Patch time allocation in male parasitoids

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Abstract. 1. Patch time allocation has been mostly studied in female parasitoids exploiting patches of hosts. Different parameters such as oviposition, host encounters, patch quality, etc. have been repeatedly shown to modify the time females invest on hosts.

2. Male parasitoids are expected to maximise their lifetime fitness by maximising the number of females inseminated during their life. Because they can be sperm and/or time limited, they should optimise their time allocation on emergence patches.

3. Patch time allocation thus appears to be an important question for both male and female parasitoids.

4. In this study, we determined the parameters used by males of the egg parasitoid *Trichogramma turkestanica* to decide when to leave the emergence patch. Among the different patch-leaving parameters tested, only contacts with parasitised hosts and presence of virgin females significantly influenced the patch-leaving tendency.

5. Our results suggest that males express behaviours that could enable them to optimise their patch exploitation time, as females do, but using different strategies.

Key words. Hymenoptera, marginal value theorem, optimal foraging, patch leaving decision, reproductive strategies, *Trichogramma turkestanica*.

Introduction

Optimality foraging models predict optimisation of an organism's behaviour in order to maximise their lifetime fitness gain. Foraging for resources (food, mate, etc.) is well suited for optimality approaches as organisms should weight foraging costs (in time, energy, risks) against potential gains. Optimal foraging has thus become an important paradigm in our quest to understand animal behaviour (Stephens & Krebs, 1986). In insect parasitoids, optimal foraging models have been applied mostly to host exploitation. Female parasitoids allocate progeny based on host size and abundance in order to optimise their rate of oviposition per time unit (reviewed by Waage, 1986). Female parasitoids also allocate the sex of their progeny based on competition among mates (Hamilton, 1967), host quality (size, species, and sex) (Charnov, 1979; Charnov *et al.*, 1981), position in oviposition sequence (Suzuki *et al.*, 1984; Wajnberg, 1993), or population's sex ratio (Rotary & Gerling, 1973; Werren & Charnov, 1978).

Optimality models have also been used to describe the allocation of time by female parasitoids exploiting patches of hosts (recently reviewed by Wajnberg, 2006). When a female parasitoid exploits a host patch, the quality of the patch decreases as she parasitises hosts and the Marginal Value Theorem (MVT) (Charnov, 1976) predicts that the female should leave the patch when the instantaneous rate of fitness gain reaches a marginal value that corresponds to the mean rate of fitness gain that can be achieved in all patches in the habitat. In the MVT model, patch time allocation depends on two factors: the quality of the patch and the travel time to reach it. The predictions associated with the MVT are: (i) females should stay longer on good quality patches; (ii) females should stay longer when travel time between patches increases; and (iii) all patches should be reduced to the same level of profitability before leaving. Proximate behavioural mechanisms have been described in several parasitoid species. A female enters a host patch with a responsiveness (or motivation) level that decreases with time and oviposition, causing the female to leave when this level reaches a threshold (Waage, 1979). This proximate mechanism can be based on either an incremental effect, when an oviposition increases the motivation level resulting in a longer residence time (Waage, 1979; Nelson & Roitberg, 1995), or a decremental (so-called *countdown*) effect, when an oviposition results in a decrease in the motivation level leading to shorter residence time in the

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patch (Driessen & Bernstein, 1999; Wajnberg *et al.*, 1999; Boivin *et al.*, 2004).

Many optimality models, including patch time allocation, have been proposed for, and tested on female parasitoids (but see Parker & Stuart, 1976; Parker, 1978). This probably reflects the impression that, in insect species, it is the female that expresses complex behaviours linked to reproduction and that males maximise their fitness by mating with the maximum number of females (Bateman, 1948). We suggest that males should also obtain higher lifetime fitness by leaving a patch at an optimal moment rather than staying to mate all available females. The lifetime fitness gain of a male parasitoid is obtained through the numbers of daughters it sires as most Hymenoptera parasitoids reproduce by arrhenotokous parthenogenesis in which males are not related to the sons of the females they mate. The fitness gain is thus influenced by the number of females mated but also to the quality of these females (i.e. their fecundity, longevity, mating status, etc.) and to the quantity of sperm transferred at each mating. As a result, male parasitoids, and not only females, should use strategies that optimise their mate acquisition throughout their life to maximise their lifetime progeny production.

