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Effects of early experience on interactions between the parasite ant *Formicoxenus provancheri* and its host *Myrmica incompleta* (Hymenoptera: Formicidae)

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Abstract. The influence of early experience on interspecific recognition in the parasite ant *Formicoxenus provancheri* and its host *Myrmica incompleta* was studied by investigating the interactions of each species with adults and with larvae. The adults tested were reared heterospecifically (host and parasite together) or homospecifically (with or without mature conspecific ergates). Adults of each species were tested with both conspecific and allospecific larval brood. Homospecifically reared *M. incompleta* were more aggressive towards their parasite than when reared with the latter. *Formicoxenus provancheri* were always attracted to *M. incompleta* brood and adults. This parasite thus prefers to rear the host-brood, especially when the parasite's early experience has been either of its own species or where it has been reared alone.

Ants of the genus *Formicoxenus* are social parasites in colonies of other ant species. Their nests may be established at the edge of or in the wall of the nest of their host, but the parasite always rears its brood in chambers separate from the brood chambers of the host. *Formicoxenus* nevertheless are completely dependent on their host for feeding (Francoeur et al. 1985). This form of social parasitism has been named xenobiosis (see Buschinger 1986).

Until recently behavioural studies had been made only on *F. nitidulus* and *F. diversipilosus*. Both of these are found in nests of species in the *Formica rufa* group. We studied the North American association of *Formicoxenus provancheri* with its host *Myrmica incompleta* using material collected in Quebec, Canada.

Adult *F. provancheri* are strongly attracted by *M. incompleta* and lick them very frequently. In the laboratory, under our experimental conditions, aggression between the species is rare and brief unless the species have been previously separated. Under these circumstances *F. provancheri* adopts an appeasement posture resembling sexual calling (Lenoir et al. 1989). However, in mother stock colonies, we observed frequent attacks by *F. provancheri* on *M. incompleta*, particularly on their antennae.

The intraspecific interactions of *F. provancheri* and *M. incompleta* adults have been described elsewhere (Lenoir et al., in press).

In the present study we carried out experiments on the development of interspecific recognition in order to elucidate the possible influence of early social experience on this phenomenon. We wanted to know whether young *M. incompleta* reared in the absence of the parasite would later accept *F. provancheri*, and whether homospecifically reared young *F. provancheri* would later accept *M. incompleta*, and consequently be able to parasitize it.

Our first concern was to analyse the interspecific behaviour of adult *M. incompleta* and *F. provancheri* and to discover the effect of rearing schemes on the development of aggressive behaviour. We then studied how adults of both species interact with conspecific or allospecific brood.

In *F. provancheri*, the laying 'queen' can be an inseminated worker, so the usual terminology for the castes is not suitable. We therefore use the terms ergates and gynes rather than workers and queens (cf. Loiselle & Francoeur 1988).

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Table I. Composition of the experimental groups

Group*	*Myrmica incompleta* 1 gyne 40 mature ergates and brood	*Formicoxenus provancheri* 1 gyne 10 mature ergates and brood	Newborn *M. incompleta* 40 ergates	Newborn *F. provancheri* 10 ergates	
1	+	+	−	+	MY+FO+
2	−	+	−	+	MY−FO+
3	+	−	−	+	MY+FO−
4	−	−	−	+	MY−FO−
5	+	+	+	−	MY+FO+
6	−	+	+	−	MY−FO+
7	+	−	+	−	MY+FO−
8	−	−	+	−	MY−FO−

*For example, group 1 is composed of 1 gyne, 40 mature ergates and brood of *M. incompleta* plus 1 gyne, 10 mature ergates, brood and 10 newborn *F. provancheri*. Groups 1–4: *F. provancheri* experimental groups. Groups 5–8: *M. incompleta* experimental groups.

