

Patch exploitation strategies of parasitic wasps under intraspecific competition

Marlène Goubault,^a Yannick Outreman,^b Denis Poinso, ^a and Anne Marie Cortesero^a

^aUPRES EA 3193, Ecobiologie des Insectes Parasitoïdes, Université de Rennes 1, Campus de Beaulieu (Bat. 25), 263, Avenue du Général Leclerc, 35042 Rennes Cedex, France, and ^bUMR INRA-Agrocampus Rennes BiO3P, 65 rue de Saint-Brieuc, CS 84215, 35042 Rennes Cedex, France

The optimal residence time of a forager exploiting a resource patch in the absence of competitors has been much studied since the development of the marginal value theorem. However, several foragers are frequently observed exploiting the same patch simultaneously, and patch residence time has been surprisingly little studied in such competitive situations. The few theoretical models developed on this topic predict that foragers should engage in a war of attrition and stay in the patch longer than when foraging alone. We tested this prediction in *Pachycrepoideus vindemmiae* (Hymenoptera: Pteromalidae), a solitary parasitoid species in which females are known to defend the hosts they are exploiting via intraspecific fighting. By measuring the effect of direct (i.e., presence of conspecifics) and indirect (i.e., presence of already-parasitized hosts) competition on patch exploitation strategies, we revealed an apparent polymorphism of strategies. Indeed, in competitive situations, some members of the population tended to retreat almost immediately from the patch whereas other members tended to remain, further exploit the patch, and be more involved in interactions with conspecifics. The proportion of “retreaters” strongly depended on competition intensity and prior experience of competition. The forager’s physiological state (age) also affects patch exploitation strategy and the intensity of interactions between competing females. Our results highlight the necessity for further theoretical studies that consider cases where contests between foragers are costly and take into account prior experience of competition and the forager’s physiological state. *Key words*: agonistic behavior, direct competition, optimal foraging, parasitoid, patch quality, physiological state, prior experience of competition, Pteromalidae. [*Behav Ecol*]

An important problem studied in behavioral ecology is the question of how animals should use patchily distributed resources to maximize their energy gain. One of the first models to describe optimal patch use is the marginal value theorem (MVT; Charnov, 1976). It predicts that a single animal exploiting a patch of resources should leave it and search for another patch when its rate of resource gain drops below the expected mean rate in the whole habitat. An animal should therefore adjust its patch residence time according to both patch quality and between-patch travel time. While this model predicts the behavior of an individual exploiting an environment without competitors, animals do not always forage alone. Individuals of a same species have similar needs for survival, growth, and reproduction and thus will often search for and exploit similar resources (e.g., food, mate partners, nests) with consequent competition (Duquet, 1995). This may lead to a different patch exploitation strategy compared to the situation of a solitary forager, especially as in presence of conspecifics, the optimal decisions of individuals are likely to depend on the decisions taken by others (Maynard-Smith, 1974). Surprisingly, few studies have investigated foraging strategies under competition (Bernstein et al., 1991; Giraldeau and Caraco, 2000; Sjerps and Haccou, 1994). According to the models developed on this topic, the MVT can be applied to competitive situations provided that competitors do not interfere with each other at all, such that

the presence of conspecifics does not change the forager’s decisions (Sjerps and Haccou, 1994). If this condition is met, the MVT predicts that all foragers will leave the patch simultaneously, that is, when the rate of gain on that patch falls below the mean gain rate expected in the habitat. Because the number of foragers on the patch determines the resource depletion rate, the more foragers, the sooner the patch-leaving gain rate should be reached (van Alphen, 1988). Consequently, competition should shorten patch residence time. Nevertheless, the presence of conspecific competitors can modify foraging behavior while on the patch. On the one hand, foragers can interfere directly via fighting or threatening behaviors. These time-consuming interactions will tend to increase time on a patch (Hassell and Varley, 1969). On the other hand, foragers can also interfere indirectly when the presence of competitors reduces the resource gain rate of each forager. In this case, foragers will benefit from the departure of their competitors and should engage in a “war of attrition” (Maynard-Smith, 1974), that is, they should try to stay on the patch longer than their competitors; this will increase patch residence times. Consequently, when there is either direct or indirect interference between competitors, foragers should stay longer in the patch than if they were alone. Factors that usually affect the optimal patch use by solitary foragers, such as habitat experience and physiological state, can also influence foraging strategies under competition (Outreman et al., 2005). For instance, previous experience of competition with conspecifics could affect patch residence time: when exploiting a patch alone, foragers should stay longer if they have a prior experience of competition (Visser et al., 1992b). Experience of long interpatch distance can also be expected to increase the duration of the war of attrition because it means that patches are costly to find. Foragers should also modify their strategies under competition according to their physiological state

Address correspondence to A.M. Cortesero. E-mail: anne-marie.cortesero@univ-rennes1.fr. M. Goubault is now at the Division of Agricultural & Environmental Sciences, School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD UK.

Received 23 July 2004; revised 26 January 2005; accepted 7 March 2005.

Table 1
List of treatments tested in the present study

| Treatment code | Number of days between emergence and the test | Number of females on the patch | Type of hosts | Number of replicates |
|--------------------|---|----------------------------------|------------------|----------------------|
| 1F _{d2} | 2 | 1 | Unparasitized | 44 |
| 2F _{d2} | 2 | 2 | Unparasitized | 60 |
| 4F _{d2} | 2 | 4 | Unparasitized | 60 |
| 1F _{pre} | 2 | 1 With competition preexperience | Unparasitized | 45 |
| 1F _{d2-P} | 2 | 1 | 24-h Parasitized | 59 |
| 1F _{d4} | 4 | 1 | Unparasitized | 30 |
| 2F _{d4} | 4 | 2 | Unparasitized | 30 |
| 1F _{d6} | 6 | 1 | Unparasitized | 30 |
| 2F _{d6} | 6 | 2 | Unparasitized | 30 |

(e.g., age, fecundity). The forager's age can, for example, affect its susceptibility to interference (i.e., the rate at which its intake rate changes with an increasing density of competitors) (Goss-Custard and Durell, 1987) and consequently its patch time allocation.

