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Original article

Social parasitism in bumble bees (Hymenoptera, Apidae): observations of *Psithyrus sylvestris* in *Bombus pratorum* nests

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Summary — Females of *Psithyrus sylvestris* (Lep) were introduced into free foraging colonies of their host *Bombus pratorum* (L) and interactions of hosts and parasites during the introduction period, and their behaviour during colony development were studied. The reactions of the host bees to the introduction of social parasites in 3 observed colonies ranged from aggressive to non-aggressive behaviour. *Psithyrus* females cohabited with host bees for several weeks following their introduction. They did not behave aggressively towards either host queens or workers, although they showed a head-rubbing behaviour, which we interpreted as dominance behaviour, possibly related to pheromone transfer. In all the observed colonies, hosts and social parasites reproduced. Host brood was reared to adults only from eggs laid prior to the usurpation by *Psithyrus*, whereas *Bombus* eggs were destroyed thereafter. *B pratorum* queens emerged earlier or at the same time as drones. In contrast, *P sylvestris* seemed to favour protandry as a reproductive strategy, with an earlier emergence of males than females. The colony with the lowest level of aggressiveness produced the greatest number of *Psithyrus* reproductives.

social parasitism / *Psithyrus sylvestris* / *Bombus pratorum* / dominance behaviour / aggressivity

INTRODUCTION

Social parasitism is widespread in the bumble bee (Hymenoptera, Apidae) where females of the genus *Psithyrus* are obligate social parasites in nests of their *Bombus* hosts. Although some parasite species have been well studied, reports about other host–parasite relationships have been rather confusing. Often they have not been supported by systematic observations or have been of an anecdotal nature. Observations range from aggressive behaviour of the social parasites towards their hosts (Hoffer, 1882, 1889; Sladen (cited in Free and Butler, 1959); Fisher, 1988) to peaceful cohabitation (Hoffer, 1889). Systematic studies have revealed that not only may the inter-

actions between social parasites and their hosts be species-specific (Röseler, 1972; van Honk *et al*, 1981a; Fisher, 1987), but that there may also be differences in the reactions of the hosts according to the age of the colony and the number of workers at the time of the introduction of the parasite (Fisher 1987, 1988).

Information about the interactions between several common European bumble bee species and their social parasites is scarce. This study provides observations about the hitherto undescribed relationship between a common bumble bee species, *Bombus pratorum* (L) and its social parasite *Psithyrus sylvestris* (Lep).

MATERIALS AND METHODS

To establish colonies of the host-species, nest-searching queens of *Bombus pratorum* were caught in the vicinity of Bochum, Germany, during March 1993, and placed in artificial hives in the Botanical Garden of the Ruhr University. The hives were checked every 3 d until the first workers emerged, when the combs were transferred to observation hives that could be heated separately, and kept at a temperature of 27–29°C. All the colonies were placed in an old bee house and the bumble bees were allowed to forage freely in the Botanical Garden.

Females of the social parasite *P sylvestris* were caught between the last week of March and the first week of May either on flowers, or while searching for nests of their host. They were kept in small wooden cages with access to sugar water and pollen for about 3 weeks until they could be introduced into colonies of their hosts.

The *P sylvestris* female was introduced into the colony on the following day after a *B pratorum* queen with her comb had been transferred into an observation hive. The parasite was placed in the entrance hole without disturbing the host bees. Screen wire was placed in front of the entrance hole of the nest, allowing only the small workers from the first brood to leave the nest, whereas the queen and the social parasite could not pass. Later, when larger workers hatched, this screen was removed. The nest was observed for 1 h following the introduction of the female and interactions, including agonistic behaviour between the social parasite and the host bees, were recorded. From the second day onward each colony was observed 2 or 3 times a day for 15 min at intervals of at least 1 h; the observation times were changed daily and from the entire observation time of 30–45 min per day the behaviour of the *Psithyrus* female and the *Bombus* queen on the comb was recorded. The behaviour was classified into 6 categories and the proportion of each particular category of behaviour during the observation time was calculated. The categories were: 'tending brood' (building new egg cells, manipulating wax and feeding larvae); 'incubating'; 'head-rubbing' (moving close to a host bee and gently rubbing against her head or thorax), which was only displayed by the social parasite; 'aggressive behaviour' (stinging, biting, and pushing of other bees), 'grooming' and 'inactivity' (when no classified activity could be observed).

