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OBSERVATIONS ON THE BEHAVIOURS OF THREE EUROPEAN CUCKOO BUMBLE BEE SPECIES (*PSITHYRUS*)

R.M. FISHER (*)

Department of Zoology, S. Parks Road, Oxford, U.K. OX1 3 PS

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SUMMARY

Females of three European species of cuckoo bumble bees (*P. bohemicus, P. vestalis,* and *P. campestris*) were introduced into free-foraging laboratory colonies of their *Bombus* hosts (*B. lucorum, B. terrestris* and *B. pascuorum,* respectively). The colony development of one successfully parasitized colony of each bumble bee species was studied. *Psithyrus* females cohabited with host queens and workers, but monopolized brood development through oophagy, larval ejection and the attempted dominance of host bees. Some *Psithyrus* brood also was destroyed, and host bees in all three colonies were successful in rearing reproductive offspring. Prolonged social contact between *Psithyrus* females and their hosts, and the possibility of host reproduction in parasitized colonies, suggest that there is considerable opportunity for coevolutionary complexity in *Bombus - Psithyrus* relationships.

RESUME

Observations sur le comportement reproducteur de trois espèces de bourdons « coucou » européens (Psithyrus)

Nous avons introduit des femelles de trois espèces européennes (*P. bohemicus, P. vestalis* et *P. compestris*) dans des colonies de laboratoire de leur hôte *Bombus* (*B. lucorum, B. terrestris* et *B. pascuorum*) pouvant fourrager librement. Pour chaque espèce de bourdon, nous avons étudié le développement d'une colonie, où des parasites avaient été introduits avec succès. Les femelles *Psithyrus* ont cohabité avec les reines et les ouvrières hôtes, mais ont monopolisé le développement du couvain à travers l'oophagie, l'expulsion des larves, et les tentatives de dominer les bourdons hôtes. Une partie du couvain *Psithyrus* a été détruite aussi, et les bourdons hôtes des trois colonies ont réussi à élever du couvain de reproducteurs. Les contacts sociaux prolongés entre les femelles *Psithyrus* et leurs hôtes, ainsi que la possibilité de reproduction de l'hôte au sein des colonies parasitées semblent indiquer que des complexités coévolutives dans les rapports *Bombus-Psithyrus* ne sont pas rares.

(*) Present address: Department of Botany and Zoology, Massey University, Palmerston North, New Zealand.

INTRODUCTION

Nest parasitism is expressed in a variety of diverse forms in bees, ranging from the usurpation of nest burrows of solitary bees to social parasitism in more advanced species. In this latter group, including the allodapine (Anthophoridae) and bumble bee (Apidae : *Psithyrus* and *Bombus*) parasites, there may be prolonged social contact between the parasite and its hosts (MICHENER, 1974). Intimacy of this sort can be studied as a means of discovering the ways in which colony social organization is maintained, and in turn manipulated by parasites for their own reproductive benefit (FISHER, 1987 *a*, *b*).

Despite the answers that studies like these provide about such questions as the acquisition and maintenance of reproductive control, the importance of colony size, and the allocation of colony resources, there is a surprising paucity of data on the behaviour of bee social parasites. For example, the behaviour of only one of the twelve European *Psithyrus* species has been described in detail (*P. vestalis* Geoffroy: VAN HONK *et al.*, 1981) although *Psithyrus* is a common and conspicuous element of the fauna. Observations of *Psithyrus* biology first made by HOFFER (1888) and SLADEN (1912), and those of VAN HONK *et al.*, (1981), suggest that the invading *Psithyrus* female effectively replaces the *Bombus* queen, although the extent of queen-parasite cohabitation and how parasites control host colony development are unknown. In this study, the reproductive biologies of the following three European species of *Psithyrus* were examined: *P. bohemicus* Seidl, *P. vestalis* Geoffroy, and *P. campestris* (Panzer). The recorded bumble bee hosts for each parasite are, respectively, *B. lucorum* L, *B. terrestris* L, and *B. pascuorum* (Scopoli), (ALFORD, 1975).

METHODS AND MATERIALS

Females of *P. bohemicus*, *P. vestalis* and *P. campestris* were field-caught in the vicinity of Oxford and Manchester, England, during the last week of May, as they searched for host nests. They were maintained in small wire cages with access to sugar-water and pollen until they were introduced into host nests. Colonies of *B. terrestris* and *B. lucorum* were reared in the laboratory from queens caught nest-searching during the first week in May. One nest of *B. pascuorum* was collected from the field on 22 June. At the time of collection it contained the queen and 24 workers. All the nests were kept in observation hives in a room at 24°C, with access to the outside through wire mesh flight tunnels.