Hymenopterous parasitoid females foraging for hosts that will allow the development of their offspring represent a particularly appropriate biological model to study the effect of intraspecific competition on foraging strategies. Indeed, because each successfully parasitized host can yield one (or more) offspring, the link between the foraging strategy and reproductive success is direct, which is not the case with herbivorous or predatory foragers. Moreover, several parasitoid females are frequently observed exploiting simultaneously the same patch of hosts (Godfray, 1994). In such a case, the females can interfere with each other either (1) directly by fighting, displaying, or hindering (Field et al., 1998; Godfray, 1994; Hardy and Blackburn, 1991) or (2) indirectly by modifying their host exploitation strategies (Visser et al., 1990, 1992a). In parasitoids, the presence of conspecific females should modify decisions of females confronted with already-parasitized hosts. In particular, females should oviposit more frequently in such hosts (i.e., superparasitize) (van Alphen, 1988; Visser et al., 1990, 1992a). Indeed, when only one parasitoid female exploits a patch, superparasitism is thus self-superparasitism (i.e., laying two eggs in the same host), which in solitary parasitoids wastes both time and eggs because only one individual can emerge from each host (van Lenteren, 1981). In contrast, when several females exploit the same patch simultaneously, laying twice in the same host increases fitness (because each egg increases the chance of winning larval competition). A war of attrition between parasitoid females is thus expected, especially because the first female that leaves a patch may lose offspring to larval competition if other females remain in the patch and continue to oviposit (Field et al., 1998; Sjerps and Haccou, 1994; van Alphen, 1988).

The aim of this study was to determine which factors affect the patch use strategy of foragers under competition and to consider their adaptive value. For this purpose, we studied the effect of both direct (i.e., presence of conspecific females) and indirect (i.e., presence of hosts already-parasitized by conspecifics) intraspecific competition on patch residence time and oviposition strategy in *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae). This solitary ectoparasitoid of the pupae of many cyclorrhaphous dipteran species has been chosen because aggressive behaviors have been observed between *P. vindemmiae* females exploiting the same host patch (Goubault M, unpublished data). We also tested

the influence of a previous experience of competition and of the forager's age on the patch exploitation strategies under competition.

MATERIALS AND METHODS

Rearing

The host, *Delia radicum* L. (Diptera: Anthomyiidae), originated from pupae collected in Le Rheu (Brittany, France) from cabbage fields in 1994. It was reared on rutabaga roots (*Brassica napus* L. [Brassicaceae]) at $20 \pm 2^\circ\text{C}$, $60 \pm 10\%$ relative humidity, and 16:8 h light:dark according to the technique described in Neveu et al. (1996). Hosts used in the experiments were 7- to 10-day-old pupae, which is the preferred host age of *P. vindemmiae* (Grandgirard et al., 2002). The *P. vindemmiae* strain was collected in Rennes (Brittany, France) in 2000 and was reared on pupae of *D. radicum* in a climate-controlled room ($25 \pm 1^\circ\text{C}$, $60 \pm 10\%$ relative humidity, 16:8 h light:dark). Adults were maintained in petri dishes (diameter = 8.5 cm; height = 2.7 cm) and supplied with honey, water, and about 150 host pupae that were replaced three times a week. Parasitized pupae were stored under the same conditions and placed in gelatine capsules in order to isolate newly emerging wasps. The day of their emergence, *P. vindemmiae* females used in the experiments were mated, by placing them with a male and observing until copulation occurred, and then individually placed in tubes (diameter = 1 cm, height = 5 cm) containing water and honey. They were then allowed to oviposit in five *D. radicum* pupae on that day and in five fresh pupae the day after.

Experimental procedures

At the beginning of the test, a given number of females (one, two, or four) were introduced simultaneously in a petri dish (diameter = 8.5 cm) containing four pupae of *D. radicum*. A plastic cone with a very small aperture was placed on top of the petri dish in order to allow females to leave the patch but not to reenter in it. The introduction of the female(s) was considered to be the starting point of the experiments and the number of females still present in the patch was checked every 15 min (i.e., 15-min steps). Experiments were stopped when all females had left the patch or after 4 h of observation.

Patch residence time, number of hosts accepted per patch, and number of eggs laid per host were tested in different situations (Table 1):

- *Level of intraspecific competition*: one, two, or four females simultaneously exploited the same patch (treatments code: 1F_{d2}, 2F_{d2}, and 4F_{d2}, respectively).

- *Experience of competition*: the tested female was maintained in isolation or experienced intraspecific competition before the test (treatments code: 1F_{d2} and 1F_{pre}, respectively). Before the tests, the experienced wasps were maintained with three other wasps in the same tube for the 2 days preceding the test in order to experience intraspecific competition.
- *Patch quality*: one female was provided with unparasitized hosts or hosts that had been parasitized 24 h previously (treatments code: 1F_{d2} and 1F_{d2-P}, respectively).
- *Level of competition and forager's age*. This combined effect was studied by using females aged 2, 4, or 6 days and exploiting a patch either alone or with one conspecific competitor (treatments code: 1F_{d2}, 1F_{d4}, and 1F_{d6} or 2F_{d2}, 2F_{d4}, and 2F_{d6}, respectively).
- *Type of competition*. By comparing treatments 1F_{d2-P} and 2F_{d2}, the effect of the competition type (indirect competition versus direct competition) on the foraging behavior of a parasitic wasp was assessed.

For the 2F_{d2}, 2F_{d4}, and 2F_{d6} treatments, the female-female interaction behaviors were recorded continuously. When females encountered each other (i.e., the distance between both females was less than 2 mm), interaction behaviors were noted: females (1) only detected each other at a distance and raised their antennae in the direction of the opponent females (a behavior called “conspecific detection”), (2) contacted each other nonaggressively with their antennae (behavior called “nonaggressive contact”), (3) attacked each other by biting or striking with their antennae (behavior called “aggressive contact”), or (4) avoided each other (behavior called “conspecific avoidance”). An encounter usually began with the detection of the conspecific. The other types of behaviors (i.e., nonaggressive contact, aggressive contact, and conspecific avoidance) could follow one another in any order. To distinguish the two females, one of them was marked on the thorax with acrylic paint after being immobilized by rapid chilling. To avoid a bias linked to chilling, both groups of females were treated in this way. Chilling and marking were performed 2 days before the experiment in order that females had time to recover. Preliminary results showed that the paint did not modify female oviposition strategies or their aggressiveness (Goubault, unpublished data).

At the end of experiments, pupae were dissected in order to check the number of eggs laid.

