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Testing competing measures of profitability for mobile resources

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Abstract Optimal diet theory often fails to predict a forager's diet choice when prey are mobile. Because they escape or defend themselves, mobile prey are likely to increase the forager's handling time, thereby decreasing its fitness gain rate. Many animals have been shown to select their prey so as to maximize either their fitness gain or their fitness gain rate. However, no study has yet compared directly these two measures of profitability by generating testable predictions about the choice of the forager. Under laboratory conditions, we compared these two measures of profitability, using the aphid parasitoid *Aphidius colemani* and its host, *Myzus persicae*. Fitness gain was calculated for parasitoids developing in each host instar by measuring life-history traits such as developmental time, sex ratio and fecundity. Fitness gain rate was estimated by dividing fitness gain by handling time, the time required to subdue the host. Fourth instar aphids provided the best fitness gain to parasitoids, whereas second instar aphids were the most profitable in terms of fitness gain rate. Host choice tests showed that *A. colemani* females preferred second instar hosts, suggesting that their decision maximizes fitness gain rate over fitness gain. Our results indicate that fitness gain rate is a reliable predictor of animal's choice for foragers exploiting resources that impose additional time cost due to their mobility.

Keywords Fitness · Handling time · Parasitoids · Optimal diet

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Introduction

Animals are expected to select resources that maximize their lifetime fitness. The optimal diet theory (ODT) has been successful in predicting the diet choice of a large number of animals (Stephens and Krebs 1986; Sih and Christensen 2001). While the ODT works generally well for foragers that exploit motionless or sessile prey, it often fails to predict adequately the choice of foragers when prey are mobile (Sih and Christensen 2001). By escaping or defending themselves, mobile prey add time and energy costs, in the form of either pursuit and capture, both of which reduce the prey's profitability.

Most models estimate prey profitability in terms of fitness return. Direct measures of fitness are difficult to obtain, and biologists usually rely on indirect measures that give absolute values, such as development time, body size, longevity or fecundity (Roitberg et al. 2001). However, in a resource acquisition context, any time cost to the forager

must be included in the estimated fitness return associated with a particular resource. When prey defend themselves, their profitability is reduced by the energy and time needed to subdue them. The inclusion of such a behavioural temporal component in the evaluation of a prey's profitability would generate better predictions concerning foragers' choices.

The ODT is usually tested in animals that forage for food, but it could also apply to the exploitation of hosts by insect parasitoids. These are ideal model organisms to study the link between host profitability and fitness because the host is the only resource available to the immature parasitoid during its development. Host quality is therefore of critical importance for the fitness of both the immature and adult parasitoids (Eggleton and Gaston 1990; Godfray 1994; Godfray and Shimada 1999; Brodeur and Boivin 2004). Moreover, female parasitoids must also often overcome host behavioural defences. These behavioural defences influence both host profitability and parasitoid behaviour, as in the hyperparasitoid *Syrphophagus aphidivorus* that exploits primary parasitoids present either as a larva in live and mobile aphids or as a pupa in dead and immobile aphids (mummies) (Buitenhuis et al. 2004). Parasitized aphids take longer to be subdued because they are mobile and fight when attacked, whereas aphid mummies cannot escape. As predicted, female *S. aphidovorus* perform better (higher intrinsic rate of increase) and prefer to lay their eggs in mummies rather than in live aphids.

Parasitoids can be confronted to patches of hosts of varying instars and hence quality (Harvey et al. 1994; Cloutier et al. 2000, 2005). The profitability of parasitoid's hosts can be measured in terms of the physiological consequences on their offspring. Parasitoid fitness can therefore be estimated from proxies such as body size at emergence, developmental time, longevity and fecundity (Roitberg et al. 2001). It has generally been assumed that late instar hosts, because they provide more nutrients, are more profitable to parasitoids (reviewed by Godfray 1994). However, larger hosts also tend to defend themselves more efficiently than smaller individuals (Brodeur et al. 1996; Walker and Hoy 2003). They can inflict injuries to the parasitoid (Brodeur et al. 1996) and impose time costs that decrease their profitability. An increase in time and energy costs when large prey are consumed has been observed in other species (Griffiths 1980b), such as coccinelids, web spiders or ant-lion larvae, which all take time to subdue large prey that may inflict them injuries. Even sit-and-wait predators, such as constricting snakes, expend a lot of energy and time subduing their prey.