Each *Psithyrus* female was introduced under red light, by placing the parasite beside the comb in the nest box, without disturbing the colony. Following its introduction, the interactions between the parasite and host bees were recorded for one hour. *P. bohemicus* females were introduced into five *B. lucorum* colonies, each containing from 4 to 12 workers and a queen (one introduction per colony). *P. vestalis* females were introduced into two *B. terrestris* nests containing three and seven workers respectively as well as a queen. Finally, two *P. campestris* females were introduced in succession into the single *B. pascuorum* colony, which contained 32 workers.

Introductions were judged to be successful if the *Psithyrus* female remained in the nest for at least 24 h. These colonies were observed under red light for 15 minutes each day (at various times) until the end of colony development. During each observation period the behaviours of the parasite and host bees were recorded. A map of the comb was drawn every other day, indicating the presence of egg cells, larval clumps and cocoons. In this way, the fate and development of egg cells and larvae could be determined retrospectively.

RESULTS

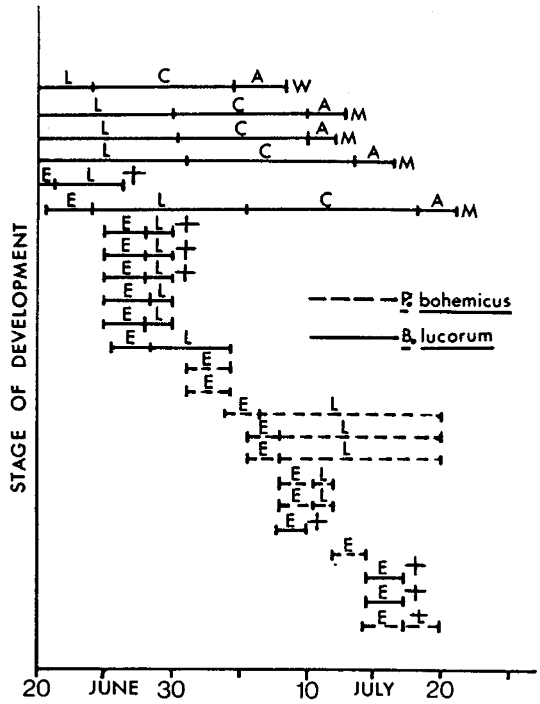
Introduction success

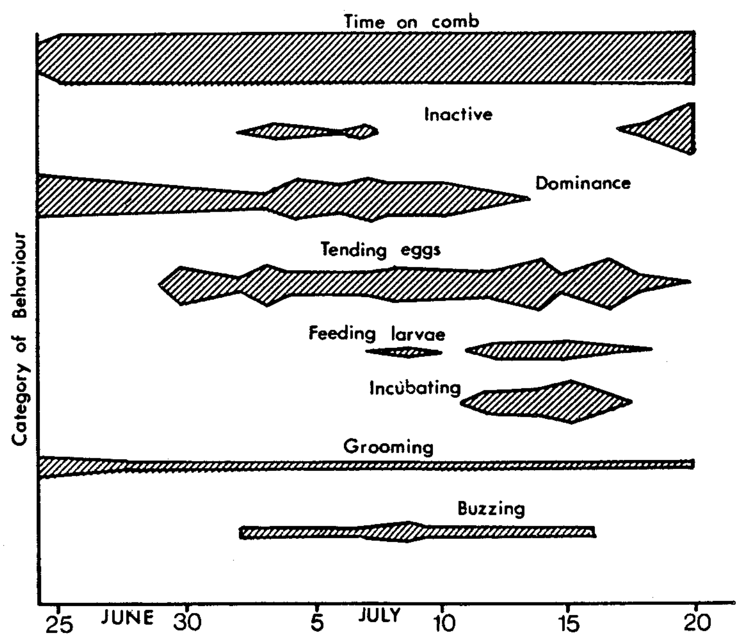
Considerable difficulty was encountered in introducing *Psithyrus* females, either because the parasites would not stay in the host nest or because they were attacked and killed by host bees. Only one of five *P. bohemicus* females, introduced into separate colonies, stayed in a *B. lucorum* nest, despite the consistent lack of animosity displayed by host bees towards them. Host queens did not respond to *P. bohemicus* females in any noticeable way, and workers did not attack them during the initial 1 h introduction period.