Statistical analysis

For each treatment, the rate of parasitism and the rate of superparasitism were analyzed by means of generalized linear models assuming a binomial distribution of error variances and a logit link function (McCullagh and Nelder, 1989). For the 2F_{d2}, 2F_{d4}, and 2F_{d6} treatments, the total number of female-female interaction behaviors observed and the frequencies (proportions) of the four interaction behaviors as a function of the forager's age were also tested. These analyses were also carried out by means of generalized linear models assuming either Poisson or binomial error variances.

Patch residence time was analyzed for each treatment. Our data showed that 20–65% of the tested females left the patch during the first 15 min of the test without ovipositing (i.e., females called “retreaters”), while the rest stayed on the patch (i.e., females called “remainers”). The patch time allocation of these two types of females was analyzed separately. The effect of the treatment on the retreat tendency (i.e., frequency of retreaters) was analyzed with a generalized linear model assuming binomial errors. The patch time allocation of the remainers was analyzed with Cox's proportional hazards

model (Cox, 1972). A thorough description of this model can be found in Collett (1994), and its use in behavioral ecology of parasitoids is explained in van Alphen et al. (2003). The purpose of this analysis is to estimate the influence of the treatment on the patch-leaving tendency in *P. vindemmiæ* remainers under all conditions tested.

All analyses were carried out using S-plus® statistical software (MathSoft, Cambridge, Massachusetts, USA) (Venables and Ripley, 1997).

RESULTS

Effect of female number (treatments 1F_{d2} versus 2F_{d2} versus 4F_{d2})

The proportion of retreaters increased with the number of females initially introduced in the patch (Figure 1A; Table 2). The tendency of the remainers to leave the patch was similar across the three treatments (Figure 2A; Table 3). The mean number of hosts exploited per patch by these females increased with the level of competition (1F_{d2}: 2.16 ± 0.27, 2F_{d2}: 2.40 ± 0.22, 4F_{d2}: 2.68 ± 0.21). The level of superparasitism also increased significantly with the number of foragers in the patch (Figure 3A; Table 2).

Effect of preexperience of competition (treatments 1F_{d2} versus 1F_{pre})

The proportion of retreating females was higher after a preexperience of competition (Figure 1B; Table 2). Concerning the remainers, the experienced females stayed longer in the patch than females that had never encountered conspecifics (Figure 2B; Table 3). A greater proportion of hosts remained unparasitized in the patches exploited by preexperienced females. In this treatment, the level of superparasitism was low and not affected by the experience status of the foragers (Figure 3B; Table 2).

Effect of patch quality (treatments 1F_{d2} versus 1F_{d2-P})

The proportion of retreaters was higher when the patch contained already-parasitized pupae (Figure 1C; Table 2). In contrast, the presence of already-parasitized hosts in the patch did not modify patch time of the remaining females (Figure 2C; Table 3). These females laid significantly fewer eggs in patches containing already-parasitized hosts (1F_{d2}: 2.16 ± 0.27, 1F_{d2-P}: 1.07 ± 0.18). In both situations, the level of superparasitism was low (Figure 3C; Table 2).

Combined effect of the level of competition and the forager's age (treatments 1F_{d2} versus 1F_{d4} versus 1F_{d6} versus 2F_{d2} versus 2F_{d4} versus 2F_{d6})

While the presence of a conspecific increased the proportion of retreating wasps, the increasing age of the foragers decreased this tendency (Figure 1D,E; Table 2). For the remainers, the tendency to leave the visited patch decreased with their age (Table 3). Overall, the presence of a conspecific competitor increased patch-leaving tendency by a factor of 1.307, but this effect depended on the age of the foragers (Table 3). When foragers were 6 days old, the presence of a competitor increased, rather than decreased, patch residence time (Table 3). The rate of hosts accepted for parasitism was similar in the six treatments (1F_{d2}: 2.16 ± 0.27, 1F_{d4}: 2.47 ± 0.27, 1F_{d6}: 1.83 ± 0.26, 2F_{d2}: 2.40 ± 0.22, 2F_{d4}: 2.27 ± 0.31, 2F_{d6}: 2.50 ± 0.25) (Table 2). However, the level of superparasitism differed between treatments: in the