METHODS

Ants were maintained in the laboratory at 20°C in petri dishes using the technique described by Alloway (1979). In control colonies (heterospecific stock cultures) the petri dishes contained a drinking trough and two circular nests, one for each species. We gave the *F. provancheri* nest an entrance of very small diameter so that *M. incompleta* were unable to enter. In homospecific colonies (homospecific stock cultures) each species was maintained in a separate single circular nest. Using ants from the stock cultures we created eight groups of experimental colonies (Table I). Four of these, two with each species, came from homospecific colonies. The homospecific colonies (*M. incompleta* and *F. provancheri*) were formed either by adding young ergates to nests containing conspecific gynes, mature workers and brood (groups 2 and 7) or by rearing newborn ergates alone (groups 4 and 8). Two groups of heterospecific colonies (groups 1 and 5) were formed by adding either young *F. provancheri* or young *M. incompleta* ergates to nests containing gynes, mature workers and brood of both species, in the same proportions as in homospecific colonies (groups 2 and 7). Two further groups of heterospecific colonies were formed by including young *F. provancheri* ergates in a *M. incompleta* colony (group 3) or by including young *M. incompleta* in a *F. provancheri* colony (group 6).

We amputated a hind tarsus of mature ants so that they could be distinguished from the young ergates.

All the tests (each of 15 min) were carried out in small petri dishes (50 mm diameter) with experimental groups from numerous colonies: we performed 10 tests per experimental group. Young ergates were tested 15 days after their emergence as it is known that when a sensitive period for post-emergence experience was observed, it is no longer than 10 days (Jaisson & Fresneau 1978; Jaisson 1985).

Interactions of Adults

Tests with F. provancheri

For each test, a single young *F. provancheri* ergate from a colony in one of the experimental groups 1–4 was placed in a small petri dish with five mature *M. incompleta* ergates. These *M. incompleta* were mature ergates taken at random from a homospecific stock culture. The behaviour of the *F. provancheri* ant and its interactions with *M. incompleta* ergates were recorded every 5 s during the first 5 min. After a further 15 min behavioural observations were continued for two additional 5-min periods, separated by a 15-min interval. Ten of these tests were conducted.

The behaviour of *F. provancheri* (previously described by Lenoir et al. 1989) was assigned to four categories.

(1) Aggression against *M. incompleta*: *F. provancheri* sometimes seize the limbs or antennae of their host. This behaviour appears relatively rarely in our experimental context.

(2) Aggression by *M. incompleta*: more frequent than category 1, and occasionally prolonged.

(3) Appeasement behaviour by *F. provancheri*: similar to that described for *F. nitidulus* (Staeger 1925). The ant raises its abdomen and extrudes the sting from which it then produces a droplet of volatile liquid. This liquid does not repel *M. incompleta* but has a pacifying action, calming the host.

(4) Non-aggressive behaviour: including all forms of behaviour with no aggressive component. The most frequent in this category are intense and prolonged licking of *M. incompleta* by *F. provancheri*. This behaviour may occupy up to 40% of the active time of a mature *F. provancheri* ergate. Solicitation, trophallaxis and very occasional licking of *F. provancheri* by *M. incompleta* were also noted (Lenoir et al. 1989).

Tests with M. incompleta

Ten young *M. incompleta* 15-day-old ergates from groups 5–8 were tested against *F. provancheri* mature ergates in a small petri dish. In each of the 10 tests one *M. incompleta* ergate was confronted with five *F. provancheri* (from a homospecific stock culture). Behaviour was classified in the same way as in the tests with *F. provancheri*.

Interactions with Brood

Tests with F. provancheri

Formicoxenus provancheri ergates (groups 1–4) were tested against brood of both species. For each of 10 tests, five ergates were put into a petri dish together with five *F. provancheri* and five *M. incompleta* larvae (from heterospecific stock cultures). The larvae were of similar size and were arranged in a circle around the centre of the dish with the species alternating. The larvae were not differentially marked but could be distinguished under the binocular microscope by their different pilosities.

Observations were made during the first 5 min of the test and, 15 min later, repeated during two periods of 5 min. During observation the behaviour of *F. provancheri* was recorded every 5 s.

Adult ants are usually strongly attracted to larvae. They readily show brood care behaviour even if the larvae are of a different species. We noted all forms of brood care behaviour: antennal examination, carrying (or simple mandibulation), licking and passive immobility near to a larva. Adults sometimes anally stimulate larvae with their antennae. The larvae then produce a droplet of clear liquid (Le Masne 1953; Wilson 1971).

Tests with M. incompleta

The tests with *F. provancheri* were repeated using *M. incompleta* young ergates from each of the experimental groups (5–8). The origin of the larvae and the observation technique were the same as for *F. provancheri*.