When exploiting resources, animals can choose between two strategies: either maximize their gain or maximize their rate of gain (which is often see as time minimization)

(Schoener 1971; Hixon 1982). Which of these strategies should be favoured depends on the constraints the animal is facing. For example, if an animal has fixed energy requirements, it should minimize the time spent acquiring this energy in order to maximize its lifetime fitness. The reverse is expected for animals that have a fixed amount of time to devote to foraging; here, the energy gain should be maximized (Schoener 1971).

Similarly, insect parasitoid females can be either time- or egg-limited (Rosenheim 1999). Female parasitoids can run out of eggs before dying (egg-limited) or, on the other hand, may die without having laid all their eggs (time-limited). Therefore, a maximization of gain rate would suggest that parasitoid females are time-limited while a maximization of the gain would suggest that they are egg-limited.

Although both gain and gain rate have been found to predict the behaviour of different animal species adequately (Cowie 1977; Lemon 1991; Gils et al. 2003), no single study has compared these two measures of profitability by evaluating their effectiveness at predicting the diet choice of a forager. In this study, we tested whether fitness gain or fitness gain rate best accounted for host selection of parasitoid females.

Methods

Study organisms

Aphidius colemani (Viereck) (Hymenoptera, Braconidae, Aphidiinae) is a solitary aphid parasitoid of several Aphididae species, including the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera, Aphididae) (Starý 1975). Parasitoid females oviposit in the haemocoel of the host, and during subsequent larval development the immature parasitoid feeds on aphid tissues. At the end of parasitoid larval development, the host is killed, and only its cuticle remains. This so-called "aphid mummy" serves as a shelter, within which the parasitoid spins a cocoon, pupates and emerges as a free-living adult. Parasitoid females typically exploit aphid colonies composed of individuals of different instars (Kouamé and Mackauer 1991; Cloutier et al. 2000; Colinet et al. 2005).

Aphids are small, sedentary, plant-sucking insects that often form dense aggregations. *Myzus persicae* has a complex life cycle, involving both sexual and parthenogenetic reproduction as well as seasonal heteroecy. Aphids are exploited by a wide array of natural enemies (predator, parasitoid, entomopathogen) and have evolved a variety of individual (kicking, dropping) and group defences (release of alarm pheromone, dilution effect) (see Villagra et al. 2002 and references therein).

A colony of *M. persicae*, established from individuals collected in greenhouses from the Horticultural Research and Development Center (HRDC), was maintained on sweet pepper plants (*Capsicum annuum* L.). *Aphidius colemani* was purchased from Koppert Canada (Scarborough, ON) and reared on *M. persicae*. Insect cultures were maintained at $20 \pm 0.5°C$ and 60–65% relative humidity and under a 16/9-h (light/dark) photoperiod; these were the standard conditions for all experiments.

In order to obtain synchronous *M. persicae* cohorts of a specific age class, about 150 apterous, parthenogenetic adult aphids were placed on a sweet pepper leaf. After 8 h, the adult aphids were removed, and the offspring were reared on excised leaves placed in a petri dish. Based on the larval developmental time of *M. persicae* under our rearing conditions, first, second, third and fourth instar larvae (here forth L1, L2, L3 and L4) and adult aphids were respectively aged 1, 3, 5, 7 and 9 days.