The comb was sketched every day and photos were taken at periodic intervals till the end of colony development, thus the development of individual larval clumps could be traced backwards. Emergence of adult bees was recorded every day. To faciliate comparison among the colonies, 'time' was expressed in days, counted from the introduction day of the social parasite (the start day). Agonistic behaviour which consisted of attacks of the bees against each other (with mandibles agape), biting, pushing and attempted stinging was recorded and the number of aggressive actions per 15 min observation period were calculated from the daily observation periods.

RESULTS

Introduction of P sylvestris *females*

Introduction of social parasites was successful in 2 of the 3 host colonies. The third colony was transferred into the observation hive with a *Psithyrus* female already living in the nest. At the time of the introduction the colonies consisted of the queen, 5 or fewer workers, cocoons, larvae and various numbers of eggs. Since the behaviour of host bees towards parasites during the introduction differed among the 3 colonies, it is described in detail for each colony separately.

Colony 1

On April 20 a *Psithyrus* female was introduced into the colony, at which time the queen and 5 workers were present. The *Psithyrus* female first walked through the nestbox without entering the comb. The queen was very agitated, vibrated her wings and searched the nestbox until she encountered the *Psithyrus* female. She attacked and tried to sting her. The parasite did not defend herself by stinging, but tried to avoid the sting of the queen and to hide under the comb. The workers did not respond to the presence of the parasite. On the following day the *Psithyrus* had left the nest *via* a breach in the gauze covering the ventilation hole.

One day later, on April 22, a second attempt was made to introduce a *P sylvestris* female into the colony. She entered the nestbox immediately, walked through the nestbox, and tried to hide under the comb. The queen was very excited, ran through the nestbox and vibrated her wings, but did not attempt to sting the parasite, nor did the workers. The *Psithyrus* female did not show any aggression such as mauling or pushing the host bees. However, she displayed 'head-rubbing' behaviour, which was observed until the end of colony development in all 3 colonies. This behaviour consisted of moving close to a worker or to the queen and rubbing her head against the head and the body of the other female.

On the following day the *Psithyrus* female behaved restlessly, and frequently sat in front of the entrance hole as if to leave the nest. The wire mesh was removed and on April 23, 27 h after the introduction, the *Psithyrus* female left the nest, but was back the next morning. Neither host bees nor parasite showed any aggression. The *Psithyrus* female displayed the head-rubbing behaviour towards the workers as during the first hour of introduction.

Colony 2

In this colony the *Psithyrus* female had established herself in the nest prior to the transfer to the observation hive, before worker emergence. Hence the reactions of the host queen to the usurpation of this nest could not be observed. The comb was transferred the day after the emergence of the first workers when the colony contained the queen and 4 workers. The day of the transfer (April 24) was considered as the beginning of observation.

Colony 3

A *P sylvestris* female was introduced on April 19. At this time the queen and 3 of the 5 workers were present on the comb. The queen did not react to the presence of the parasite, but the workers were very aggressive. Within the first 20 min after the introduction, they attacked the parasite and tried to sting her. They followed her off the comb, pushed her and tried to shove her off the comb. The *Psithyrus* female did not attack host bees, but lifted her middle leg in the typical gesture of the bumble bees. Head-rubbing behaviour was first observed on April 20, the day following the introduction. Within 4 h of observations this behaviour was displayed 25 times towards different workers, 8 times towards the *Bombus* queen, and later only towards workers.

Behaviour of Bombus *queens and* Psithyrus *females on the comb*

The 3 *Psithyrus* females who had successfully usurped a host colony stayed there for 20, 28 and 33 d respectively. They incubated cocoons, manipulated the wax of larval clumps and built egg cups together with their hosts.

In each of the 3 colonies the *Bombus* queen spent large proportions of time tend-

ing brood, later an increasing amount of time was spent incubating cocoons. Interactions with her workers were only rarely observed. Only when she defended a new egg cell did she behave aggressively towards workers who came close to her eggs.

The *Psithyrus* female spent the same amount of time as the *Bombus* queen tending brood. However, the amounts of time she spent incubating brood decreased over time. At the end of colony development, she walked through the nest-box neither tending the remaining brood nor incubating cocoons. Both females spent approximately the same amount of time grooming themselves.