In contrast, queens and workers of *B. terrestris* attacked *P. vestalis* females. In one of two colonies, all three workers and then the queen attempted to sting the parasite. The *Psithyrus* female mauled the queen, which then left the nest. The queen returned three minutes later, but continued to leave the comb at the approach of the parasite. The *P. vestalis* female left the nest after 19 minutes and did not return. Similar behaviour was exhibited by host bees in the other nest; both workers and the queen attacked the parasite, after which the queen temporarily abandoned the nest. The *P. vestalis* female mauled workers and the queen. By the end of the 1-h introduction period, no animosity by host bees was evident, and the host queen and parasite jointly occupied the comb.

Similarly, the first *P. campestris* female was attacked by host workers as soon as she was introduced. Workers formed a ball around the parasite as they attempted to sting her. The queen left the comb, and stayed at the entrance of the nest for seven minutes. Although she then returned to the comb, she did not attack the *Psithyrus* female at any time during the attempted introduction. A total of seven workers (22 % of the total worker force) were stung and killed by the parasite before it was killed, 35 minutes after introduction.

One hour later, the second, *P. campestris* female was introduced into the same nest. Prior to this introduction, nest material (dry grass) was added to the nest to provide the parasite with a possible refuge from worker attack. However, the responses of the parasite and host bees were similar to that observed during the first introduction: the queen abandoned the


STAGE OF DEVELOPMENT
P. bohemicus
B. lucorum
L C A W
L C A M
E L
E L C A M
20 JUNE 30 10 JULY 20


Category of Behaviour
Time on comb
Inactive
Dominance
Tending eggs
Feeding larvae
Incubating
Grooming
Buzzing
25 JUNE 30 5 JULY 10 15 20

comb while workers attacked the *Psithyrus* female. To assist the parasite in gaining access to the nest, all the workers were removed, leaving the queen and parasite on the comb. Neither of the two bees attacked the other, and they were observed incubating adjacent cocoons 15 minutes later. Five workers were reintroduced, 16 h later. These workers did not attack the parasite, and no further interspecific antagonism was observed.

P. bohemicus - B. lucorum **colony development**

The parasite female stayed in the *B. lucorum* colony for 28 days, from 24 June until her death on 22 July. An ethogram for this female was constructed (*fig. 1*), based on an analysis of daily observation periods. Eight categories of behaviour were quantified. These included the relative amount of time in each observation period during which the parasite was seen on the comb, irrespective of what type of behaviour it was exhibiting. "Inactivity" was defined as lack of movement. "Dominance behaviour" included any attempts by the *Psithyrus* female to push or maul host bees. Parasites "tended" their egg cells by defending them against host bee attack (see below), as well as feeding and incubating their developing offspring. Two other commonly observed behaviours were grooming and buzzing.

During the first few days of nest occupation the parasite appeared to attempt to establish a position of dominance by mauling and pushing the queen and workers. Mauling was accomplished by grabbing a bee as if to sting it, and then letting it go. Attempts to subordinate host bees in this way continued throughout colony development. Dominance behaviour was exhibited towards both queen and workers, although the queen received more attention from the parasite (62 % of total encounters directed at the queen versus 38 % toward all other adults (workers) combined). Host bees

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Fig. 1. — (top) Ontogeny of brood development in the parasitized *B. lucorum* colony. Horizontal lines indicate relative durations of development of individual clumps of eggs (E), larvae (L), cocoons (C), and periods of adult emergence (A). Adults which emerged were workers (W), males (M), or reproductive females (F). (+ denotes brood which the parasite was observed eating or ejecting). (Bottom) Ethogram of *P. bohemicus* reproductive behaviour. Depths of hatched areas indicate the relative amounts of time the parasite was engaged in the various behaviours during each observation period.

Fig.1. — En haut : ontogenèse du couvain dans les colonies parasitées de *B. lucorum*. Les lignes horizontales indiquent les durées relatives du développement des groupes d'œufs (E), des larves (L), des cocons (C), et les périodes d'émergence des adultes (A). Les adultes ayant éclos étaient soit des ouvrières (W) soit des mâles (M), soit des femelles reproductrices (F). (+ indique le couvain que nous avons vu être mangé ou expulsé par les parasites). En bas : Ethogramme du comportement reproducteur de *P. bohemicus*. La largeur des zones hachurées indique la durée relative des diverses activités des parasites pendant chaque période d'observation.

responded to the parasite by moving away, and did not attack at any time during or subsequent to parasite introduction.

Included under the heading of dominance behaviour were attempts by the *P. bohemicus* female to control brood development by eating host eggs and ejecting larvae. Larval ejection was first noticed on 28 June, four days before the parasite began to lay eggs. The parasite uncovered larvae and dropped them beside the brood clump. These larvae were subsequently picked up by workers and carried from the nest. If interrupted by the approach of a worker, the parasite ceased uncovering host brood and moved away. It then returned to the brood clump once the worker had resealed the waxen envelope surrounding each clump and left. Egg cells were treated similarly, although the eggs were eaten rather than ejected.