Parasitoid females used in this study were standardized as follows. Third instar aphids were exposed to female parasitoids for 4 h, at a parasitoid:host ratio of 1:10. Parasitized aphids were then reared in petri dishes on excised leaves of sweet pepper. Following emergence, males and females remained caged together to allow mating and had access to a dilute honey solution (20%). Prior to each test, 1- to 2-day-old naive females (no previous encounter with hosts) were selected at random.

Life-history trait measurements

A first set of experiments was conducted to measure developmental time, sex ratio and potential fecundity of parasitoid offspring developing in five different aphid instars. Female parasitoids were individually introduced in petri dishes (diameter 9 cm) containing a sweet pepper leaf with 25 aphids of either L1, L2, L3, L4 or adults. After 4 h, the female was removed and the aphids reared on the leaf until mummification. Aphids were supplied with a fresh excised leaf every 3 days. Mummies were isolated in capsules (300-μl Beem polyethylene capsules), and parasitoid emergence was monitored twice daily. Adults were collected and sexed, and females were frozen to prevent further egg production.

The secondary sex ratio (percentage of females at emergence) and development time (oviposition to emergence) were noted. Potential fecundity was estimated by counting the number of mature eggs from the ovaries at the time of emergence. Females of *A. colemani* live for about 5 days when they have access to water and hosts (Hofsvang and Hågvar 1975a), and they can lay up to 88% of their eggs during their first 2 days of life (Hofsvang and Hågvar 1975b). Females were dissected in 1% saline solution

within 48 h of emergence, the ovaries extracted from the abdomen under a stereomicroscope, the eggs expelled and the number of mature eggs recorded (a mature egg has a lemon shape).

Twelve experimental blocks were carried out per treatment (host instar), with five females per block each parasitizing 25 aphids of a given instar (L1, L2, L3, L4 and adult aphids). Sixty 60 replicates per instar were carried out (12 blocks × 5 females). In total, 1500 aphids were parasitized (300 per instar). For each life-history trait, the means per instar were calculated for each block.

Handling time

In a second set of experiments, we measured handling time: the duration of a parasitoid attack from the first antennal contact with an aphid host to the end of a successful oviposition. Typically, the following sequence of events leads to a successful oviposition: the foraging parasitoid female contacts the host with her antennae, bends her abdomen forward in preparation of oviposition and then quickly inserts her ovipositor into the host. The tests started by introducing a parasitoid female in an arena $(2 \times 1.5 \times 0.5 \text{ cm})$ with three aphids of a given instar previously placed on a sweet pepper leaf disk (diameter 1 cm). The behaviour of *A. colemani* females was video-recorded for subsequent description and quantification using the software Observer VideoPro version 5.0 (Noldus Information Technology, Leesburg, VA). Hosts were free to walk in the arena and to defend themselves. Each contact with a host leading to an insertion of the ovipositor was considered in the measurement of handling time. Tests ended when 5 min had elapsed without parasitism, and they were discarded if no oviposition occurred in the first 5 min. Females were used only once, and twenty replicates were carried out for each of the five host instars.

Host profitability

To estimate the profitability of each host instar, we used four fitness proxies: potential fecundity, number of female progeny, development time and handling time. For each aphid instar, we estimated two measures of host profitability (currencies): fitness gain and fitness gain rate. The fitness gain was estimated as:

Fitness gain:

$$\frac{(\text{potential fecundity} \times \text{number of females produced})}{\text{development time}}$$

The fitness gain rate was estimated by dividing the fitness gain by the handling time:

$$\text{Fitness gain rate}: \frac{(\text{potential fecundity} \times \text{number of females produced})/\text{development time}}{\text{handling time}}$$

Choice of host instar

We used the ranking derived from the two measures of profitability to test whether *A. colemani* female host selection maximizes fitness gain or the fitness gain rate per host. Paired choice tests were performed to determine the choice of females when offered both L2 and L3 or L3 and adults. These conditions were chosen because they enabled us to distinguish between the two following predictions, assuming that the abundances are sufficient to allow for specialisation. If female choice maximizes fitness gain, they should specialize on L3 over L2 and on adults over L3. On the other hand, if female choice maximizes fitness gain rate, we should observe the opposite choice patterns.