P sylvestris females never displayed mauling behaviour, which is accomplished by grabbing and attempting to sting workers and queens. Parasites showed head-rubbing behaviour, following the host bees across the comb. Sometimes the *Psithyrus* uncoiled her proboscis, rubbing it gently over the workers' back. This behaviour was observed particularly towards foragers who came back into the nest from a foraging trip.

Ethograms for *Psithyrus* females and *Bombus* queens were constructed showing the relative amounts of different actions during observation periods (fig 1).

Aggressive interactions

Agonistic behaviour of the social parasite was similar to the aggressive behaviour of the hosts, and consisted of biting, stinging and pushing. The host queen was seldom attacked either by her workers or by the *Psithyrus* female, even at times when workers displayed agonistic behaviour towards each other; the *Psithyrus* was frequently attacked at that time, and responded aggressively to attacks. However, neither host bees nor social parasites were killed during these encounters.

In colony 1 workers showed aggressive behaviour towards each other and towards the social parasite. Attacks were very violent and included attempted stinging. When a climax of aggressive interactions was reached with 15 attacks per 15 min, worker bees also attacked the *Bombus* queen (0.5 attack per 15 min). In colony 2 agonistic behaviour only reached a low level with an average of 1.5 attacks per 15 min. Aggressive actions here were not as violent as in colony 1 (0.5 to 9 attacks per 15 min), they merely consisted of pushing other bees away (fig 2).

Ejection of larvae was only recorded in colony 2, where large larvae were ejected on the 23rd and 27th day, some of them alive. This occurred at a time when only *Psithyrus* larvae were present in the nest, and aggressive behaviour was no longer recorded.

Social parasites were not pushed from the comb. However, in all 3 colonies the *Psithyrus* female did not stay in the nest until the end of colony development. Each left the nest, on the 20th day in colony 1, the 28th day in colony 2 and the 33rd day in colony 3. In contrast, the *Bombus* queens stayed on the comb till the 30th day, the 33rd day, and the 34th day respectively.

Colony development

Psithyrus females started egg-laying between the second and the seventh day following their introduction into host nests. This was verified by direct observation, and by observations of the developing brood. In all 3 colonies there was a peak in egg-laying between the fourth and the 18th day, when at least 1 new egg batch was recorded every day. Some egg batches and larval clumps were opened and destroyed, or did not grow because the larvae had not hatched or small larvae died. Later in colony development, larger larvae were not fed and consequently died (observed twice). Some egg cells built on old cocoons did not develop because they were removed together with the tops of the cocoons when the adult bees emerged.