Maximisation of the lifetime mate acquisition and progeny production depends on the sperm production and allocation by males. Recent data indicate that male parasitoids have species-specific strategies of sperm production and allocation. The lifetime production of gametes can be used to classify female parasitoids as proovigenic when they emerge with all their egg supplies or synovigenic when they produce eggs during their adult life (Flanders, 1950; Jervis *et al.*, 2001). In a similar fashion, males can be prospermatogenic when they emerge with all their sperm stock or synspermatogenic if they produce sperm during their adult life (Boivin *et al.*, 2005). This suggests that sperm production incurs non-trivial cost for male parasitoids and therefore that selection should act on behaviours that optimise sperm use. These behaviours could even express themselves after sperm depletion, as in some species males continue to mate when sperm depleted (Gordh & DeBach, 1976; García-González, 2004). In *Trichogramma turkestanica* (=*evanescens*) Meyer (Hymenoptera: Trichogrammatidae), sperm-depleted males continue to mate and, while they do not transfer sperm, they transfer seminal fluid, preventing subsequent males to fully inseminate the female. A female mated by a sperm-depleted male has to mate with three additional males to fill her spermatheca (Damiens & Boivin, 2006).

In gregarious parasitoid species, where several individuals can develop per host, and quasi-gregarious species that attack aggregated hosts, several individuals emerge on a host patch and on-patch mating generally occurs before emigration from the patch. The sperm capacity of males of several of these species is higher than that needed to inseminate all females on a patch (Gordh & DeBach, 1976; Ode & Strand, 1995) and males therefore disperse with sperm still available (Martel & Boivin, 2007) searching for off-patch females to inseminate. This mating structure where mating occurs both on- and off-patch is called partial local mating (Hardy, 1994), and occurs in many species (Kazmer & Luck, 1991; West & Herre, 1998; Gu & Dorn, 2003). For these males, and especially in time-limited species, time can

then be a limiting factor and behaviours should tend to optimise time allocation by maximising the number of females inseminated during the life of a male. How much time to invest in a patch before leaving is therefore a question as important for male as for female parasitoids.

As an emergence patch is gradually depleted of its virgin females, males will encounter an increasing proportion of mated females. Mating with an already mated female brings a variable fitness to a male depending on sperm precedence (utilisation of sperm from each male stored by a female). While in most insects there is last male sperm precedence, that is the last male to mate sires more progeny (Arnaud, 1999; reviewed by Simmons, 2001), in most parasitoid wasps the first male to mate fathers more offspring than the subsequent ones (reviewed by Quicke, 1997). In *T. turkestanica*, the second male mating a female sires only about 10–20% of the female's progeny (Damiens & Boivin, 2006). Males thus face a trade-off between continuing to exploit a patch with a decreasing quality and leaving that patch to search for off-patch mates.

In this paper, we determined the parameters that are used by male parasitoids to leave the emergence patch to search for off-patch mates. We thus observed male egg parasitoids from their emergence until they left the host patch. Using a Cox regression model, their behaviours and encounters with females and parasitised hosts were then used to determine the factors used by males to decide when to leave the patch.

Materials and methods

Insects

Trichogramma turkestanica is an egg parasitoid attacking mainly Lepidoptera. Males are prospermatogenic (Boivin *et al.*, 2005) and emerge with all their sperm stock. However, their sperm supply is higher than what is needed to inseminate the available females on the patch (Boivin & Lagacé, 1999; Damiens & Boivin, 2005) and most males disperse with enough sperm to inseminate off-patch mates (Martel & Boivin, 2007).

The strain used in this study originated from Egypt. The cultures were maintained at $25 \pm 1\,°C$, $50 \pm 5\%$ RH, and LD 16:8 h on eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). Before emergence, the insects were maintained under the conditions of the culture but experiments were conducted under ambient conditions ($23 \pm 2\,°C$, 40–70% RH).

Patch preparation

One less than 24 h-old mated female, unfed and taken from the culture, was provided with ca. 100 cold-killed host eggs on a filter paper. All ovipositions were observed under a binocular magnifying glass at $40 \times$. When an interruption in abdominal contractions occurred during oviposition, the egg was considered as a daughter, and when no interruption occurred, the egg was considered as a son (Cole, 1981). For all experiments, we used these parasitised hosts with known sex to create patches of one male and five

females. This ratio corresponds to the sex ratio deposited by female *T. turkestanica* (=*evanescens*) exploiting a patch alone (Boivin & Lagacé, 1999). Host eggs were glued on a strip made of 3M Post-it® message pad of 9×4 mm which was itself glued in the centre of a filter paper of a diameter of 45 mm.