The development of individual brood clumps from egg cell to maturity in the parasitized *B. lucorum* colony is shown in *figure 1*. At the time of introduction, the nest contained developing *Bombus* worker and male brood. Some male and female brood clumps were left undisturbed by the parasite. As a result, the worker population increased from 8 at the time of introduction to 28 at the peak of colony development. In addition, a total of 20 *Bombus* males were reared from eggs laid before and during nest occupation by the *P. bohemicus* female.

Psithyrus egg cells were rougher in shape than those of hosts, and were constructed from wax collected from destroyed host egg cells and wax nectar pots. As *Psithyrus* eggs hatched, the parasite as well as the host workers fed the young larvae by regurgitating food collected from nearby pollen receptacles through the waxen envelope surrounding brood clumps. Notwithstanding the assistance it received from workers in caring for its offspring, the *P. bohemicus* female failed to reproduce because all of its offspring were eventually eaten or ejected by host bees (*fig. 2*). The *B. lucorum* queen lost dominance over her workers on 6-7 July (for quantification of queen dominance, see Fisher 1987 *a*), which coincided with the first loss of *Psithyrus* brood. The parasite attempted to protect its offspring by pushing host bees away from its egg cells while buzzing loudly, and by frequent examination of cells. However, this failed to protect its developing larvae from host attack. From 12 July onward, the *Psithyrus* female spent increasing amounts of time either incubating host cocoons, or inactive beside the comb. It died on 22 July.

The *B. lucorum* queen continued to lay eggs while the *Psithyrus* female was in the nest, and one worker also laid eggs on July 15. This brood was eaten by the *Psithyrus* female. The last host bees, including the queen and four workers, died on 26 July. Besides the host males that developed from eggs laid prior to parasite introduction, no other reproductive offspring of either species were reared.

Fig. 2. — *Psithyrus bohemicus* female in a nest of *Bombus lucorum.* The parasite is attempting to push a worker away from a destroyed egg cell, the remains of which can be seen atop a cocoon below the *Psithyrus* female.

Fig. 2. — Femelle de *Psithyrus bohemicus* dans un nid de *Bombus lucorum.* Le parasite tente de repousser une ouvrière à l'écart d'une cellule à œuf détruite, dont les restes, visibles, se trouvent sur un cocon au-dessous de la femelle *Psithyrus.*

P. vestalis - B. terrestris **colony development**

Like the parasitized *B. lucorum* nest, an extended period of nest cohabitation took place between the *P. vestalis* female and *B. terrestris* host bees, from 21 June until the parasite's death on 6 August (46 days). The *P. vestalis* female attempted to dominate the queen and workers by mauling and pushing them. It began to eject host larvae and eat eggs within a day of being introduced, and laid its first eggs on 27 June. Some host brood which was present in various stages of development at the time of nest usurpation were reared to adulthood (see *fig. 3*), including 25 workers and 19 host males. Dominance behaviour by the parasite diminished over time, although the *Psithyrus* female continued to guard its egg cells by pushing bees away from them and by mauling host bees. The parasite queen also incubated host and parasite cocoons at irregular intervals throughout colony development.

On 8 July, the host queen was found dead on the comb. The workers moved very rapidly about the comb, and the *Psithyrus* female was attacked