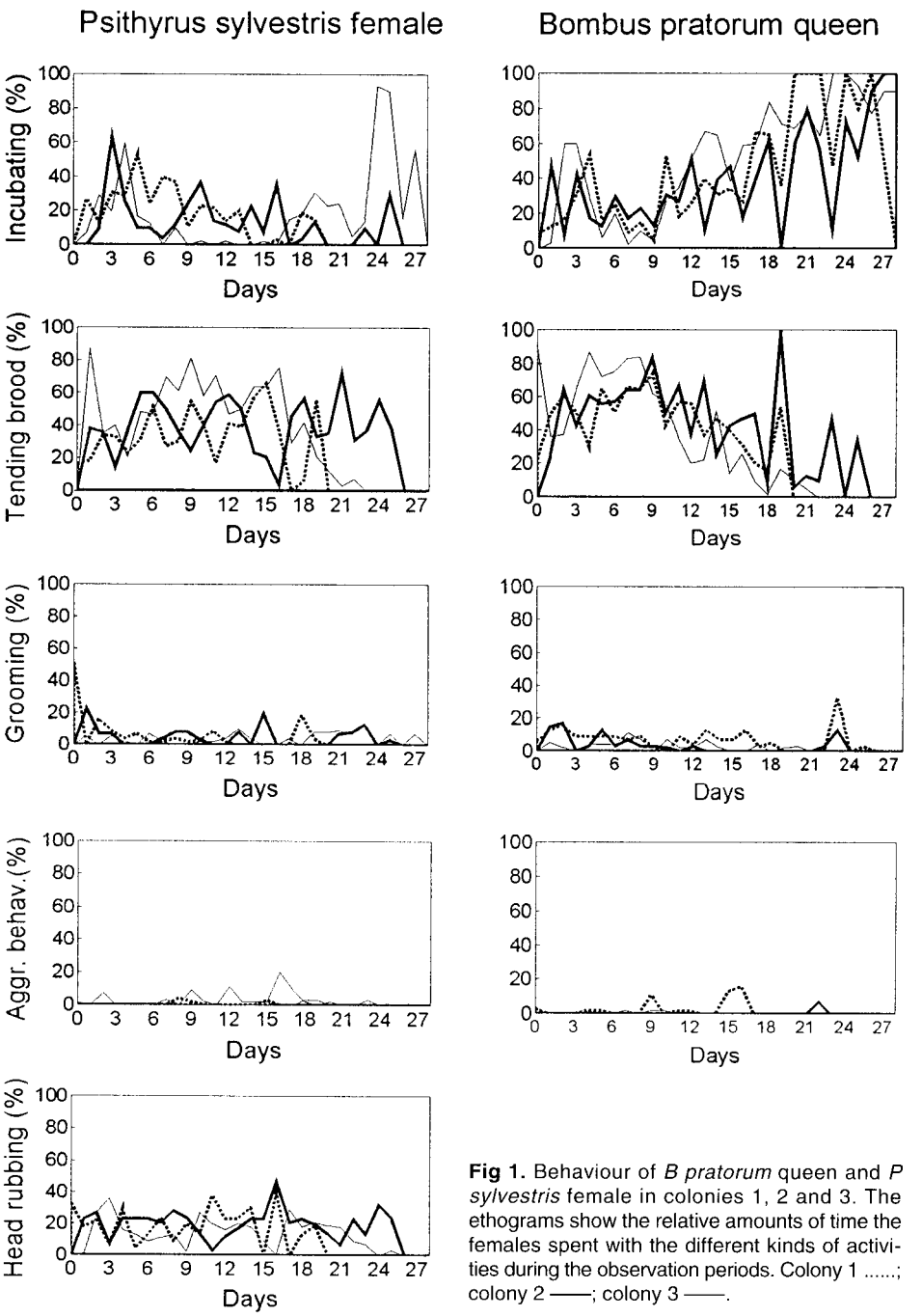

Fig 1. Behaviour of *B pratorum* queen and *P sylvestris* female in colonies 1, 2 and 3. The ethograms show the relative amounts of time the females spent with the different kinds of activities during the observation periods. Colony 1 .....; colony 2 ——; colony 3 ——.

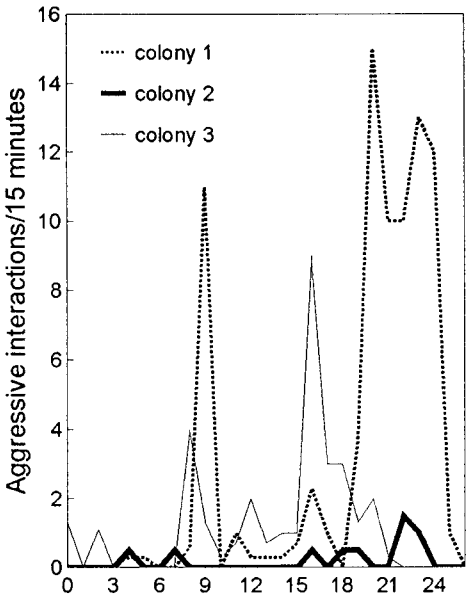

Fig 2. Aggressive interactions between *B pratorum* workers, the *Bombus queen* and the *P sylvestris* female in colonies 1, 2 and 3 from the day on which aggressions between workers started. The number of aggressive interactions per 15 min is calculated from daily observation periods.

The host queens continued to lay eggs even when *Psithyrus* brood was in the nest; brood from these eggs, however, was not reared to adults. Nonetheless, *Bombus* adults emerged only until the 22nd day after the introduction of the *Psithyrus* females (see table I). Considering the duration of pre-pupal stages for *Bombus* (18–19 d for workers (N = 12) and 16–24 d for drones (N = 22)), we can conclude that from *Bombus* eggs deposited later than 6 d after the introduction of the *Psithyrus* females (when they had laid their first eggs) no offspring was reared.

In all 3 colonies *Psithyrus* males and females did not emerge at the same time as *Bombus* adults, but 2–6 d after the last *Bombus* had emerged (*eg,* colony 1, fig 3). The durations of development for *Psithyrus* were found to be 14–19 d for drones (N = 21) and 22–27 d for females (N = 39). Total numbers and *Bombus/Psithyrus* ratios were different in all 3 cases. In addition, the colony which produced the greatest number of workers (colony 3) did not produce the greatest number of reproductive offspring (table II).