RESULTS

Interactions of Adults

Behaviour of the parasite

Aggressive behaviour by *F. provancheri* towards *M. incompleta* was infrequent and there were no significant differences between the groups (Fig. 1a). In contrast, young *F. provancheri* reared together with mature ones in the absence of *M. incompleta* (group 2) were attacked by *M. incompleta* significantly more often than were young *F. provancheri* ergates reared in the absence of mature conspecifics ($F_{1,36}=2{\cdot}47$, $P<0{\cdot}05$; Fig. 1b). This difference occurred whether or not the *F. provancheri* had been reared with *M. incompleta*.

Appeasement behaviour towards *M. incompleta* was significantly more frequently shown by *F. provancheri* reared in the absence of mature conspecifics ($F_{1,36}=7{\cdot}56$, $P<0{\cdot}01$), or in the absence of *M. incompleta* ($F_{1,36}=7{\cdot}57$, $P<0{\cdot}01$). The interaction of these two factors was also highly significant ($F_{1,36}=8{\cdot}96$, $P<0{\cdot}01$) and gave rise to the spectacularly high frequencies of appeasement behaviour recorded for young *F. provancheri* reared alone (MY – FO –; Fig. 1c).

The same trends were evident in the frequencies of non-aggressive behaviour (Fig. 1d). This behaviour was significantly more frequent for *F. provancheri* reared without mature conspecifics ($F_{1,36}=43{\cdot}00$, $P<0{\cdot}005$) or without *M. incompleta* ($F_{1,36}=32.34$, $P<0{\cdot}005$). These factors interacted significantly and non-aggressive behaviour was very frequent for *F. provancheri* reared with neither mature conspecifics nor *M. incompleta* (Fig. 1d).

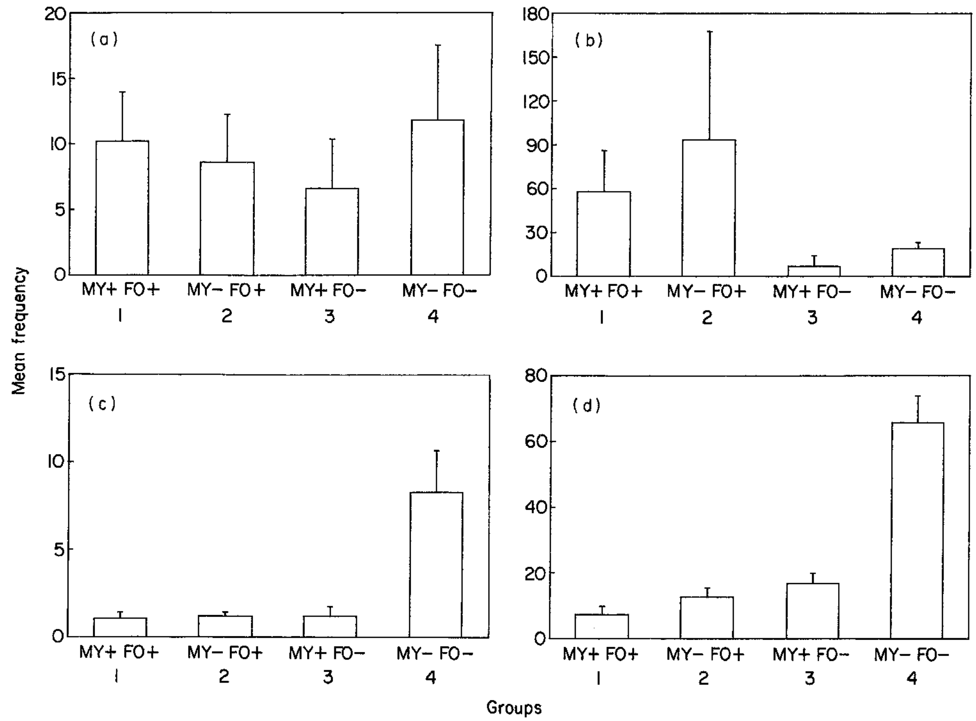

Figure 1. Mean frequency of interactions between *F. provancheri* (from the differently reared experimental groups) and *M. incompleta* (from homospecific stock culture). Vertical bars indicate the standard error. (a) Agonistic behaviour of *F. provancheri* towards *M. incompleta*. (b) Agonistic behaviour of *M. incompleta* towards *F. provancheri*. (c) *F. provancheri* appeasement behaviour. (d) Licking of *M. incompleta* by *F. provancheri*. See Table I for composition of groups.