Host instar selection of *A. colemani* females was assessed using paired-choice tests. The order of tests was balanced. Twenty replicates were carried out for each experimental condition. In each test, a female was placed in a petri dish (diameter 5.5 cm) with 20 aphids (ten of each instar tested). During a test, the female contacted a majority (at least 75%) of the hosts present. The female's behaviour was recorded using the Noldus Observer XT version 6.0 software. The following behaviours and parameters were either directly observed or derived from the observations.

Observed behaviours:

(1) antennal contact: the parasitoid contacts the aphid with antennae
(2) bending: the parasitoid bends its abdomen
(3) insertion: the parasitoid inserts its ovipositor in the host.

Derived parameter:

(4) Proportion of acceptance: number of insertions/number of antennal contacts.

Statistical analyses

The results were analysed using regression analyses, following verification that the residuals of the regressions conformed to a normal distribution. The best model was selected based on the Aikake Information Criterion (AIC), a measure of the goodness of fit of an estimated statistical model (Akaike 1974). For life-history trait measurements, the sample sizes (>40 per model tested) were large enough

to use the AIC values directly (Anderson and Burnham 2002) while for handling time, we used the AICc (AIC corrected for small sample size; Anderson and Burnham 2002). The extent of specialization was established by testing whether the frequencies of antennal contact, abdomen bending and ovipositor insertion of the ovipositor between host instars were significantly different from a 50:50 ratio based on chi-squared analysis.

Results

Life-history traits measurements

Development time of *A. colemani* decreased with increasing host instar. Parasitoids took almost 20% longer to develop when eggs were laid in L1 hosts than when laid in adult hosts. For any given host instar, parasitoid males developed faster than females (Fig. 1a). Potential fecundity at emergence increased with host instar and was maximum when females developed in L4 aphids (Fig. 1b). Akaike Information Criterion values are shown in Appendix 1 (Electronic Supplementary Material).
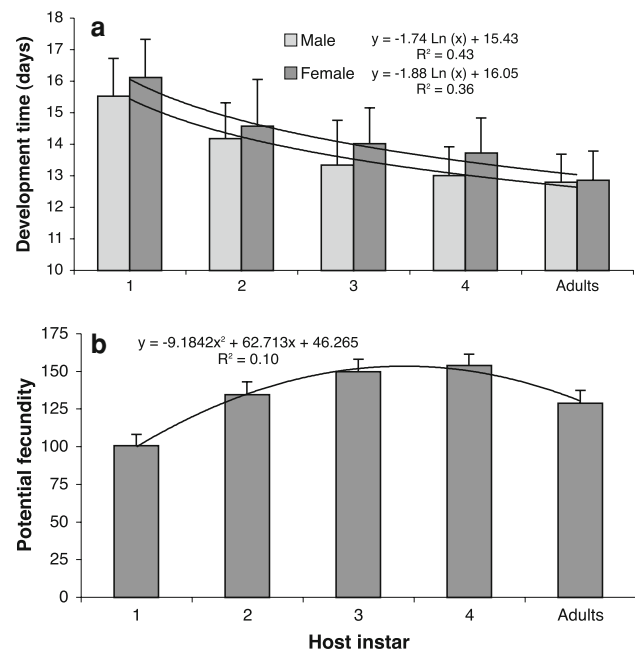