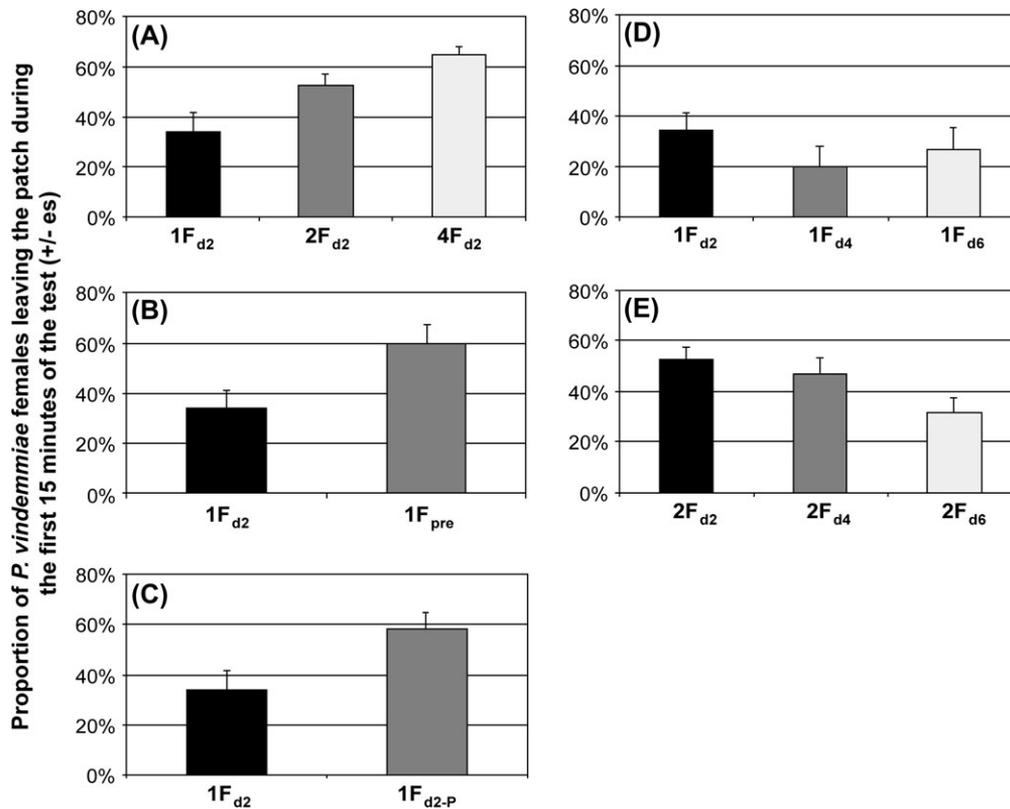


Figure 1

Proportion of retreating *Pachycrepoideus vindemmiae* females (i.e., females that leave the patch during the first 15 min of the test). (A) Effect of the number of females exploiting the patch simultaneously (1F_{d2}, 2F_{d2}, 4F_{d2}), (B) effect of previous competition experience (1F_{d2}, 1F_{pre}), (C) effect of patch quality (i.e., exploitative competition) (1F_{d2}, 1F_{d2-P}), (D) effect of female age (1F_{d2}, 1F_{d4}, 1F_{d6}), and (E) combined effect of intraspecific competition and female age (2F_{d2}, 2F_{d4}, 2F_{d6}).

presence of a competitor, the frequency of superparasitism increased significantly (Figure 3D,E; Table 2). The generalized linear model suggested that in the presence of competition, the level of superparasitism tended to increase

with the age of the foragers, although this effect was marginally nonsignificant ($p = .058$).

The mean number of female-female interaction behaviors increased significantly with their age ($\chi^2 = 22.63$, $df = 2$,

Table 2

Generalized linear models showing the effect of various factors on the foraging strategy of *Pachycrepoideus vindemmiae* females foraging on patches containing pupae of the cabbage root fly *Delia radicum*

| Treatment | Source | Variables (distribution family) | | | | | | | | |
|--|---|--|----------|-----------|---------------------------------|----------|-----------|---------------------------------|----------|-----------|
| | | Departure in the first 15 min (binomial) | | | Host acceptance rate (binomial) | | | Superparasitism rate (binomial) | | |
| | | df | χ^2 | p Value | df | χ^2 | p Value | df | χ^2 | p Value |
| Level of intraspecific competition (treatments 1F _{d2} versus 2F _{d2} versus 4F _{d2}) | <i>N</i> females | 2 | 17.19 | <.001 | 2 | 7.50 | <.05 | 2 | 23.26 | <.001 |
| | Error | 401 | | | 161 | | | 161 | | |
| Experience of competition (treatments 1F _{d2} versus 1F _{pre}) | Experience | 1 | 6.06 | <.05 | 1 | 30.54 | <.001 | 1 | 0.01 | .971 |
| | Error | 87 | | | 87 | | | 87 | | |
| Patch quality (treatments 1F _{d2} versus 1F _{d2-P}) | Patch quality | 1 | 5.66 | <.05 | 1 | 31.84 | <.001 | 1 | 2.39 | .121 |
| | Error | 101 | | | 101 | | | 101 | | |
| Competition and physiological state (treatments 1F _{d2} versus 1F _{d4} versus 1F _{d6} versus 2F _{d2} versus 2F _{d4} versus 2F _{d6}) | <i>N</i> females (1) | 1 | 9.99 | <.005 | 1 | 3.21 | .073 | 1 | 24.83 | <.001 |
| | Female's age (2) | 2 | 7.00 | .030 | 2 | 1.27 | .538 | 2 | 5.68 | .058 |
| | Interaction (1) × (2) | 2 | 1.97 | .373 | 2 | 5.71 | .057 | 2 | 0.81 | .664 |
| | Error | 338 | | | 218 | | | 218 | | |
| | Competition type (treatments 2F _{d2} versus 1F _{d2-P}) | Competition type | 1 | 0.41 | .516 | 1 | 54.87 | <.001 | 1 | 17.49 |
| | Error | 178 | | | 118 | | | 118 | | |

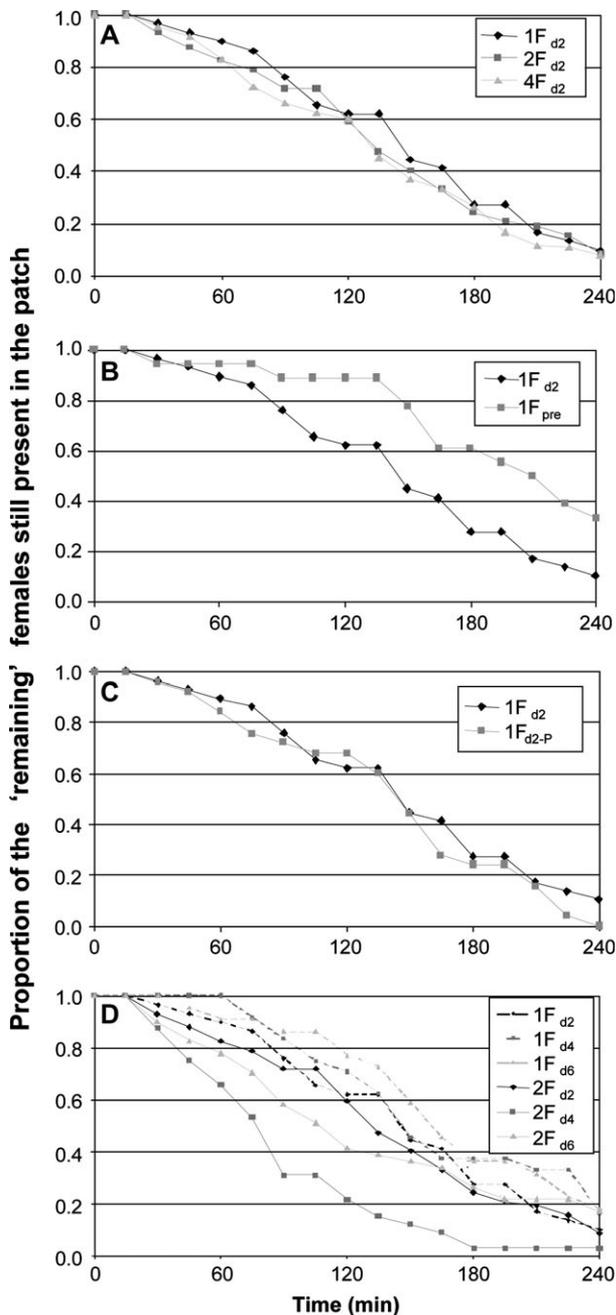


Figure 2 Proportion of remaining *Pachycrepoideus vindemmiae* females (i.e., females that stay more than 15 min in the patch) as a function of time. (A) Effect of the number of females exploiting the patch simultaneously (1F_{d2}, 2F_{d2}, 4F_{d2}), (B) effect of previous competition experience (1F_{d2}, 1F_{pre}), (C) effect of patch quality (i.e., exploitative competition) (1F_{d2}, 1F_{d2-p}), and (D) combined effect of intraspecific competition and female age (1F_{d2}, 1F_{d4}, 1F_{d6}, 2F_{d2}, 2F_{d4}, 2F_{d6}).