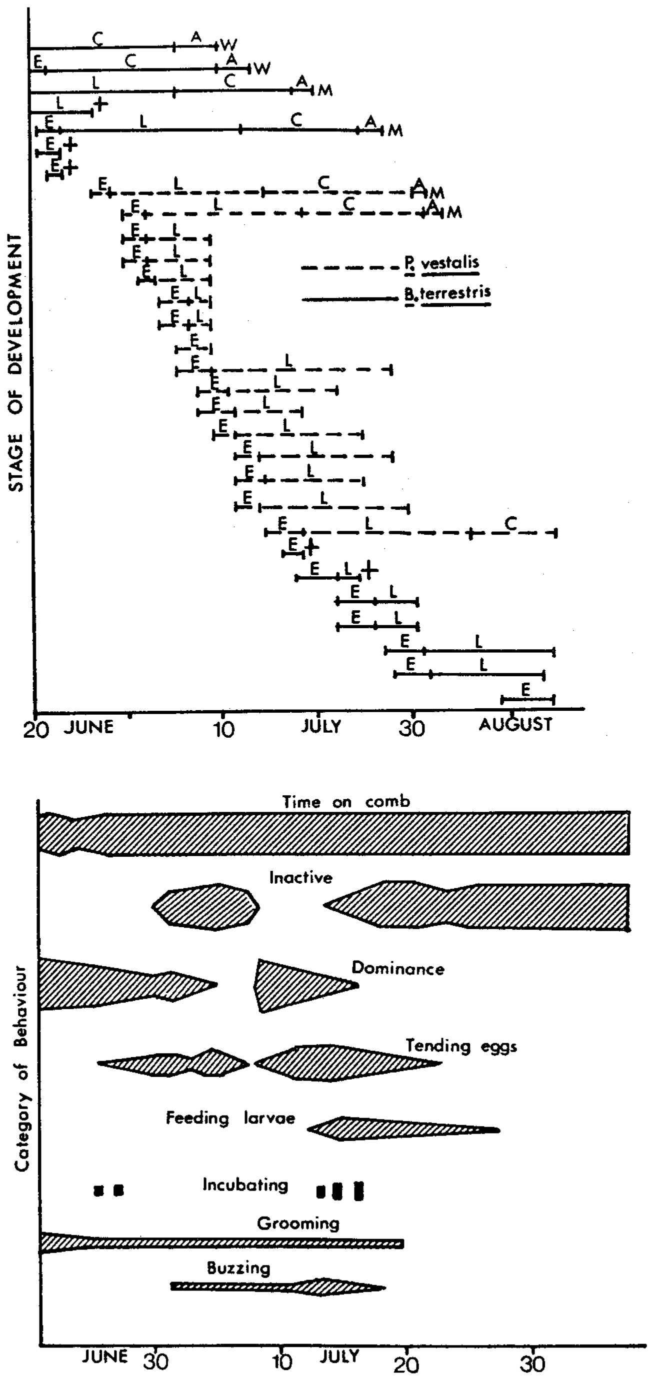

Fig. 3. — Brood development in the parasitized *B. terrestris* nest, and ethogram of the *P. vestalis* female. Legend as in figure 1.

Fig. 3. — Développement du couvain dans le nid parasite de *B. terrestris* et éthogramme de *P. vestalis* femelle. Légendes identiques à celles de la figure 1.

twice during the observation period. In addition, 6 of 11 *Psithyrus* brood clumps had been destroyed since the previous day (see *fig. 3*). *Psithyrus* dominance behaviour returned to levels comparable to those when the parasite was first introduced, but diminished again over the course of the next few days. Further loss of *Psithyrus* brood did not occur until July 20, after which all *Psithyrus* brood gradually were ejected, with the exception of brood from the first two egg cells constructed by the parasite. This loss occurred despite attempts by the parasite to protect offspring by pushing workers away from egg cells while buzzing loudly.

One attempt to reproduce by host workers was prevented when the *Psithyrus* female ate the eggs. Further brood loss occurred when workers ejected the larvae of other host bees. Workers guarded their brood, as did the *Psithyrus* female, by pushing and mauling other bees that contacted their egg cells.

In all, a total of 18 host males and 14 *P. vestalis* males were reared in the parasitized *B. terrestris* colony. The *Psithyrus* female became inactive towards the end of July, and died on 8 August. None of the remaining *Psithyrus* and *Bombus brood* were reared to adulthood.

P. campestris - B. pascuorum **colony development**

Following its introduction, and for long periods throughout its occupation of the comb, the most common behaviour exhibited by the *P. campestris* female was inactivity (*fig. 4*). It stayed beside the comb, periodically grooming itself for the first eight days (range = 1 to 5 grooming bouts/observation period), although increasing amounts of this apparent inactivity were spent on the comb, rather than beside it. On 30 June, the parasite began to interfere with host brood development by uncovering and ejecting host larvae, and by eating eggs. Unlike the behaviour of the other two *Psithyrus* females, no pushing or mauling behaviour accompanied the manipulation of host brood, or any other parasite activity.

Like the other parasitized colonies, some host brood was allowed to develop, resulting in an increase in the number of workers from 5 on the date of introduction to a peak of 45 on 14 July. The first destruction of host brood coincided with the appearance of parasite egg cells on 2 July (*fig. 4*). These egg cells were constructed with the wax of destroyed host egg cells, although not necessarily on the same site (only 1 of 4 egg cells). Unlike those of *P. vestalis* and *P. bohemicus* females, *P. campestris* egg cells were difficult to distinguish from host egg cells. They were identified by later examination of brood maps, and by the behaviour of the *Psithyrus* female. It stayed near its egg cells until the eggs hatched, periodically manipulating the wax of each cell with its jaws.

