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REVIEW

Éric Wajnberg

Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms

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Abstract As most parasitoids are time limited, they usually die before they have laid all their eggs. In such cases, optimal foraging theory predicts that female parasitoids will adopt behavioral reproductive strategies enabling them to maximize progeny production per unit of time. One key situation in which parasitoid females must optimize their time budget is related to the fact that most of their hosts are distributed in discrete patches in the environment. In this review, I first present the results of basic theoretical models predicting female wasp search duration on a patch of hosts. I then compile and analyze all studies investigating the effect of different factors on parasitoid patch time allocation and patch-leaving decision rules. Different patch-leaving mechanisms that were proposed to explain the results obtained are discussed, along with statistical methods that should be used to estimate them from experimental data. Finally, ideas for future research are presented.

Keywords Time-foraging strategies · Patch-time allocation · Patch-leaving rules · Optimal foraging models · Behavioral mechanisms · Statistical methods

Introduction

Insect parasitoids have been widely used to develop and test theory in behavioral and evolutionary ecology. Parasitoid host searching and oviposition strategies are directly linked to offspring production and fitness gain, making them particularly good biological models for testing optimization theories of reproductive behavior (van Alphen and Vet 1986; Godfray 1994). Some parasitoids are egg limited, running out of eggs before dying (Rosenheim 1996). However, most parasitoid species are rather time limited as females die before they can deposit all their eggs (Driessen and Hemerik 1992; Seventer et al. 1998; Rosenheim 1999). Hence, parasitoid should maximize their offspring gain per unit of time. In fact, time is often considered to be the sole mediator of the cost of reproduction (e.g., Charnov and Skinner 1984; Skinner 1985; Visser et al. 1992a; Rosenheim 1999).

In this paper, time is considered to be the main variable driving the evolutionary responses of time-limited insect parasitoids to the selective pressures of natural selection. In this context and following the seminal works of Emlen (1966) and MacArthur and Pianka (1966), a large amount of theoretical and experimental research was developed, leading to consider the foraging behaviors and especially time allocation strategies of parasitoid females to be those that have been selected to produce the higher rate of progeny production.

The main situation in which female parasitoids must optimize their time allocation strategy when exploiting their hosts comes from the fact that hosts of most species occur in discrete patches in the environment (Godfray 1994). In this review, following Hassell and Southwood (1978), a patch is defined as a spatial subunit of the foraging area in which aggregations of hosts occur. Examples of patches are aphid colonies for aphid parasitoids or host egg masses for egg parasitoids. Patches of hosts are usually of different quality (e.g., in terms of the number of hosts to attack) and, thus, of different profitability for the foraging females. Therefore, the central issue is to understand how parasitoid females should allocate their foraging time in each host patch before leaving it to find another patch in the environment. Time invested by parasitoid females to different patches has arguably probably been the most-studied problem in behavioral ecology over the past few decades (van Alphen et al. 2003).

In this paper, I successively examine: (1) the ultimate predictions of standard optimality models in behavioral ecology that indicate the optimal time parasitoid females

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É. Wajnberg (✉)
INRA, 400 Route des Chappes,
BP 167, 06903 Sophia Antipolis Cedex, France
e-mail: wajnberg@antibes.inra.fr
Tel.: +33-4-92386447
Fax: +33-4-92386557

should remain on a host patch under different environmental conditions, (2) the proximate mechanisms that have been experimentally observed on different parasitoids, and (3) a detailed discussion of patch-leaving behavioral mechanisms proposed to explain how parasitoid females determine their patch residence time and what sort of statistical tools can be used to estimate these patch-leaving rules from experimental data. Lastly, ideas for future research will be presented in the discussion.

What should females do to behave optimally?

The general framework of optimal foraging models for time-limited parasitoids assumes that females should maximize their encounter rate with unparasitized hosts (e.g., Cook and Hubbard 1977; Hubbard and Cook 1978; Comins and Hassell 1979; Henneman 1998). Such an assumption has been tested several times, both in the laboratory (e.g., Cook and Hubbard 1977; Hubbard and Cook 1978) and in the field (Stamp 1982; Waage 1983; Thompson 1986; Janssen 1989; Heimpel et al. 1996). The theoretical models that I present here follow this general assumption.

The marginal value theorem

The most important rate maximization model predicting the optimal time a parasitoid female should remain on a host patch is the Marginal Value Theorem (MVT) (Charnov 1976). This model assumes that, upon entering a patch, the rate of fitness gained by the female is initially high but progressively drops as a function of patch residence time, as available hosts are progressively depleted. In such a case, Charnov's MVT predicts that female parasitoids should leave the patch when their instantaneous rate of host encounter and exploitation falls below the average rate that can be achieved in the environment. As can be graphically seen in Fig. 1a, this theoretical model predicts that females should stay longer on patches of better quality (McNair 1982). As host encounter rate will be lower if females spend, on average, more time traveling in the environment to discover host patches, the MVT also predicts that females should stay longer on patches when they spend, on average, a larger amount of time traveling to discover patches to be exploited (Charnov 1976) (see Fig. 1b). Finally, the MVT predicts that patches of different quality should be reduced to the same level of profitability before leaving (Cook and Hubbard 1977; Bell 1991).