$p < .001$) (2F_{d2}: 4.81 ± 0.97 , 2F_{d4}: 5.53 ± 1.05 , 2F_{d6}: 7.40 ± 1.52). The rate of nonaggressive contacts and the rate of conspecific avoidance were not affected by the age of the foragers ($\chi^2 = 4.60$, $df = 2$, $p = .10$; $\chi^2 = 2.63$, $df = 2$, $p = .26$; respectively) (Figure 3). The rates of conspecific detection decreased significantly with the age of the wasps ($\chi^2 = 12.90$, $df = 2$, $p < .005$), while the rate of aggressive contacts increased with the age of foragers ($\chi^2 = 6.38$, $df = 2$, $p < .05$) (Figure 4).

Effect of the competition type (treatments 2F_{d2} versus 1F_{d2-p})

The frequency of retreaters (Figure 1A,C; Table 2) and the patch residence time of the remainders (Figure 2A,C; Table 3) were similar whatever the competition type. However, the oviposition strategy differed between the two treatments: the females laid significantly fewer eggs under indirect competition (2F_{d2}: 2.40 ± 0.22 , 1F_{d2-p}: 1.07 ± 0.18), and the level of superparasitism was higher in the presence of a competitor (i.e., direct competition) (Figure 3A,C; Table 2).

DISCUSSION

Our results showed that the level of competition between *P. vindemmiae* females modified their patch residence time and their host acceptance strategy. Contrary to expectations (based on Sjerps and Haccou, 1994; van Alphen, 1988; Visser et al., 1992a), *P. vindemmiae* females spent less time in patches with increasing numbers of competitors. Thus, no war of attrition was observed, in contrast with the situation described in *Leptopilina heterotoma* (Visser et al., 1990). Nevertheless, Visser and collaborators used a number of females proportional to the patch unit (one female searched in a single-unit patch with 20 hosts, two females searched a double-unit patch of 40 hosts, etc.), whereas in our experiment the unit of patch used was kept constant whatever the number of females introduced. Despite this difference, our results showed that, when *P. vindemmiae* females were introduced in unparasitized patches, the intensity of competition clearly affected the proportion of females leaving the patch early: this proportion of “retreating” females increased with the number of females initially introduced. After these first 15 min, the patch-leaving tendency was similar whatever the initial number of competitors. Because oviposition in *P. vindemmiae* lasts about 12 min (Goubault et al., 2004), early-leaving females left the patch before any eggs could be laid. Therefore, in *P. vindemmiae*, the decision to leave a patch sooner under competition is essentially due to the presence of competitors (direct competition) and not to patch depletion (indirect competition).

When females decided to stay in the patch, their oviposition strategy was affected by the level of direct competition: these “remaining” females were more willing to superparasitize when the number of competitors increased. This effect on superparasitism level was expected because in time-limited parasitoids superparasitism becomes advantageous in the presence of conspecific competitors (Visser et al., 1990, 1992a). Nevertheless, self-superparasitism was also observed in females foraging alone in a patch, even when they had never encountered any conspecific female (no preexperience of competition). This kind of self-superparasitism could be adaptive if the natural level of intraspecific competition is high. Indeed, in such a case, the risk that conspecific females will later exploit the same patch is high, and females could anticipate this risk by laying two eggs in some hosts as a safeguard. Field studies would be needed to determine the natural level of intraspecific competition in *P. vindemmiae* and confirm this hypothesis.

The *P. vindemmiae* females used in this experiment were apparently able to assess overall quality of the patch quickly, not only concerning the direct competition intensity but also the indirect competition level. Indeed, the females were able to detect the presence of already-parasitized hosts quickly and stayed shorter in such depleted patches. Thus, *P. vindemmiae* females exhibit a similar patch time allocation whatever the type of competition (either direct or indirect): they tend to leave earlier from patches where there is competition. In

Table 3

Estimated regression coefficients (β), standard errors (SE), and hazard ratios $\exp(\beta)$ for covariates that could affect the patch-leaving tendency of *Pachycrepoideus vindemmia* females foraging on patches containing pupae of the cabbage root fly *Delia radicum*

| Treatment | Covariates | | β | SE (β) | Exp(β) | χ^2 (df) | <i>p</i> Value |
|--|-----------------------|--------------------------|------------|----------------|----------------|---------------|----------------|
| Level of intraspecific competition (treatments 1F _{d2} versus 2F _{d2} versus 4F _{d2}) | Level of competition | One female | 0.0000 | 0.0000 | 1.000 | 0.65 (2) | .732 |
| | | Two females | 0.0567 | 0.1202 | 1.060 | | |
| | | Four females | 0.0408 | 0.0554 | 1.041 | | |
| Experience of competition (treatments 1F _{d2} versus 1F _{pre}) | Experience | No experience | 0.0000 | 0.0000 | 1.000 | 5.34 (1) | <.05 |
| | | Experience | -0.3940 | 0.1774 | 0.674 | | |
| Patch quality (treatments 1F _{d2} versus 1F _{d2-p}) | Patch quality | Healthy hosts | 0.0000 | 0.0000 | 1.000 | 0.86 (1) | .352 |
| | | Parasitized hosts | 0.132 | 0.1411 | 1.141 | | |
| Competition and physiological state (treatments 1F _{d2} versus 1F _{d4} versus 1F _{d6} versus 2F _{d2} versus 2F _{d4} versus 2F _{d6}) | N females (1) | One female | 0.0000 | 0.0000 | 1.000 | 11.74 (1) | <.005 |
| | | Two females | 0.268 | 0.0796 | 1.307 | | |
| | | Age (2) | 2 Days old | 0.0000 | 0.0000 | | |
| | 4 Days old | 0.1500 | 0.0940 | 1.162 | | | |
| | 6 Days old | -0.1032 | 0.0580 | 0.902 | | | |
| | Interaction (1) × (2) | Competition × 2 days old | 0.0000 | 0.0000 | 1.000 | 8.1 (2) | <.05 |
| Competition × 4 days old | | 0.2640 | 0.0943 | 1.302 | | | |
| Competition × 6 days old | | -0.0464 | 0.0579 | 0.955 | | | |
| Competition type (treatments 2F _{d2} versus 1F _{d2-p}) | Competition type | Direct competition | 0.0000 | 0.0000 | 1.000 | 0.41 (1) | .521 |
| | | Indirect competition | 0.079 | 0.1230 | 1.081 | | |

