supports an earlier observation of DeJonghe [11] that the subspecies *B. terrestris xanthopus* from Sardinia, Italy is more susceptible to a given *Nosema* infection than *B. t. terrestris* from Central Europe. Both bee races can otherwise be hybridized with each other. Hybrids also show higher susceptibility.

However, a strong result is that the intrinsic variation among colonies can over-

shadow differences among species. This is suggested by the results of *table III*, as well as by the fact that colony-wide averages for infection intensity or prevalence did not differ sufficiently to generate significant species effects (*figure 2*). To be sure, our results do suggest that *Nosema* from *B. terrestris* does not perform as well on other species (*figure 2*). However, strong colony effects have come to light in both experiments. In fact, similar differences in the susceptibility of different honey bee colonies to infection by *N. apis* have been reported in a number of studies, for example in Furgala [19] (see also [3, 30]). Such colony versus parasite strain effects are important for understanding the ecological and evolutionary dynamics of host–parasite interactions. In the current case, it suggests that colony-level variation may be important in determining the dynamics of *Nosema* infections in field populations and perhaps entire communities of co-existing *Bombus* species.

In the honey bee, *N. apis* seems unable to infect the larvae, as freshly emerged bees are normally free of the disease [1, 3, 21]. Spores detected in other organs, e.g. fat body and hypopharyngeal glands, are probably not *N. apis* [2]. Nevertheless, other species of microsporidia in honey bees have been found to kill the pupae by infection [9]. We now find that *N. bombi* is able to infect both brood and adults of bumble bees, contrary to the study of Eijnde and Van den Vette [14] who only found larvae to be susceptible. However, these authors checked their adults 10–12 days post-infection. This may sometimes be too early, since we found that new spores are often shed by an infected host only after a considerable length of time (up to 2–3 weeks). Unfortunately, the data did not allow a firm statistical inference for this issue. Similarly long periods have also been reported by L'Arrivée [24] for *N. apis* in honey bees, but other studies report a period of around 5 days [3] or even shorter (2 days: Kellner 1980, cited in Fries [18], who found 3 days). These differences appear to be dose dependent [18]. In careful investigations of infected tissue, McIvor and Malone [27] found that mature spores of *N. bombi* – which are typically recognized in the faeces – appear 5 days (120 h) post-infection in its host *B. terrestris* at the earliest. These time spans must be compared to the average life span of bumble bee workers which is normally around 20–30 days [20], or to a mean weekly mortality rate in the order of 20–35 % [34]. Assuming a maximum prepatent phase of approximately 20 days and immediate infection after emergence from the pupa, the chances of the host to reach this age are around 50 % and half of the infections would be lost before they can be transmitted further. Hence, the temporal dynamics of *N. bombi* infections warrants further studies.

Similarly, the overall level of infection success (28.7 % in the first experiment; 19.7 % in the second), despite forced inoculations, is remarkably low. Of course, temperature and condition of the host are likely to affect the cycle of *Nosema*, as is known for *N. apis* in honey bees. In honey bees, sporonts produced in summer differ from those in winter bees [39, 40, 42]. Weiser [40] concluded that diapause in the host also arrests microsporidian development. Recent studies also found that the observation of emptied spores of *N. apis* is similar to observations of dimorphic spores in other *Nosema* spp., although it is doubtful whether true dimorphism occurs [10, 18, 33]. Perhaps, some spores of *N. apis* germinate inside the host cytoplasm, whereas others spores remain ungerminated and spread to other hosts or reinfect the gut epithelium (I. Fries, pers. comm.). Such characteristics could be relevant for microsporidia in hosts with annual life cycles as in the bumble bees. More studies are clearly indicated to further elucidate the intricate relationship of these microsporidia with their hosts. According to our results, such studies should be highly rewarding.