DISCUSSION

Reactions of host bees to the introduction of a *Psithyrus* female as observed in this study were different in all 3 observed colonies, although their size and the treatment of the *Psithyrus* females prior to introduction were similar.

Different types of usurpation of a *Bombus* colony by social parasites seem to exist

Table I. Period of emergence of *Bombus* and *Psithyrus* adults in the 3 observed colonies in days (calculated from the day of the introduction of the *Psithyrus* female).

Colony	*Period of emergence (d)*				
	Bombus pratorum			Psithyrus sylvestris	
	Workers	*Queens*	*Males*	*Females*	*Males*
1	0–19	8–17	18–19	31–32	25–33
2	0–20	–	19–22	29–42	25–41
3	0–18	16–22	17–20	26–36	24–38

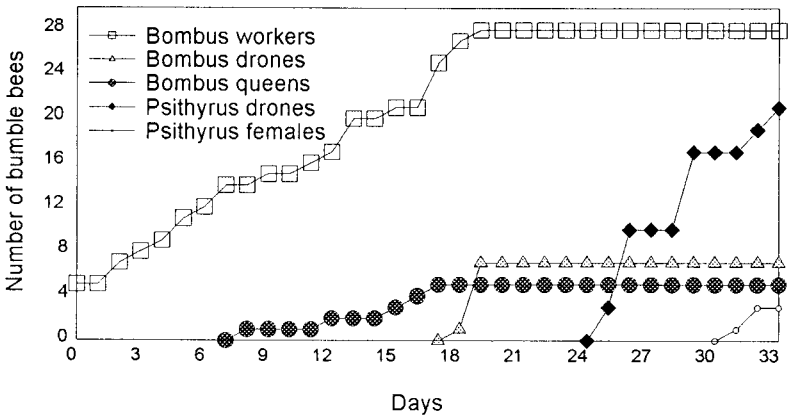

Fig 3. Emergence of *B pratorum* and *P sylvestris* adults in colony 1.

according to the *Bombus* and *Psithyrus* species involved: an aggressive type may occur as in *B terrestris* responses towards *P vestalis* (van Honk *et al*, 1981a; Fisher, 1988) and a non-aggressive type may occur between *B affinis* and *P ashtoni* (Fisher, 1987), *B agrorum* and *P campestris* (Hoffer, 1889; Fisher 1988) and *B lucorum* and *P bohemicus* (Fisher, 1988).

Our sample size was too small to state definitely to which type of interaction *P sylvestris* belongs. Further investigations will be necessary. As we chose colonies of a size which seems to be attractive to *P sylvestris* females under natural conditions (Küpper and Schwammberger, 1992/1993), differences in the reactions of host bees to the introduction cannot be attributed to different colony sizes. However, it might be possible that the physiological condition of the *Psithyrus* females plays a role in their reception in the host nests, thus explaining to some extent the different responses we observed. *Psithyrus* females, which were held singly in cages with access to sugar-water and pollen for about 3 weeks, showed a behaviour similar to that of broody *Bombus* queens prior to egg-laying. Possibly this condition is favourable for the usurpation of the host nest.

Agonistic behaviour between hosts and parasites was only observed during a short period following the introduction of the *Psithyrus* female, and then a period with-

Table II. Number of adults in colonies 1, 2 and 3.

Colony	Bombus pratorum			Psithyrus sylvestris	
	No of workers	*No of queens*	*No of drones*	*No of females*	*No of drones*
1	28	5	7	3	21
2	29	0	17	20	40
3	42	6	19	28	3

out aggressions followed. Later, when workers started laying eggs, aggressive behaviour between the worker bees reoccurred. Aggressions also occur in non-parasitized colonies at the time when the dominance of the queen decreases and the workers start laying eggs (Röseler and Röseler, 1977; van Honk *et al*, 1981b; Duchateau and Velthuis, 1988).

P sylvestris females did not show agonistic behaviour towards the host females during the first part of colony development prior to the competition point (for definition of the competition point, see Duchateau and Velthuis, 1988), and they only defended themselves when attacked. None of the queens were killed or seriously molested, in contrast to colonies invaded by *P rupestris* and *P vestalis* (Sladen, cited in Free and Butler 1959) and *P citrinus* (Fisher, 1984). Moreover, the queens were not pushed from the comb as observed in *P vestalis* invasions (van Honk *et al*, 1981a).