χ^2 Corresponds to the likelihood ratio tests.

contrast, their oviposition strategies differ in relation to the type of competition: females superparasitize more often in presence of conspecifics. This difference in oviposition strategy appears adaptive because in this species, when

a female parasitizes a host just after a conspecific (i.e., direct competition situations), the chance of winning the larval competition is approximately 50% (Goubault et al., 2003). Moreover, in that case, females can also try to destroy the egg

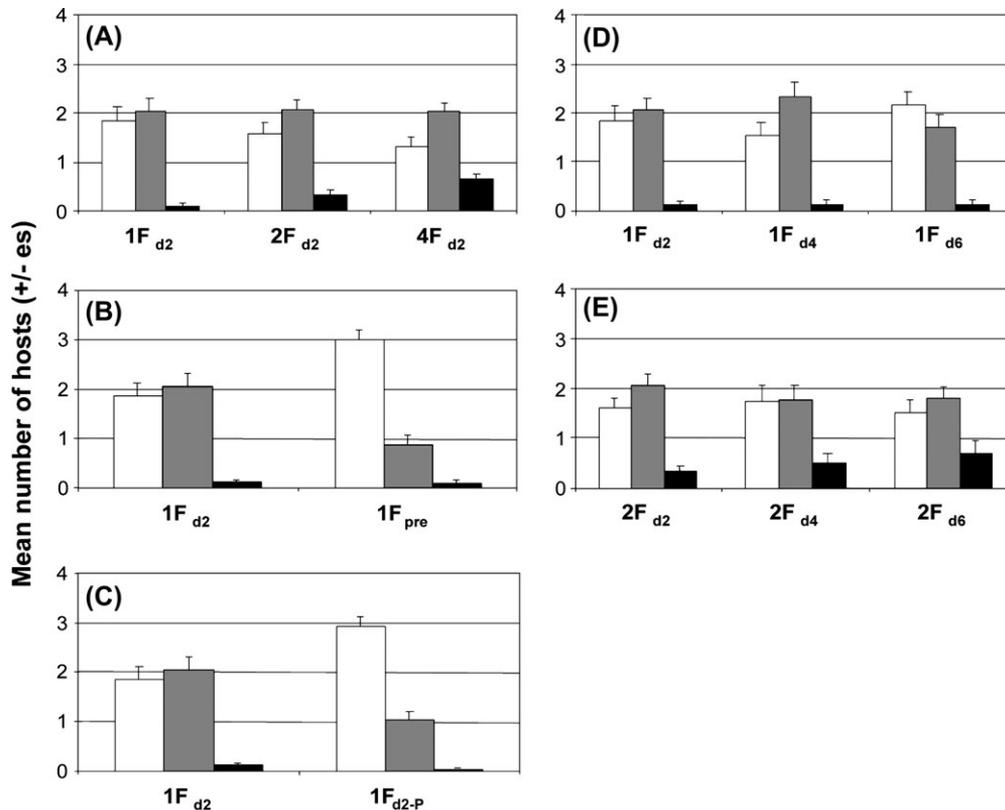


Figure 3

Egg distribution of remaining *Pachycrepoideus vindemmia* females among hosts. (A) Effect of the number of females exploiting the patch simultaneously (1F_{d2}, 2F_{d2}, 4F_{d2}), (B) effect of previous competition experience (1F_{d2}, 1F_{pre}), (C) effect of patch quality (i.e., exploitative competition) (1F_{d2}, 1F_{d2-p}), (D) effect of female age (1F_{d2}, 1F_{d4}, 1F_{d6}), and (E) combined effect of intraspecific competition and female age (2F_{d2}, 2F_{d4}, 2F_{d6}). White, gray, and black bars correspond to the mean number of hosts per patch that received respectively no egg, one egg, and more than one egg during the test.

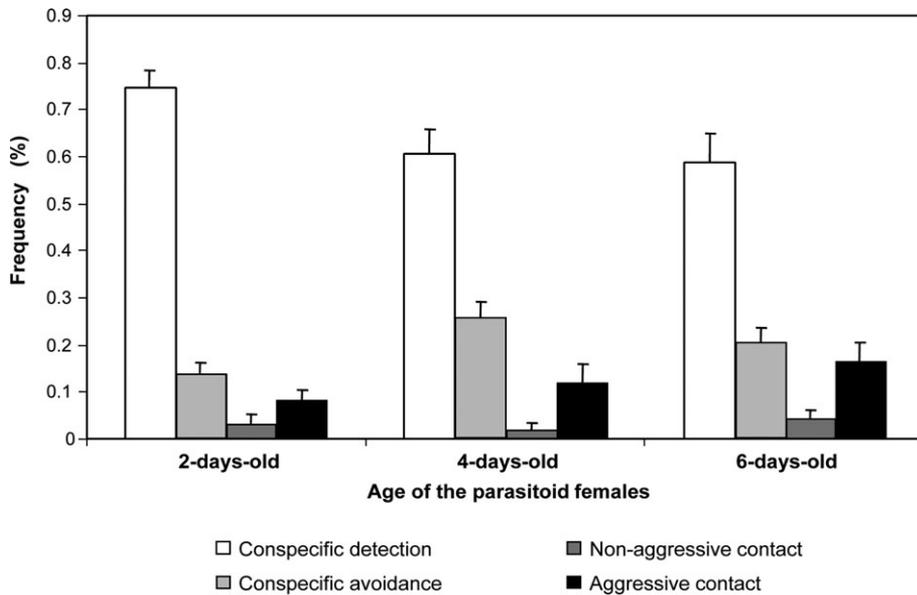


Figure 4
Frequencies of the different female-female interaction behaviors according to the age of the foraging *Pachycrepoideus vindemmiae* females (2F_{d2}, 2F_{d4}, 2F_{d6}).

already present on the host (i.e., ovicide) before laying (Goubault et al., 2004). In contrast, when hosts have been parasitized for a longer period (i.e., indirect competition situations), the chances of winning the larval competition decrease and are <40% when hosts have been parasitized for 24 h (Goubault et al., 2003), as was the case in our experiments.