The *P. campestris* female collected wax from *Bombus* larval clumps and nectar pots and added it to its own brood clumps as larvae increased

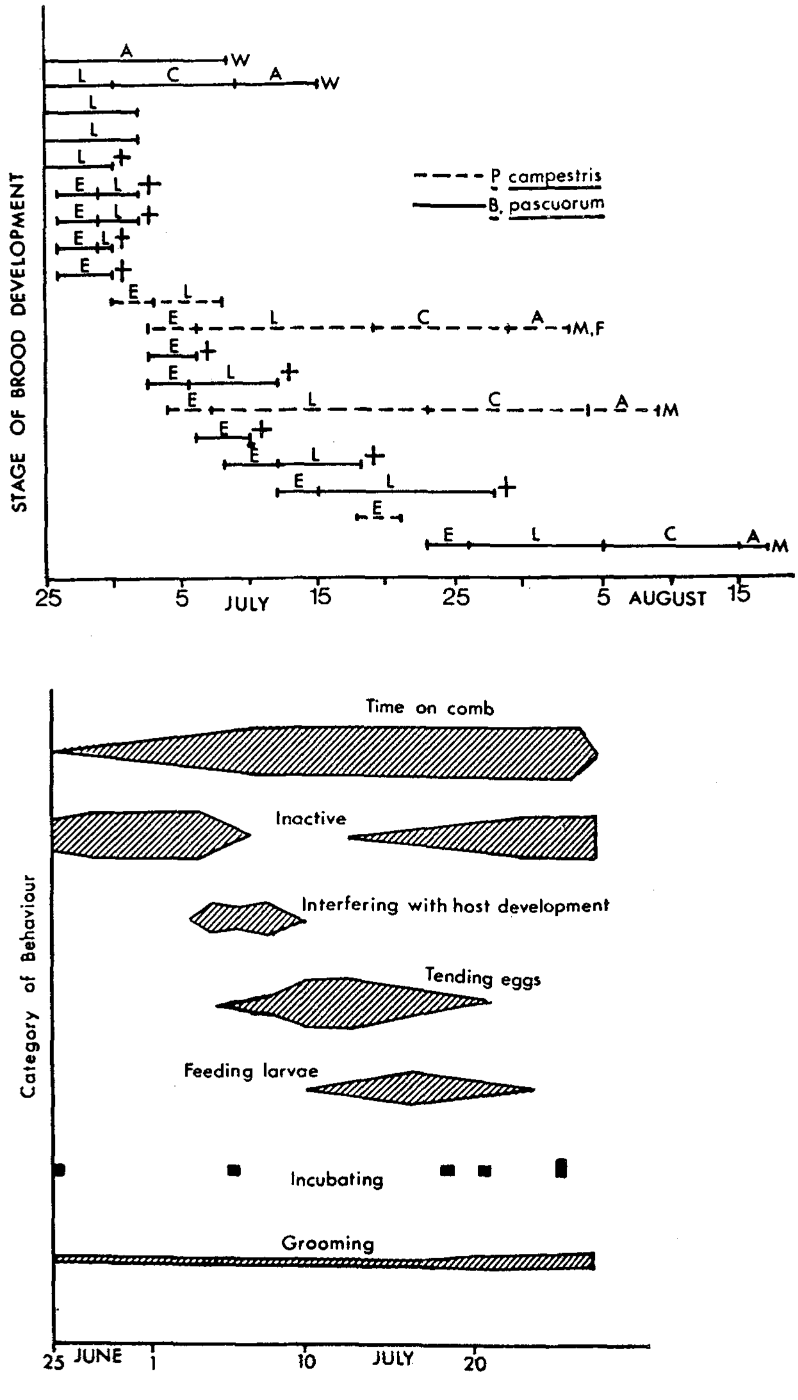

Fig. 4. — Brood development in the parasitized *B. pascuorum* nest, and ethogram of the *P. campestris* female. Legend as in figure 1.

Fig. 4. — Développement du couvain dans le nid parasité de *B. pascuorum* et éthogramme de *P. campestris* femelle. Légendes identiques à celles de la figure 1.

in size. *Psithyrus* larval development was similar to that of host bees: larvae were enclosed in waxen envelopes containing outpouchings (= pockets *sensu* SLADEN 1912 when describing the brood development of members of the bumble bee subgenus to which *B. pascuorum* belongs). Pollen was deposited in these pockets by returning foragers. The parasite and workers collected the pollen and fed it to larvae via regurgitation, after biting a small hole in the top of larval clumps. The parasite never fed host larvae It did however exhibit a novel method of caring for its own larvae. In 30% of all observed feedings by the *P. campestris* female, it chewed a hole in the tops of larval clumps, and then moved away from the clump. Upon encountering these open holes, workers regurgitated into the clump and resealed it. In this way, the amount of feeding care carried out by the parasite was reduced.