Mauling, a dominance behaviour described for different *Psithyrus* species (Free and Butler, 1959; Alford, 1975), *P ashtoni* (Fisher, 1983a, 1987), *P vestalis* (van Honk *et al*, 1981; Fisher, 1988), *P bohemicus* (Fisher, 1988), and *P citrinus* (Fisher, 1984) was never observed in our colonies. Mauling is also not exhibited by *P campestris* (Fisher, 1988), and may not be a necessary usurpation behaviour.

The head-rubbing behaviour of the *P sylvestris* females described in this paper is identical to that described for *P citrinus* in North America (Fisher, 1983b). Its function is unknown, and may involve pheromonal communication. Further investigations will be made to show to what extent workers might be influenced by this behaviour.

Free and Butler (1959) suggested that *Psithyrus* brood was tended only by *Bombus* workers without the help of the *Psithyrus* female. In the observed colonies *P sylvestris* females cared for her brood as do *P vestalis*, *P bohemicus* and *P campestris* (Fisher, 1987, 1988). This was previously suggested by Hoffer (1889) for various *Psithyrus* species. As host females and parasites both built the waxen envelopes of the egg batch, the *Psithyrus* egg batch could not be distinguished from the *Bombus* egg batch, as in the case of *B affinis* and *P ashtoni* (Fisher, 1987) and *B lucorum* and *P bohemicus* (Fisher, 1988). Observations of *B pascuorum* and *P campestris*, where egg batches of the 2 species cannot be distinguished either, suggest the possibility that some species may build their egg batches together as did the bumble bees observed in this study.

Although *Bombus* queens and, probably, workers laid eggs while parasites were present, *Bombus* adults were only reared from the brood already present at the time of introduction of the social parasites, or from eggs laid before the *Psithyrus* females started egg-laying. *Psithyrus* females of different species interfere with the reproduction of their hosts by destroying egg batches, eating eggs, and destroying larvae (Sladen and Plath, cited in Free and Butler, 1959; Alford, 1975; van Honk *et al*,1981; Fisher, 1987, 1988; von Hagen, 1988). Although not observed in the 3 colonies described in the present paper, we tend to assume that egg-eating also took place here. This is inferred from recent observations of other colonies in which egg-eating and destroying of larvae were recorded (Küpper, unpublished data).

In all 3 colonies both *Bombus* and *Psithyrus* females had reproductive success. Fisher (1985) and Alford (1975) have assumed that the quantity of reproductives is related to the number of workers in the colonies. Whether there exists such a correlation in *B pratorum* and *P sylvestris* cannot yet be decided. In this study the colony with the largest cohort of workers did not produce the greatest number of reproductive offspring. However, there seems to be a relationship between the level of aggressiveness and the reproduction. The colony

with the smallest amount of aggressive interactions produced the greatest number of *Psithyrus* reproductives. As in other *Psithyrus/Bombus* relationships (Fisher, 1987), control of the workers may be more important than resource quantity in dictating parasite reproductive success.

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Résumé — Le parasitisme social chez les bourdons (Hymenoptera, Apidae) : observations de *Psithyrus sylvestris* dans des nids de *Bombus pratorum*. Le parasitisme social est largement répandu chez les bourdons : les femelles du genre *Psithyrus* sont des parasites sociaux obligés des nids de leurs hôtes, les *Bombus*. Généralement une espèce de *Psithyrus* préfère une espèce de *Bombus* donnée. Cette étude fournit des informations concernant les relations non encore étudiées d'un bourdon commun, *Bombus pratorum* (L), et de son parasite social, *Psithyrus sylvestris* (Lepeletier). Des femelles de *P sylvestris* ont été introduites dans des colonies de leur hôte *B pratorum* composées d'une reine et de 5 ouvrières maximum. Les abeilles hôtes ont réagi à l'introduction des parasites sociaux par des comportements agressifs et non-agressifs. Aucune des femelles de *Psithyrus* n'a été tuée. Elles n'ont pas réagi de façon agressive aux attaques mais ont essayé d'éviter le contact avec leurs hôtes. Le comportement agressif des abeilles hôtes avait cessé plusieurs heures après l'introduction. Les agressions ont repris plus tard dans le cycle de la colonie, d'abord entre les ouvrières, puis avec le parasite. La proportion d'interactions agressives a varié d'une colonie à l'autre (fig 2). Les femelles de *P sylvestris* ont présenté un comportement de «frottement de la tête» : elles s'approchaient d'une abeille hôte, reine ou ouvrière, et frottaient doucement leur tête, le proboscis souvent étendu, contre la tête et le thorax de celle-ci. Nous interprétons cela comme un comportement de dominance, peut-être lié à un transfert de phéromone. Les femelles de *Psithyrus* ont cohabité plusieurs semaines avec les abeilles hôtes et ont pris part aux soins du couvain (fig 1). Dans toutes les colonies étudiées les hôtes aussi bien que les parasites se sont reproduits (tableau II), mais les abeilles hôtes n'ont été élevées qu'à partir d'œufs pondus avant les premiers œufs de *Psithyrus*. Par la suite les œufs de *Bombus* ont été détruits. Le nombre d'ouvrières dans une colonie n'a pas été corrélé avec la descendance des *Psithyrus*. Néanmoins la colonie la moins agressive a produit le plus grand nombre d'individus reproducteurs de *Psithyrus*. Il se peut donc que la proportion d'interactions agressives influence le succès reproducteur des parasites.