P. vindemmiae females modified their patch use decisions according to their information level about the environment. When exploiting a patch alone, females that had already experienced an important level of competition behaved differently from females that had never encountered any competitor. Such a modification of foraging behavior due to earlier competition has only been shown in a few studies (Hoffmeister et al., 2000; Michaud and Mackauer, 1995; Visser et al., 1990, 1992b), and the decisions of *P. vindemmiae* females clearly differed from those found in other species. Females of *L. heterotoma* (Visser et al., 1990, 1992b), *Monoctonus paulensis* (Michaud and Mackauer, 1995), or *Ageniaspis fuscicollis* (Hoffmeister et al., 2000) self-superparasitized hosts more frequently when they had previously experienced competition. In contrast, about 60% of *P. vindemmiae* females that had experienced previous competition left the patch during the first 15 min of the test without ovipositing. This behavior that allows the females to avoid losing time in a poor-quality habitat (i.e., where competition level is high) and to invest this time in the search for a better habitat, appears adaptive only if better patches are easily available. *P. vindemmiae* is a generalist pupal parasitoid attacking many dipteran species such as the fruit fly *Drosophila melanogaster* Meigen, and the true fruit flies *Ceratitis capitata* Weidemann and *Rhagoletis* sp. (Rueda and Axtell, 1985). During summer, many host patches should be available without substantial interpatch travel time. The remaining 40% of *P. vindemmiae* females that had experienced previous competition, in contrast, invested more time in the patch but laid only a few eggs, leading to partial patch exploitation and a low rate of superparasitism. In conditions where many host patches are available, this strategy also appears advantageous because it can allow females (1) to exploit patches efficiently by selecting hosts accurately (even if it takes time) and (2) to distribute their eggs in many patches instead of depositing all their eggs in the same patch with the

risk that this patch would be destroyed (e.g., by predators or bad weather).

Other factors such as physiological state (e.g., age, egg load) can influence parasitoid patch exploitation strategies (Charnov, 1976; Mangel, 1989; Outreman et al., 2005; Rosenheim, 1999; Sirot et al., 1997) and may also affect how females respond to direct competition (Hughes et al., 1994; Stokkebo and Hardy, 2000; Visser et al., 1992b). Here, we tested the effect of female age, but this effect could not be separated from the effect of patch travel time: the older the females, the longer the “travel time” between patches they had experienced (because older females were deprived of hosts for a longer time than younger females). As predicted by the MVT (Charnov, 1976), in the absence of direct competition, patch residence time of *P. vindemmiae* females increased with the “distance” (here, the time interval) between patches. However, direct competition increased the tendency of females to leave the patches. This effect clearly depended on their age. Indeed, although there is no linear relationship between increasing age of females and their patch-leaving tendency, old females tended to stay longer in patches where conspecifics were present, and they also displayed much more interaction behaviors than younger females. Moreover, the interaction behaviors expressed by old females were more aggressive than those expressed by younger females. This age effect could be explained by older females becoming time limited, hence the higher value of the hosts for them. Recently, Wajnberg et al. (2004) have shown that competitive interactions between females strongly influence patch residence time in *Trissolcus basalidis*: contacts and fights with conspecifics increase patch-leaving tendency. In our case, *P. vindemmiae* females tended to avoid contests by leaving the patch early. The females seemed to remain in the patch and to become aggressive only when host value increased (i.e., when female age and/or patch travel time increased). In fact, *P. vindemmiae* females are able to bite or strike each other with their antennae (Goubault M, unpublished data), leading to time and energy wastage and to the risk of injury (although we never observed *P. vindemmiae* females losing body parts or being killed, as seen in some species; Lawrence, 1981; Pérez-Lachaud et al., 2002). Therefore, leaving patches early when conspecifics are present appears adaptive. Such patches may

even be avoided at distance by the females as shown in some species (Castelo et al., 2003; Janssen et al., 1995).

Finally, in contrast to the predictions of the war of attrition model (Maynard-Smith, 1974; Visser et al., 1992a), it appears that in *P. vindemmiæ*, while a part of the population almost immediately leaves the patch, the other part stays (but not longer than if they were alone), (super)parasitizes, and gets involved in aggressive contacts. Consequently, neither the retreaters nor the remainers plays a war of attrition strategy and a Hawk-Dove-like polymorphism of patch exploitation strategies seems to exist in this parasitoid species.

In fact, as pointed out by Giraldeau and Caraco (2000) and van Alphen et al. (2003), theoretical models on group foraging strategies are still underdeveloped, and empirical data are lacking not only on parasitoids searching for hosts but also on predators searching for prey or herbivores searching for plants. According to current models, foragers should leave the patch earlier when under competition than when foraging alone, provided that they do not interfere (directly or indirectly) with one another. On the contrary, they should stay longer in situations of interference (Sjerps and Haccou, 1994; van Alphen, 1988; Visser et al., 1992a). Even if these predictions are supported by some empirical results (Field et al., 1998; Visser et al., 1990), by this study we have shown that other behavioral strategies need to be considered. More specifically, the current theory may not be applicable when (1) finding other patches is not a limiting factor or (2) female-female contests are costly in time and energy or can lead to serious injuries. Accordingly, new models need to be developed in order to take these parameters into account. The effect of competition experience as well as the forager's physiological state also need to be integrated in these models because they clearly affect the group foraging strategies of animals.

We are grateful to E. Wajnberg for his valuable comments on earlier versions of this manuscript and to Ian Hardy and two anonymous reviewers for their helpful comments. We thank M. Rault, C. Jammoneau-Paty, and S. Dourlot for their technical assistance. M.G. was supported by a grant from the French Ministry of Research.