Patch residence time

Nine days after oviposition, the prepared patch was placed on a Petri dish, just before the onset of light. Observations started as soon as the male emerged, generally around 15 min before females (Doyon & Boivin, 2006) and ended when he left the patch (delimited by the filter paper) for at least 60 s, whether or not all females already emerged. All experiments were video-taped and analysed using the computer software package The Observer (Noldus, 1991). We recorded events and behaviours that were informative about patch quality for the male: male or females (i) emerging, (ii) leaving or (iii) returning on the patch; male visiting (iv) empty and (v) not yet emerged parasitised host eggs; male (vi) courtship, (vii) pursuit or (viii) mating with a virgin or mated female. Thirty-three replicates were done.

Analysis

Patch-leaving decisions used by males on a patch of females were analysed by means of a Cox proportional hazards model (Cox, 1972). A thorough description of this model can be found in the literature dealing with survival analysis (Kalbfleisch & Prentice, 1980; Collett, 1994). Its application to patch-leaving decisions in parasitoids has been described on several occasions (Haccou *et al.*, 1991; van Roermund *et al.*, 1994; Driessen & Bernstein, 1999; Wajnberg *et al.*, 1999). The proportional hazards model expresses the data in terms of patch-leaving tendency (i.e. hazard rate), which is the probability per unit of time that a male leaves the patch, given that he is still on it. The model assumes that the leaving tendency is the product between an innate leaving tendency and an exponential factor (the so-called hazard ratio) representing the joint effect of all the explanatory variables (i.e. covariates) taken into account. The equation of the model is:

$$h(t) = h_0(t)\exp\left\{\sum_{i=1}^{p} \beta_i z_i\right\} \qquad (1)$$

in which $h(t)$ is the hazard rate, $h_0(t)$ is the baseline hazard, t is the time passed since the male emerged, and β_i the regression coefficients that give the relative contributions of p covariates z_i. A hazard ratio above one indicates an increasing effect on the male's patch-leaving tendency, while a hazard ratio below one shows a reduction in the patch-leaving tendency. In this study, all covariates are time dependent. The baseline hazard is the patch-leaving tendency when all the covariates are equal to zero. Successful ovipositions and host rejections are the usual covariates used when studying females leaving decision (Haccou *et al.*, 1991; van Roermund *et al.*, 1994; Wajnberg *et al.*, 1999). Among the information available to the male to estimate patch quality, we selected parameters indicating the remaining re-

sources on the patch such as presence and contact with virgin females and unemerged hosts, and other indicating patch depletion such as mated females and empty eggs. We therefore used for our analysis male interactions with females (pursuit, courtship followed or not by mating, and mating), cumulated pursuit time, number of females present on the patch (virgin, inseminated, total), number of female's emergence and leaving, and male contacts with parasitised eggs (already emerged or not) as covariates to measure their influence on males patch-leaving tendency. This enabled us to quantify the associated incremental or decremental effect on patch residence time. Females' emergence and mating was continuously recorded to allow us to discriminate between males visiting empty or not yet emerged eggs, and between virgin and mated females when interaction occurs. The parameters were estimated from the data by means of partial likelihood maximisation (Cox, 1975). The significant effects of the covariates on the males' patch-leaving tendency were tested using a standard likelihood ratio test through an iterative procedure described in Wajnberg *et al.* (1999).

Results

The mean ($\pm$SE) patch residence time for *T. turkestanica* males was 87.74 ± 10.82 min. Most females were inseminated only once (68 out of 90 females that emerged before male's dispersal), although 19 females dispersed still virgin and 3 females were inseminated twice, resulting in an average number of matings of 2.2 ± 0.3 per male.

Fitting a Cox proportional hazards model to the data led to a final model with three significant parameters. Table 1 gives the estimated effect of the covariates that had a significant influence on the patch-leaving tendency of *T. turkestanica* males. The patch-leaving tendency was significantly decreased by a factor of 0.001 for each virgin female still present on the patch and by a factor of 0.973 with each contact with a host not yet emerged. In contrast, each contact with an empty host significantly increased the patch-leaving tendency by a factor of 1.025.

Discussion

Among the 11 covariates tested in the model, only three had a significant incremental or decremental effect on the male's

Table 1. Estimated regression coefficients (β), standard errors (SE) and hazard ratio [exp(β)] for covariates having a significant effect ($P < 0.05$) on the patch-leaving tendency of males *Trichogramma turkestanica*.

	β	SE	exp(β)	χ^2 (d.f.)	P-value
Number of virgin females	−6.908	17.08	0.001	6.2 (1)	0.013
Contact with an unemerged egg	−0.027	0.011	0.973	6.9 (1)	0.009
Contact with an empty egg	0.025	0.008	1.025	10.2 (1)	0.001

All tests were computed with all the other significant terms present in the model.

patch leaving tendency: the contacts with hosts already emerged or not, and the number of virgin females still present on the patch. All the other covariates had no effect on the patch leaving tendency including mating with a female, either virgin or already inseminated (all *P*-values >0.05).