During the early and middle stages of colony development, two *Psithyrus* brood clumps were destroyed, either as eggs or young larvae. The relative involvement of the queen and workers in this destruction was unknown. On 22 July, the first instance of worker oophagy was observed. From this day until 27 July, the workers harassed the *Psithyrus* female and each other by pushing other bees off the comb. On 22 July (33 days after introduction), the *P. campestris* female was found outside the nest, in the front portion of the observation hive. An attempt was made to reintroduce it, but it was attacked by workers, and pushed off the comb. The next day, the *Psithyrus* female was once again found outside the nest. Although it was reintroduced, it was again pushed off the comb by workers and did not return.

The host queen continued to occupy the nest with her workers. She was observed laying eggs twice aferwards, and the *B. pascuorum* colony succeeded in rearing 16 males, in addition to 10 male and 3 female *Psithyrus*.

DISCUSSION

The results of this study are noteworthy in the way that a small sample size has produced observations which contradict the anecdotal studies of *Psithyrus* behaviour by early students of bumble bee biology. These early views of *Psithyrus* females as unwelcome bumble bee guests which usurp the queens' role, contribute nothing towards brood development (either their own or that of their hosts), and direct colony resources exclusively towards their own reproduction have been perpetuated in the literature (e.g. WILSON, 1971), and do not emphasize the potential longevity and complexity of interactions between a given *Psithyrus* female and its hosts. To some extent, this study is also at fault, in that a lack of replication may lead to erroneous conclusions about the general pattern of *Psithyrus* reproduction. Tempered by the cautionary view that variability in host-parasite relationships can and does occur (see FISHER, 1987 *a*), the major findings of this study may nonetheless help to dispel the apparent simplicity of *Psithyrus-Bombus* interactions, and may be summarized as follows:

Queen-parasite and worker-parasite cohabitation may be extensive in duration

In some species, including those of this study, and in others observed by Webb (1961: *P. variabilis*) and FISHER (1987 *a: P. ashtoni*), cohabitation can persist throughout colony development, although the *Psithyrus* female and its brood can be at great risk from attack by the host queen and workers. Indeed, the two *P. vestalis* females observed by VAN HONK *et al.*, (1981) both were ejected from their respective host colonies by queenless workers. The success of the *P. vestalis* female of this study in quelling attempts by host workers to expel it after the death of the queen may have been a function of colony size (only 15 workers were present at the time of queen death), and the free-foraging conditions under which the bees were kept. Confined laboratory workers like those studied by VAN HONK *et al.*, (1981) experience unnatural longevity and maximal opportunities for ovarian growth and subsequent increases in dominance behaviour (TOD, 1986).

Psithyrus **females contribute a substantial amount of parental care to their offspring.**

This care may included protection from host attack, feeding, and incubation of cocoons. The time spent by parasites in apparent inactivity may represent a time pool which can be allocated to the varying needs for dominance, egg-laying and brood care. While a parasitical lifestyle has reduced brood care behaviours by *Psithyrus* females, these behaviours can be evoked should the need arise. As pointed out by G.C. EICKWORT (personal communication), brood care by parasites may be especially important if *Psithyrus* females are attempting to rear reproductive offspring before their hosts normally do so, or in colonies of host species in which *Psithyrus* reproductives are larger than those of hosts.

Parasite control over brood development is not absolute, and does not necessarily involve overt dominance by the parasite

Control of brood development by the *P. campestris* female, for example, was accomplished not by behavioural dominance and suppression of egg laying by hosts, but by destruction of host brood. The *B. pascuorum* queen continued to lay eggs, and monopoly of brood-rearing was achieved by the *P. campestris* female through oophagy and larval ejection. Similarly, *B. terrestris* and *B. lucorum* host bees continued to lay eggs after *Psithyrus* females had been introduced. Buzzing by parasites may assist them in advertising a position of behavioural dominance within a nest (FISHER and

WEARY, 1988). Although some species of *Psithyrus* (and some facultative bumble bee social parasites) appear to be capable of suppressing ovarian development in queenless workers (FISHER 1984, 1987 *b*), such an ability is not a prerequisite for reproductive success.