Behaviour of the host

Myrmica incompleta ergates tested 15 days after their emergence displayed little aggressive behaviour. Those reared homospecifically were more aggressive to *F. provancheri* than those reared with the parasite ($F_{1,36}=8{\cdot}59$, $P<0{\cdot}005$; Fig. 2a). In contrast, *M. incompleta* from all experimental groups were attacked with the same intensity by *F. provancheri* ($F_{1,36}=0{\cdot}72$, NS; Fig. 2b). The number of attacks on young *M. incompleta* ergates reared alone (group 8) was slightly higher than for the other groups but this difference was not significant (Fig. 2b).

Appeasement behaviour by *F. provancheri* appeared to be less frequent in tests with young *M. incompleta* reared alone than with *M. incompleta* from the other groups although not significantly so ($F_{1,36}=3{\cdot}26$, $P<0{\cdot}10$; Fig. 2c). The frequency of non-agonistic behaviour by *F. provancheri* was greatest towards *M. incompleta* that had early social experience with the parasite (groups 5 and 7; $F_{1,36}=9{\cdot}21$, $P<0{\cdot}005$; Fig. 2d).

Interactions with Brood

Behaviour of the parasite

Heterospecifically reared ergates (group 1) showed more care behaviour towards conspecific than heterospecific larvae (Wilcoxon $T=4$; $P<0{\cdot}01$; Fig. 3). However, ergates reared under different regimes (groups 2–4) all showed more care behaviour to *M. incompleta* larvae than to conspecifics. This was true for both homospecific *F. provancheri* groups, with and without mature ergates, and also for young *F. provancheri* ergates reared heterospecifically ($T=0$; $P<0{\cdot}005$ in all cases).

Behaviour of the host

Brood care behaviour (licking and transport) of conspecific larvae was only significantly more frequent than care of allospecifics (Wilcoxon $T=0$; $P<0{\cdot}005$; Fig. 4) when young *M. incompleta*