The information used by males to decide when to leave the patch are thus the number of virgin females and the number of host eggs contacted, either emerged or not. The number of virgin females present on the patch is likely an indication of the instantaneous patch quality and, correspondingly, an increase in the number of virgin females results in an increase in males' patch time allocation. Neither the number of mated females (which are poor quality mates) nor the total number of females on the patch influenced the patch-leaving tendency of males. These data strongly suggest that males *T. turkestanica* are able to detect the presence of virgin females and discriminate them from mated ones. Male parasitoids can generally detect virgin females using sex pheromones (see Silva & Stouthamer, 1997) and the presence of such sex pheromones have been found in some *Trichogramma* species. Virgin *T. brassicae* Bezdenko females produce a substrate-borne sex pheromone that causes males to stay in the marked zone and initiate courtship behaviour (Pompanon *et al.*, 1997). Such a sex pheromone allows short-distance location of virgin females by males. The production of a substrate-borne sex pheromone by virgin females could be responsible for the increase in time spent on the patch by a male. A volatile sex pheromone has also been found in *T. brassicae* (=*maidis*), where males are attracted to females over short distances (Pintureau & Toonders, 1983). In *T. turkestanica*, two compounds from a sex pheromone have been identified in virgin females, and males react to these extracts by exhibiting a courtship response (van Beek *et al.*, 2005). In addition, male *T. turkestanica* prefer virgin females over mated ones, suggesting a discrimination capacity (Martel *et al.*, 2008). Our results thus seem to confirm the presence of a sex pheromone, either volatile or substrate borne, emitted by virgin *T. turkestanica* females.

Encounters with parasitised hosts also influenced the patch-leaving decisions of males. Encounters with unemerged hosts are probably indicating to the male that there are still potentially unemerged virgin females on the patch and males should in this case stay longer to have the opportunity to inseminate these females upon emergence. The reverse is true when males encounter hosts from which a parasitoid already emerged. These hosts are probably providing an indication of patch depletion and are thus leading to an increase in the propensity of males to leave the patch. These data suggest that males are able to detect the presence of parasitoids developing inside the host. This capacity to discriminate has been confirmed in some parasitoid species. Males from *T. brassicae* (=*maidis*) (Pintureau & Toonders, 1983), *Itoplectis maculator* (Fabricius) (Hymenoptera: Ichneumonidae) (Aubert, 1959) and *Pimpla inquisitor* Say (Hymenoptera: Ichneumonidae) (Wagner, 1909 in Pintureau & Toonders, 1983) aggregate around parasitised hosts from which females are about to emerge. In *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae), males can distinguish between parasitised and unparasitised hosts, and

prefer hosts where parasitoids are about to emerge (King *et al.*, 1969). Moreover, males from this species are more likely to stay on patches where females are close to emergence, or on patches with a female-biased sex ratio, suggesting a capacity to distinguish between hosts containing a female or a male parasitoid (Shuker *et al.*, 2005). In *Diadromus pulchellus* Westmeal (Hymenoptera: Ichenumonidae), males are attracted to hosts from which females will emerge within 48 h (Rojas-Rousse, 1973).

Results suggest that the number of matings performed by males had no influence on their patch-leaving decision indicating that under the conditions tested, males were likely not sperm-limited, or that sperm limitation had no effect. However, to be sperm limited, males must have more mating opportunities then their insemination capacity. As the male *T. turkestanica* are sperm depleted after an average of 20 matings (Damiens & Boivin, 2005) and the number of females available for males in our experiments was only five, it is unlikely that these males became sperm depleted, even if females can mate several times.

The fact that male mating had no influence on their patch-leaving tendency also suggests that mating is probably not used as a cue for patch quality. As the number of matings increases, the number of virgin females available decreases and so does patch quality. Because the initial patch quality varies depending on the number of virgin females initially available, the decrease in quality after the insemination of a virgin female will be greater in a patch with high sex ratios (proportion of males) than in a highly female-biased patch.

Our results show which parameters are used by males in their patch-leaving decisions. However, the impact of the different variables could vary depending on the conditions of the experiments (sex ratio, patch density, etc.) Females' ability to adjust their patch residence time during host patches exploitation has already been demonstrated. In most parasitoid species, females increase their patch residence time on a patch with more hosts or with a higher proportion of healthy hosts, both indicators of patch quality (recently reviewed by Wajnberg, 2006). Our results suggest that males express behaviours that could enable them to optimise their patch exploitation time, as females do, but using different strategies. We could expect males to adjust their strategy depending on time and gamete limitation. Further studies are needed to look at the functional aspects of male patch allocation.

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