Because parasite control is not absolute, host bees have a chance to reproduce in parasitized nests

Observations have been made of host reproduction in bumble bee nests parasitized by the European species *P. sylvestris* (HOFFER, 1888), and *P. bohemicus* (CUMBER, 1949) and in North America in nests parasitized by *P. variabilis* (WEBB, 1961), *P. ashtoni* (FISHER, 1987 *a*), *P. suckleyi*, *P. insularis* and *P. fernaldae* (K.W. Richards, personal communication). Some of this reproduction can be explained as a consequence of the conflict between the queen and her workers over the rearing of queens and males (TRIVERS and HARE, 1976). If queens are unable to suppress worker ovarian development, workers may engage in oophagy as they attempt to rear male offspring (FREE *et al.*, 1969). The queen may even be killed or expelled (VAN HONK *et al.*, 1980). Host reproduction in the *B. pascuorum* colony was achieved after the *P. campestris* female was ejected by fecund workers, following the loss of queen dominance. Similarly, *B. terrestris* workers attempted to reproduce, and ejected large quantities of *Psithyrus* brood after their queen was dead.

The failure of *Psithyrus* females to reproduce in parasitized colonies is not uncommon (see the data for *P. ashtoni* in FISHER, 1987 *a*), and may be due in part to the destruction of brood by the host queen and her workers. It has been sugested that *Psithyrus* females distinguish their eggs from those of hosts by differences in surface sculpting (C. O'TOOLE, personal communication, and see SALKELD (1978) for electron micrograph studies of *Psithyrus* and *Bombus* eggs). If such a difference in egg morphology exists, one might expect that selection would favour similar discriminatory powers by host bees which reproduce in parasitized colonies.

Bumble bee nest parasitism involves potentially complex interactions between parasite and host. The response of host bees to parasites and their brood suggests that there is considerable scope for coevolution in these relationships. However, further studies of parasite invasion frequency and success, and host reproduction will be required before the magnitude and scope of these coevolutionary forces can be determined.

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References

ALFORD D.V., 1975. — Bumblebees, *Davis-Poynter*, publ., London, 352 pp.

CUMBER R.A., 1949. — Humble-bee parasites and commensals found within a thirty mile radius of London. *Proc. R. ent. Soc. Lond., A 24*, 119-127.

FISHER R.M., 1984. — Dominance by a bumble bee social parasite (*Psithyrus citrinus*) over markers of its host (*Bombus impatiens*). *Anim. Behav., 32*, 303-304.

FISHER R.M., 1987 a. — Queen-worker conflict and social parasitism in bumble bees. *Anim. Behav., 35*, 1026-1036.

FISHER R.M., 1987 b. — Temporal dynamics of facultative social parasitism in bumble bees. *Anim. Behav., 35*, 1628-1636.

FISHER R.M., WEARY D.M., 1988. — Buzzing bees: communication between bumble bee social parasites (Hymenoptera: Apidae) and their hosts. *Bioacoustics, 1*, 3-12.

FREE J.B., WEINBERG I., WHITEN A., 1969. — The egg-eating behaviour of *Bombus lapidarius L. Behaviour, 35*, 313-317.

HOFFER E., 1888. — Die schmarotzerhummeln Steiermarks. Lebensgeschichte und beschreibung derselben. *Mitt. naturw. Ver. Steirermark, 25*, 82-158.

HONK C.G.J. VAN, VELTHUIS H.H.W., RÖSELER P.F., MALOTAUX M.E., 1980. — The mandibular glands of *Bombus terrestris* queens as a source of queen pheromones. *Ent. Exp. & Appl., 28*, 191-198.

HONK C. VAN, RÖSELER P.F., VELTHUIS H., MALOTAUX M., 1981. — The conquest of a *Bombus terrestris* colony by a *Psithyrus vestalis* female. *Apidologie, 12*, 57-67.

MICHENER C.D., 1974. — The Social Behavior of the Bees. *Harvard Univ. Press*, publ., Cambridge, 404 pp.

SALKELD E.H., 1978. — The chorionic structure of the eggs of some species of bumblebees (Hymenoptera: Apidae: Bombinae), and its use in taxonomy. *Can. Entomol., 110*, 71-83.

SLADEN F.W.L., 1912. — The humble-bee, its life history and how to domesticate it. *Macmillan and Co.*, publ., London, 283 pp.

TOD C., 1986. — Socio-economic effects on colony size in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae). *MSc Thesis, Massey University*, New Zealand, 85 pp.

TRIVERS R.L., HARE H., 1976. — Haplodiploidy and the evolution of the social insects. *Science, 191*, 249-263.

WEBB, 1961. — The biology of the bumble bees of a limited area in eastern Nebraska. *Ph.D. thesis, Univ. Nebraska*, Lincoln, 337 pp.

WILSON E.O., 1971. — The Insect Societies. *Harvard Univ. Press, publ.*, Cambridge, Mass, 548 pp.