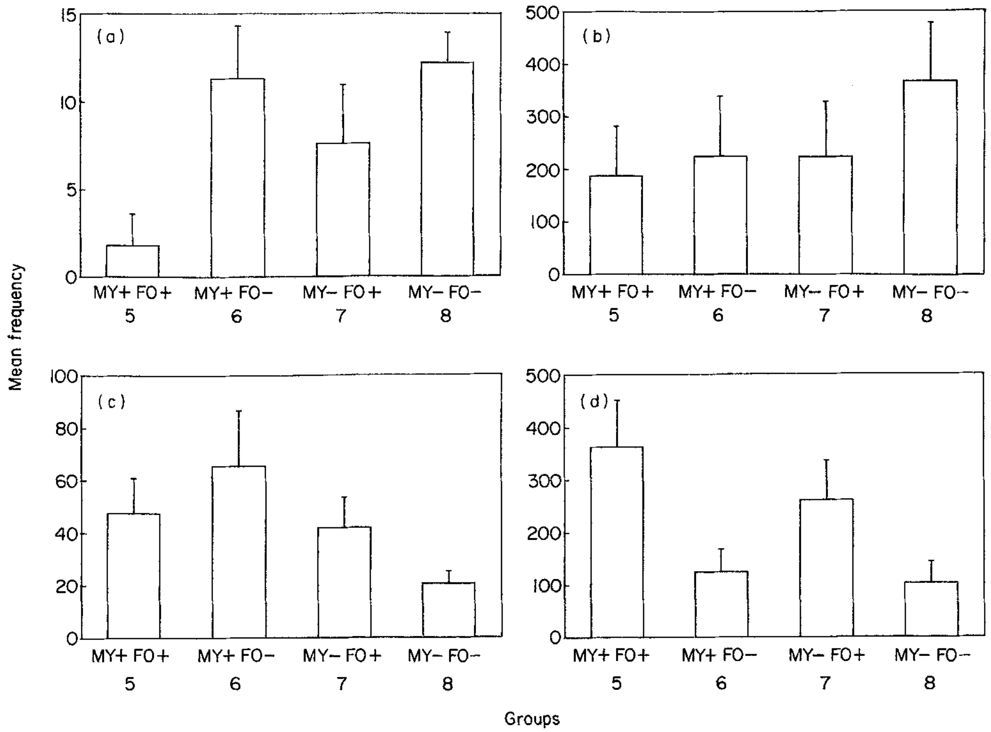

Figure 2. Mean frequency of interactions between *M. incompleta* (from the differently reared experimental groups) and *F. provancheri* (from homospecific stock culture). Vertical bars indicate the standard error. (a) Agonistic behaviour of *M. incompleta* towards *F. provancheri*. (b) Agonistic behaviour of *F. provancheri* towards *M. incompleta*. (c) *F. provancheri* appeasement behaviour. (d) Licking of *M. incompleta* by *F. provancheri*. See Table I for composition of groups.

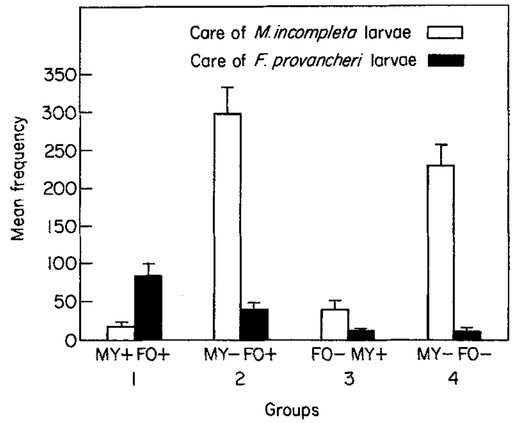

Figure 3. Mean frequency of care behaviour by *F. provancheri* ergates (from the differently reared experimental groups) towards *F. provancheri* (conspecific) and *M. incompleta* (allospecific) larvae. Vertical bars indicate the standard error. See Table I for composition of groups.

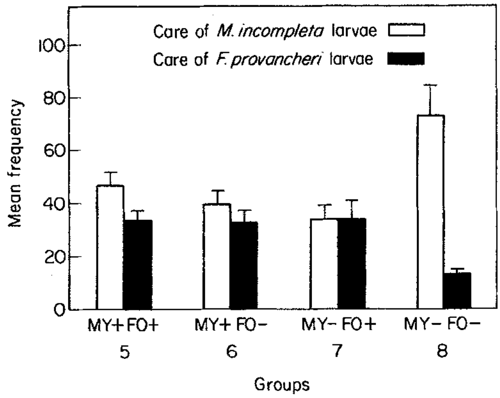

Figure 4. Mean frequency of care behaviour by *M. incompleta* ergates (from the differently reared experimental groups) towards *M. incompleta* (conspecific) and *F. provancheri* (allospecific) larvae. Vertical bars indicate the standard error. See Table I for composition of groups.

were reared homospecifically without mature conspecific ergates (group 8). In all the other groups (5–7) there was no significant difference in the frequency of care given to conspecific and allospecific brood (respectively, $T=19$, $T=28$, $T=22$, NS).

DISCUSSION

Interactions of adults

Aggression by the parasite *F. provancheri* towards it host *M. incompleta* was rare and was not influenced by the way in which either the parasite or the host had been reared. However, *F. provancheri* reared alone were more non-aggressive and showed more appeasement. The host's behaviour, in contrast, depended on both its and the parasite's rearing conditions. Thus, *F. provancheri* reared with mature conspecifics appeared to be recognized and accepted less readily by the host, receiving more aggression. Also, *M. incompleta* reared in the absence of the parasite were more aggressive to it, whereas when they were reared in the parasite's presence they were licked more frequently.

Interactions with brood

To prevent its brood being rapidly eaten by *M. incompleta* ergates, *F. provancheri* always isolates its eggs and larvae from those of *M. incompleta* (personal observations). In nature, therefore, the nests of the two species are always separate. When only limited isolation is offered in artificial nests *F. provancheri* defends its brood chamber or area against the occasional incursions of *M. incompleta*. Both species recognize their own brood but *F. provancheri* foragers are also strongly attracted by *M. incompleta* larvae. They lick these larvae just as frequently as they lick *M. incompleta* adults (Lenoir et al., in press).