Fig. 1 Influence of host instar on development time (**a**) and fecundity (**b**) of *Aphidius colemani* parasitizing *Myzus persicae*
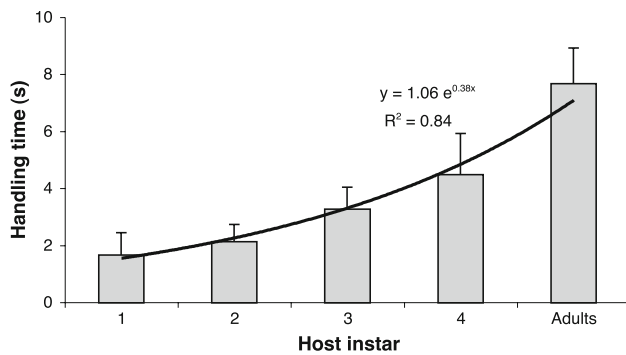
Fig. 2 Influence of host instar on the handling time of *A. colemani* parasitizing *M. persicae*

Handling time

Handling time increased with increasing host instar (Fig. 2), and females took more time to parasitize older hosts than younger hosts. Time to parasitize an adult aphid was fourfold longer than that for an L1 aphid.

Measures of profitability

Fitness gain increased with host instar, with the L4 aphids representing the best fitness return per host for the parasitoid and the L1 aphids being the least profitable (Fig. 3a).
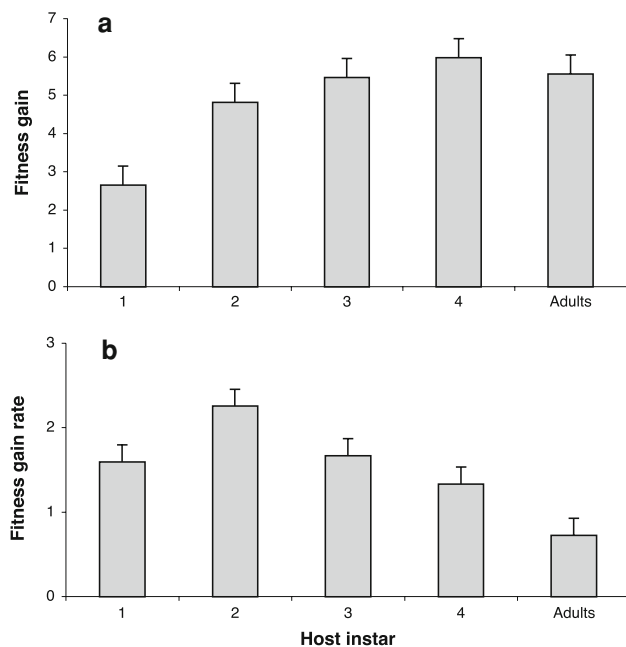

Fig. 3 Host profitability in function of host instar in *A. colemani* parasitizing *M. persicae*. **a** Fitness gain per host estimated with life-history traits measurement (development time, sex ratio, potential fecundity), **b** fitness gain rate estimated with life-history traits measurement (development time, sex ratio, potential fecundity) and handling time

However, when handling time was integrated into the measure of profitability, the relative overall profitability of aphid instar changed, and fitness gain rate was maximized for L2 hosts and declined with older host instars (Fig. 3b).

Choice of host instar

Based on host acceptance, parasitoid females significantly preferred L2 over L3 aphids and L3 aphids over adult aphids (Table 1). Of significance, for the L2 versus L3 host pair, females expressed their preference for L2 hosts even though they made more contacts with L3 hosts; i.e. they actively rejected the latter more frequently (Table 1). Frequencies of bending and oviposition behaviours followed the same pattern; females bent their abdomen and inserted their ovipositor more often with L2 aphids than with L3 and more often with L3 than adult hosts.

Discussion

Our results highlight the importance of taking time into account when estimating the profitability of diet items used to predict an animal's choice. In the case of parasitoids exploiting hosts that can defend themselves, fitness gain rate was a better currency predicting animal's choice than simply fitness gain. The result suggests that parasitoid females assess host profitability from a combination of physiological characteristics and handling time.