REFERENCES

- Bernstein C, Kacelnick A, Krebs JR, 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *J Anim Ecol* 60: 205–225.
- Castelo MK, Corley JC, Desouhant E, 2003. Conspecific avoidance during foraging in *Venturia canescens* (Hymenoptera: Ichneumonidae): the roles of host presence and conspecific densities. *J Insect Behav* 16:307–318.
- Charnov EL, 1976. Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136.
- Collett D, 1994. Modeling survival data in medical research. London: Chapman and Hall.
- Cox DR, 1972. Regression models and life tables. *Biometrics* 38:67–77.
- Duquet M, 1995. Glossaire d'écologie fondamentale. Paris: Nathan.
- Field SA, Calbert G, Keller MA, 1998. Patch defence in the parasitoid wasp *Trissolcus basalis* (Insecta: Scelionidae): the time structure of pairwise contests, and the 'waiting game'. *Ethology* 104:821–840.
- Giraldeau LA, Caraco T, 2000. Social foraging theory. Princeton: Princeton University Press.
- Godfray HCJ, 1994. Parasitoids: behavioral and evolutionary ecology. Princeton: Princeton University Press.
- Goss-Custard JD, Durell SEA le V Dit, 1987. Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference. *J Anim Ecol* 56: 521–536.
- Goubault M, Fourrier J, Krespi L, Poinot D, Cortesero AM, 2004. Selection strategies of parasitized hosts in a generalist parasitoid depend on patch quality but also on host size. *J Insect Behav* 17: 99–113.
- Goubault M, Plantegenest M, Poinot D, Cortesero AM, 2003. Effect of expected offspring survival probability on host selection in a solitary parasitoid. *Entomol Exp Appl* 109:123–131.
- Grandgirard J, Poinot D, Krespi L, Nénon JP, Cortesero AM, 2002. Costs of the secondary parasitism in the facultative hyperparasitoid *Pachycrepoideus dubius*: does host size matter? *Entomol Exp Appl* 103:239–248.
- Hardy ICW, Blackburn TM, 1991. Brood guarding in a bethylid wasp. *Ecol Entomol* 16:55–62.
- Hassell MP, Varley GC, 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* 223: 1133–1137.
- Hoffmeister TS, Thiel A, Kock B, Badendriener D, Kuhlmann U, 2000. Pre-patch experience affects the egg distribution pattern in a polyembryonic parasitoid of moth egg batches. *Ethology* 106: 145–157.
- Hughes JP, Harvey IF, Hubbard SF, 1994. Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): interference—the effect of mature egg load and prior behavior. *J Insect Behav* 7:433–454.
- Janssen A, van Alphen JJM, Sabelis MW, Bakker K, 1995. Odour-mediated avoidance of competition in *Drosophila* parasitoids: the ghost of competition. *Oikos* 73:356–366.
- Lawrence PO, 1981. Interference competition and optimal host selection in the parasitic wasp, *Biosteres longicaudatus*. *Ann Entomol Soc* 74:540–544.
- Mangel M, 1989. Evolution of host selection in parasitoids: does the state of the parasitoid matter? *Am Nat* 133:688–705.
- Maynard-Smith J, 1974. The theory of games and the evolution of animal conflicts. *J Theor Biol* 47:209–221.
- McCullagh M, Nelder JA, 1989. Generalized linear model, 2nd ed. London: Chapman and Hall.
- Michaud JP, Mackauer M, 1995. Oviposition behavior of *Monoctonus paulensis* (Hymenoptera: Aphidiidae): factors influencing reproductive allocation to hosts and host patches. *Ann Entomol Soc* 88: 220–226.
- Neveu N, Kacem N, Nénon JP, 1996. A method for rearing *Trybliographa rapae* W. on *Delia radicum* L. OILB/SROP Bull 19: 173–178.
- Outreman Y, Le Ralec A, Wajnberg E, Pierre J-S, 2005. Effect of within and among patch experiences on the patch leaving decision rules in insect parasitoids. *Behav Ecol Sociobiol* (in press).
- Pérez-Lachaud G, Hardy ICW, Lachaud JP, 2002. Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biol Control* 25:231–238.
- Rosenheim JA, 1999. The relative contributions of time and eggs to the cost of reproduction. *Evolution* 53:376–385.
- Rueda LM, Axtell RC, 1985. Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and the other muscoid flies associated with poultry and livestock manure. North Carolina Agric Res Serv Bull; 278:2.
- Siroit E, Ploye H, Bernstein C, 1997. State dependent superparasitism in solitary parasitoid: egg load and survival. *Behav Ecol* 8: 226–232.
- Sjerps M, Haccou P, 1994. Effects of competition on optimal patch leaving: a war of attrition. *Theor Popul Biol* 46:300–318.
- Stokkebo S, Hardy ICW, 2000. The importance of being gravid: egg load and contest outcome in parasitoid wasp. *Anim Behav* 59: 1111–1118.
- van Alphen JJM, 1988. Patch-time allocation by insect parasitoids: superparasitism and aggregation. In: Population genetics and evolution (de Jong G, ed). Berlin: Springer-Verlag; 215–221.
- van Alphen JJM, Bernstein C, Driessen G, 2003. Information acquisition and time allocation in insect parasitoids. *Trends Ecol Evol* 18:81–87.
- van Lenteren JC, 1981. Host discrimination by parasitoids. In: Semiochemicals, their role in pest control (Nordlund DA, Jones RL, Lewis WJ, eds). New York: Wiley; 153–179.
- Venables WN, Ripley BD, 1997. Modern applied statistics with S-plus, 2nd ed. New York: Springer-Verlag.

- Visser ME, van Alphen JJM, Hemerik L, 1992a. Adaptive superparasitism and patch time allocation in solitary parasitoids: an ESS model. *J Anim Ecol* 61:93–101.
- Visser ME, van Alphen JJM, Nell HW, 1990. Adaptive superparasitism and patch time allocation in solitary parasitoids: the influence of the number of parasitoids depleting a patch. *Behaviour* 114:21–36.
- Visser ME, van Alphen JJM, Nell HW, 1992b. Adaptive superparasitism and patch time allocation in solitary parasitoids: the influence of pre-patch experience. *Behav Ecol Sociobiol* 31:163–171.
- Wajnberg E, Curty C, Colazza S, 2004. Genetic variation in the mechanisms of direct mutual interference in a parasitic wasp: consequences in terms of patch-time allocation. *J Anim Ecol* 73:1179–1189.