When reared with their host, *F. provancheri* have numerous opportunities to lick *M. incompleta* larvae and adults. This behaviour resembles feeding. In the present study, these contacts seem to have been sufficient for *F. provancheri* ergates and they therefore did not require to seek out *M. incompleta* larvae. When reared in the absence of mature conspecifics, young *F. provancheri* neglected conspecific larvae. This discrimination may have arisen from the greater attraction of *M. incompleta* larvae (possibly because they provide a nutritious resource) to young *F. provancheri* ergates reared homospecifically (group 4). This may influence the development of the parasite's colony if any perturbation occurs.

Myrmica incompleta did not appear to care preferentially for larvae of their own species except when young ergates were reared in isolation in the absence of mature conspecifics. However, 'larval care' may not be a coherent behavioural category and the transport of larvae may have other purposes. *Myrmica incompleta* may, for example pick up and transport *F. provancheri* larvae in order to eat them later. We had to reduce the opening of *F. provancheri* nests in heterospecific cultures to prevent predation by *M. incompleta* on the *F. provancheri* brood.

Fifteen-day-old *F. provancheri* and *M. incompleta* ergates thus apparently differed in their response to early social experience. The development of behaviour in the two species was affected to a variable degree by the social environment: *M. incompleta* showed little preference for their own versus the parasite's larvae, whereas the parasite, under certain treatments, preferred to rear the brood of the host *M. incompleta*. The present study shows for the first time that a parasite preferred to rear the host's brood, especially when the parasite's early experience had been either of its own species (MY−FO+) or isolation (MY−FO−). We would least expect a parasite, whatever else it did, to tend the host's brood after these particular treatments. A partial explanation may be that the host's brood provides a resource via a secretion. It would be interesting to know what the function of the secretion was with respect to *M. incompleta*, i.e. how it might benefit *M. incompleta* to a degree that offsets the cost of making their larvae attractive to a parasite.

In numerous species, for example in the genera *Formica*, *Camponotus* and *Myrmica* (see Jaisson 1985), social experience in the days or hours immediately after emergence is extremely important. The polygynous *Myrmica* spp. show very plastic responses and therefore easily learn to tolerate intruding allospecific ants (Vienne et al., in press). *Formicoxenus provancheri*, however, are evidently attracted to their host. These results resemble those of Jaisson (1985) which showed that young *Formica sanguinea* workers do not learn to care preferentially for pupae other than those of their own species. Alloway & Hare (1989) showed that early learning need not be involved to account for the acceptance of a *Harpagoxenus* brood by enslaved *Leptothorax* workers.

Heterospecific colonies of *F. Nitidulus* and *Leptothorax acervorum* can be created if *L. acervorum* pupae are introduced to the *F. nitidulus* nest (Buschinger 1976). *Leptothorax acervorum* is a species in the *Leptothorax* subgenus closest to *Formicoxenus* but we were unsuccessful in our attempts to induce *F. provancheri* to adopt pupae of species in other *Leptothorax* subgenera (unpublished data). In contrast we were easily able to cause newly emerged *Myrmica rubra* from Europe to adopt *F. provancheri*, whereas it is impossible with mature *M. rubra*.

The cuticular chemical compounds of the host and the parasite have been determined by gas chromatography coupled to mass spectrometry: the first results of this analysis (Lenoir et al. 1990) show that the tolerance between *F. provancheri* and *M. incompleta* is facilitated by the existence of similar cuticular hydrocarbons and their close relative percentage variations in each species. A similar situation occurs with myrmecophilous beetles where individuals are tolerated because of chemical mimicry (Howard et al. 1980; Vander Meer & Wojick 1982). Franks et al. (1990) discovered that the parasitic ants *Leptothorax kutteri* pick up host odours through grooming. A different situation is observed in mixed colonies: if two independent ant species are experimentally forced to live together immediately after emergence we can detect an intermediate chemical pattern. Although impossible in Nature, such an association can be achieved artificially through the formation of a mixed colonial odour from the hydrocarbons of the two species (Errard & Jallon 1987; Errard et al. 1990; Vienne et al. 1990; Bagnères et al. 1991; Errard & Jaisson 1991).

For the parasitic association *F. provancheri/M. incompleta* the ethological, chemical and ecological data bring to light a rather rigidly preadapted system. It is also known that a parent association exists including a sibling parasitic species, *F. quebecensis*, and a sibling host species, *M. alaskensis* (Francoeur et al. 1985). A comparison of their behavioural development remains to be investigated. It should be a most interesting case of coevolution, as it is in terms of morphology.

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