Although many studies have shown that animals maximize their rate of gain (Stephens and Krebs 1986), surprisingly few studies have tested concurrently two currencies to determine which is the best predictor of behavioural decisions (Kacelnik 1984; and see Ydenberg et al. 1994 for discussion). One example of such a test involves a study on central place foraging in starlings (*Sturnus vulgaris*), which confronts different predictions derived from four optimality models (Kacelnik 1984). Kacelnik (1984) found that maximization of the energy available for growth (a measure called "family gain" in his paper) was the best predictor of parent foraging decisions. To our knowledge, our study is the first that tests alternative fitness currencies in an arthropod and which shows that fitness gain rate is a better predictor of behavioural decisions than fitness gain.

Fitness gain measures: development time and fecundity

Our results support the expected concordance between fitness gain and common life-history traits in parasitoids. For instance, development time of *A. colemani* decreased with increasing host instar, a consistent pattern for parasitoids that can attack different stages of the same host

Table 1 Number of contacts, abdomen bendings and ovipositions of *Aphidius colemani* parasitizing different instars of *Myzus persicae* in the choice tests

Choice	Host instar[a]	n	$n_{contacts}$ (mean ± SE)	$n_{bending}$ (mean ± SE)	$n_{ovipositions}$ (mean ± SE)	Proportion of acceptance (mean ± SE)[b]
L2 versus L3	L2	15	11.87 ± 0.87b	9.13 ± 0.80a	9.00 ± 0.80a	0.75 ± 0.04a
	L3		16.67 ± 2.05a	6.27 ± 0.95b	3.47 ± 0.72b	0.19 ± 0.03b
L3 versus adults	L3	15	13.13 ± 1.29a	10.00 ± 0.88a	9.80 ± 0.86a	0.76 ± 0.03a
	Adults		15.13 ± 1.62a	4.07 ± 0.73b	1.47 ± 0.27b	0.09 ± 0.02b

Within an experimental condition, values followed by a different letter denote a significant difference between host instars (Chi test $\alpha = 0.05$)

[a] L2, L3, Second and third instar larvae, respectively

[b] The proportion of acceptance represents the number of ovipositions in a given instar divided by the number of antennal contacts. SE, Standard error

species (Mackauer and Sequeira 1993; Harvey et al. 1994). Koinobiont parasitoids (whose hosts continue to feed, grow and develop following parasitization) adapt their growth trajectories to the nutritional and physiological attributes of the host. Likely, *A. colemani* developing in early aphid instars would favour increased body size and fecundity (the two traits being correlated) over a shorter development time. However, those developing in large aphid nymphs or adults would allocate extra nutritional resources to maximize all life-history traits. Differential development rates may have important consequences on both parasitoid survival and competitive interactions. A shorter development time would reduce the risks of mortality from natural enemies, as predicted by the slow-growth-high-mortality hypothesis (Benrey and Denno 1997). Parasitoids that develop faster would also have the competitive advantage of being the first ones to exploit resources from the habitat.

Reproductive success in *A. colemani* is correlated with host size at the time of parasitization with L4 hosts providing females with the highest potential fecundity. Similar results have been reported for *Aphidius nigripes* (Cloutier et al. 2000), but our results do differ from those of Qayyum (2001) where the potential fecundity of *A. colemani* reared on *M. persicae* increased linearly with host age. However, in the latter study, a different biotype of parasitoid was used, and the aphids were reared on a different plant species (*Brassica oleracea*), which possibly modified the impact of host instar on the females' fecundity.

Aphidius colemani does not perform equally well on all instars of *M. persicae*. Based on our measures of life-history traits, parasitoid females should select L4 instar aphids if they rely on fitness gain to estimate host profitability.