***Psithyrus sylvestris* / *Bombus pratorum* / parasitisme social / relation hôte–parasite / dominance/ agressivité**

Zusammenfassung — Sozialparasitismus bei Hummeln (Hymenoptera, Apidae): Beobachtungen von *Psithyrus sylvestris* in Nestern von *Bombus pratorum*. Sozialparasitismus ist bei Hummeln weit verbreitet: Weibchen der Gattung *Psithyrus* sind obligate Sozialparasiten in Völkern der Gattung *Bombus*, die einzelnen Arten sind spezialisiert auf einen oder wenige Wirte. In dieser Studie wird das Verhalten von *Psithyrus sylvestris* (Lep) in Völkern ihres Wirtes *Bombus pratorum* (L), die Reaktionen des Wirtes auf den Sozialparasiten sowie die Entwicklung der parasitierten Völker

untersucht. Die *Psithyrus sylvestris*-Weibchen wurden in frei fliegende Völker eingesetzt, die aus der Wirtskönigin und fünf oder weniger Arbeiterinnen bestanden. Die Reaktion der Wirte auf das Einsetzen reichten von aggressiv bis zu völliger Nichtbeachtung des Sozialparasiten. In keinem Falle wurde das *Psithyrus*-Weibchen getötet, es verhielt sich passiv und versuchte, den Angriffen auszuweichen. Das aggressive Verhalten hörte nach wenigen Stunden auf, erst später setzten Aggressionen innerhalb des Volkes ein, die zwischen den Arbeiterinnen begannen und das *Psithyrus*-Weibchen einbezogen. Das Ausmaß dieser Aggressionen war in den untersuchten Völkern unterschiedlich hoch (Abb 2). Alle *Psithyrus*-Weibchen zeigten ein Verhalten, das wir als Dominanzverhalten, möglicherweise in Zusammenhang mit Pheromon-Transfer, interpretierten: das 'Kopfreiben', bei dem das Weibchen mit Kopf und manchmal mit ausgestrecktem Rüssel über eine Arbeiterin oder die Königin des Wirtsvolkes reibt. *Psithyrus sylvestris*-Weibchen blieben einige Wochen zusammen mit den Wirtsköniginnen im Nest und beteiligten sich an Brüten und Brutpflege (Abb 1). Alle parasitierten Völker produzierten sowohl *Bombus*- als auch *Psithyrus*-Geschlechtstiere (Tabelle II), wobei *Bombus*-Imagines nur aus Eiern aufgezogen werden, die vor der ersten Eiablage der *Psithyrus* gelegt worden waren. Später angelegte *Bombus*-Einäpfe wurden zerstört. Die Anzahl der geschlüpften *Psithyrus*-Nachkommen war nicht mit der Anzahl der Arbeiterinnen korreliert. Es scheint jedoch, daß das Ausmaß der Aggressionen innerhalb eines Volkes einen Einfluß auf die Anzahl der *Psithyrus* Nachkommen hat, so wurden in dem Volk mit dem niedrigsten Aggressionslevel die meisten *Psithyrus*-Nachkommen produziert.

***Psithyrus sylvestris / Bombus pratorum* / Sozialparasitismus / aggressives Verhalten / Dominanzverhalten**

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