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Résumé – Contribution à la connaissance des infections dues à *Nosema* chez les bourdons, *Bombus* spp. Le but de ce travail est d'étudier quels stades de l'hôte peuvent être parasités par la microsporidie *Nosema bombi* et s'il existe des résistances entre les colonies et entre les diverses espèces de bourdons. Le parasite a été prélevé sur des ouvrières de *Bombus terrestris* et a servi à infecter expérimentalement des larves, des ouvrières et des mâles de *B. terrestris*. Les deux stades et les deux sexes ont pu être infectés avec succès. En moyenne 19 à 29 % des infections ont réussi. Aucune différence n'a été mise en évidence entre les diverses catégories d'hôtes. Dans une première expérience on a utilisé deux sources de spores de *N. bombi* (provenant de deux colonies de *B. terrestris*). Là, on a observé des différences dans la réussite de l'infection selon la colonie hôte ($n = 3$; de 4,2 à 40,5 %) et selon la source de spores (de 17,6 à 44,4 %) (*figure 1*). En outre il existe une interaction génotype-génotype entre l'origine du parasite et la colonie hôte. Dans une seconde expérience on a pu transmettre *N. bombi* provenant de l'hôte *B. terrestris* à des ouvrières de 28 colonies de *B. lapidarius, B. hypnorum* et *B. terrestris*. Le succès et l'intensité de l'infection sur les hôtes étrangers a été légèrement plus faible que sur l'hôte propre (*figure 2* ; *tableau II*). En revanche, la mortalité finale chez les hôtes étrangers a été plus élevée que chez *B. terrestris* (37,1 % contre 16,4 % ; *figure 2*). En outre l'intensité de l'infection (nombre de spores) était plus élevée chez les ouvrières mortes jeunes, alors que la probabilité de survie des insectes infectés était inférieure à celle des insectes non infectés. Une attaque intense par *N. bombi* conduit donc à la mort prématurée de l'hôte. L'analyse factorielle de la résussite de l'infection fait ressortir que la variation entre colonies au sein d'une même espèce hôte est plus importante que les composantes de la variation entre les espèces hôtes. Des différences entre les colonies au sein d'une même espèce hôte peuvent donc cacher les différences entre espèces hôtes. © Inra/DIB/AGIB/Elsevier, Paris

***Bombus* / *Nosema bombi* / parasite / spécificité hôte / couvain**

Zusammenfassung – Ein Beitrag zur Kenntnis der *Nosema*-Infektionen bei Hummeln. Das Ziel dieser Studie war, zu untersuchen, welche Stadien des Wirts von *Nosema bombi* befallen werden können und ob es Unterschiede in der Resistenz zwischen Kolonien und verschiedenen Arten von *Bombus* gibt.Das Mikrosporidium *Nosema bombi* wurde aus Arbeiterinnen von *B. terrestris* gewonnen und experimentell Larven und adulte Arbeiterinnen, sowie adulte Männchen von *B. terrestris* infiziert. Beide Stadien und Geschlechter konnten infiziert werden. Durchschnittlich waren 19–29 % der Infektionen erfolgreich. Es wurde kein Unterschied zwischen diesen Wirtskategorien festgestellt. Im Versuch wurden zwei verschiedene Quellen von *Nosema*-Sporen verwendet (ursprünglich isoliert aus zwei verschiedenen Kolonien von *B. terrestris*). Dabei zeigten sich Unterschiede im Infektionserfolg von 4.2 % bis 40.5 % zwischen drei getesteten Wirtskolonien, und ebenfalls zwischen den beiden verwendeten Sporen-Quellen (17.6 %, 44.4 %; *Abb. 1*). Ausserdem wurde eine Interaktion deutlich, was auf Genotyp-Genotyp Inter-

aktion in bezug auf Parasiten-Herkunft und Wirtskolonie schliessen lässt. In einem zweiten Experiment konnte *N. bombi* aus der Wirtsart *B. terrestris* auf die Arbeiterinnen aus 28 Kolonien von *B. lapidarius, B. hypnorum* , sowie auf *B. terrestris* selber übertragen werden. Der Erfolg und die Intensität der Infektion von *N. bombi* in den fremden Wirtsarten war leicht geringer als auf der eigenen Wirtsart (*Abb. 2, Tabelle I*). Andererseits war die Fallmortalität in den fremden Wirtsarten höher als in *B. terrestris* (37.1 % gegenüber 16.4 %; *Abb. 2*). Ausserdem war die Infektionsintensität (Sporenzahl) bei früh gestorbenen Arbeiterinnen höher, während die Überlebenswahrscheinlichkeit infizierter Tiere kleiner war als diejenige nicht infizierter Tiere. Intensiver Befall durch *Nosema* führt daher zum vorzeitigen Tod des Wirts. Eine faktorielle Analyse des Infektionserfolgs ergab ausserdem, dass die Variation zwischen Kolonien innerhalb der gleichen Wirtsart bedeutsamer war als die Variationskomponente zwischen den Wirtsarten. Unterschiede zwischen den Kolonien innerhalb Wirtsart können deshalb die Unterschiede zwischen den Wirtsarten verdecken.

***Bombus / Nosema bombi* / Parasit / Wirtsspezifizität / Brut**

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