Fitness gain rate measures: handling time

Handling time generally increases with prey size (Griffiths 1980b), as has been observed in shore crabs (*Carcinus maenas*) where handing time has recently been demonstrated to be the most important factor explaining their

prey-handling behaviour (Rovero et al. 2000). Similar results can also be found in other animals [insects, Griffiths 1980a; fish, Gill and Hart 1994; mammals, Griffiths 1980b; a number of aphid parasitoid species (*Ephedrus cerasicola*, Hofsvang and Hågvar 1986; *Monoctonus paulensis*, Chau and Mackauer 2001; *Lipolexis oregmae*, Walker and Hoy 2003)].

In our study, late host instars were more profitable to *A. colemani* in terms of fitness gain, but they imposed a significant cost because of increased handling time. Handling time, which included time required to subdue host and oviposit, increased with increasing host instar, an expected trend as older aphids tend to escape and fight more frequently and more aggressively than younger aphids (see Villagra et al. 2002 and references therein). Parasitoid females thus have to invest more time to parasitize an older host. *Aphidus colemani* does not have the same ability to attack all instars of *M. persicae*. Based on our estimation of handling time, parasitoid females should neglect large hosts if they rely on fitness gain rate to estimate host profitability.

Profitability and choice of host instar

The ODT predicts that an organism should specialize on the most profitable resource when sufficiently abundant and become a generalist with no preference otherwise. Our findings do not support either prediction; parasitoid females showed behavioural plasticity towards host acceptance but expressed partial preferences for one host instar. This preference for the host that provided the highest rate of gain (as seen in host choice test) is consistent with the hypothesis that the parasitoids have been selected to maximize gain rate rather than simply gain. The type of partial preference we have observed for *A. colemani* has been reported in virtually every test of ODT (Stephens and Krebs 1986) and is usually attributable to violations of some of the model's assumptions. For instance, it is unlikely our female parasitoids were

omniscient. More likely, they had to sample an aphid patch to learn how many hosts of each type were available. Moreover, females did not experience unchanging rates of encounter with each host type within the patch as they parasitized the preferred hosts. As patch quality declined with the abundance of the most profitable hosts, the parasitoid female reduced the density of the most profitable host such that a generalist policy became optimal. We are confident, therefore, that the host preferences we observed in our tests indicate that parasitoids have been selected to maximize gain rate rather than total gain.

Maximizing the rate of fitness gain rather than fitness gain should be optimal in other activities, such as reproduction, where animals look for resources and where costs are important. Male insect parasitoids can be limited in either their sperm stock or time (Boivin et al. 2005; Damiens and Boivin 2006). The fact that males adjust their patch residence time based on the availability of virgin females tends to support the fact that males are selected to optimize the rate of female acquisition rather than the total number of females mated per patch (Martel et al. 2008).

This maximization of gain rate suggests that *A. colemani* females are time-limited. Time limitation in parasitoids is expected when the female is likely to die before having laid all its eggs (Seventer et al. 1998; Rosenheim 1999). Our data are consistent with the notion that parasitoid females can assess their rate of fitness gain, but we have not identified the proximate mechanisms involved. Several hypotheses could be examined. Recently, the egg parasitoid *Trichogramma brassicae*, has been shown to have a fixed innate estimate of habitat quality and to exploit host patches according to this estimate (Wajnberg et al. 2000). Such innate estimates would be expected for specialist species, but they are unlikely to be effective for generalist parasitoids, such as *A. colemani*, which can parasitize hosts from different species that vary in terms of size and quality. For such generalist species, estimation of host profitability is more likely learned. Mechanisms such as memory window could provide an animal with an estimation of the average rate of gain based on its last encounters (Valone 1992) and has already been proposed to explain how parasitoids could forage optimally (Pierre et al. 2003). Alternatively, parasitoid females may base their estimate of host profitability on their first few encounters. Recent empirical evidence of this mechanism has been reported in the egg parasitoid *Anaphes victus* that estimates patch quality based on the first patch encountered rather than on a fixed innate estimate (Boivin et al. 2004). Which proximate mechanisms parasitoid females are using to assess their fitness gain rate remain to be examined.

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