Despite being 30 years old, the MVT is still used and constantly being improved. It is based on several assumptions that are likely overly simplistic, missing important aspects of biological realism (Nonacs 2001). The most important assumption is that female parasitoids should "know" the average host attack rate that can be achieved in the environment. For this, they need complete information on the quality of all patches in the habitat and on the average time to reach them (Stephens and Krebs 1986), an assumption that is unlikely to occur in nature. Several theoretical studies have relaxed this assumption by considering that animals, through a continuous sampling of host patches, can assess the quality of all patches in the habitat and the average travel time to reach them (Ollason 1980; McNamara and Houston 1985, 1987). Female parasitoids do learn the features of their habitat (Turlings et al. 1993). Then, if a sufficient number of patches are visited, theoretical models that incorporate females' ability to learn result in predictions similar to those of the MVT (Ollason 1980; McNamara and Houston 1985, 1987).

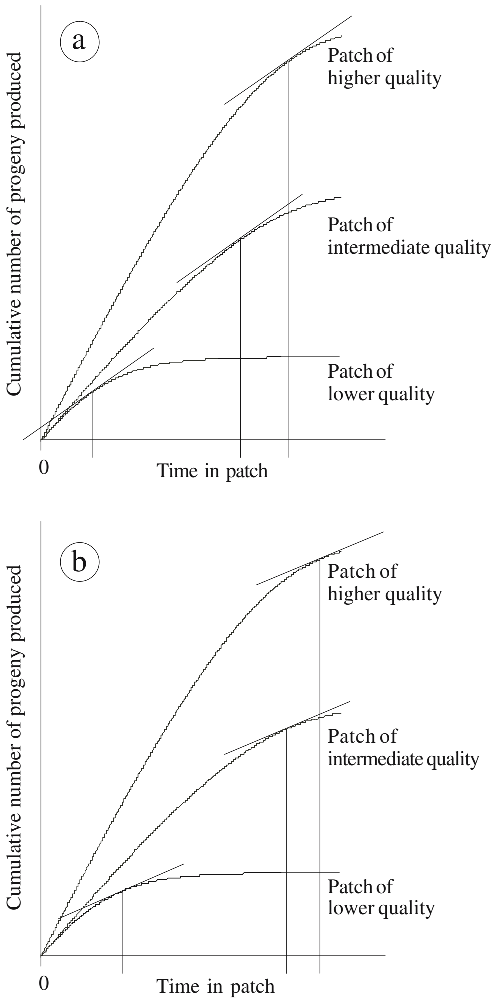

Fig. 1 A graphical representation of Charnov's (1976) Marginal Value Theorem. Both graphs are examples of the cumulative fitness curves of female parasitoids foraging on patches of three different qualities. Female parasitoids should leave the patch when their instantaneous rate of fitness gain (i.e., the slope of the cumulative fitness curve) falls to the average rate that can be achieved in the environment, which is represented by the three parallel slopes tangent to the cumulative fitness curves. **a** Patches of better quality should be exploited during a longer period of time. **b** The parasitoids have to travel, on average, a longer time before finding a patch to exploit, so the average host attack rate in the environment is lower and females should stay longer on each patch

The MVT also assumes that there is no competition between females, as they are assumed to forage alone in each patch (Yamamura and Tsuji 1987). In natural habitats, however, many female parasitoids can exploit host patches simultaneously (Godfray 1994). When several females are competing, optimal patch residence time of each of them may depend on the time that the others are willing to invest (van Alphen 1988; Wajnberg et al. 2004). Using game theory (Maynard Smith 1982), Sjerps and Haccou (1994), Haccou et al. (1999), and, more recently, Haccou et al. (2003) and Hamelin et al. (2006a,b) demonstrated theoretically that, in most cases, females should enter a "war of attrition" when foraging simultaneously on a patch. More specifically, if parasitoid females are interfering with each other, their optimal patch residence times should be longer than those predicted by the MVT.

Finally, the MVT also assumes that females avoid any mortality risks such as predation or starvation. Theoretical models based on stochastic dynamic programming (Clark and Mangel 2000), that include predation and/or starvation, show that the optimal time females should remain on a host patch is longer than the optimal time predicted by the classic, static MVT (Newman 1991; Nonacs 2001). More generally, stochastic dynamic models have been used on several occasions to find optimal patch time allocation of female parasitoids (Nonacs 2001; Wajnberg et al. 2006). On the contrary to the static MVT, their aim is to find optimal behavioral strategies, taking into account the state of the foraging females (McNamara and Houston 1986; Houston et al. 1988; Clark and Mangel 2000). As far as patch residence time is concerned and besides the effect of predation and/or starvation, dynamic programming approaches have been used to model the ability of females to learn patch quality while foraging (Keasar et al. 2001), the ability to discriminate between healthy or parasitized hosts (Li et al. 1993; Rosenheim and Mangel 1994; Keasar et al. 2001; Tenhumberg et al. 2001a), or the effect of variation in average habitat quality (Roitberg et al. 1992, 1993; Tenhumberg et al. 2001a). Optimal patch time allocation for time-limited parasitoids was also recently addressed using such a modeling approach (Wajnberg et al. 2006).

The ideal free distribution

Now, suppose that there are several parasitoid females simultaneously foraging in a habitat where several host patches can be exploited. In this context, the Ideal Free Distribution (IFD) is a simple theoretical model that predicts the stable distribution of the foragers over all available patches (Fretwell and Lucas 1970). Just like for the MVT, foragers in the IFD are assumed to "know" the quality of all patches in the habitat, and this is why individuals are referred to be "ideal." In contrast to the MVT, patches cannot be depleted and there is no time cost for traveling between patches. This last assumption is why the foraging animals are referred to as "free." Under such restrictive hypotheses, parasitoids are predicted to distribute themselves among host patches in such a way that the encounter rate with hosts is equal for all of them. Hence, host patches of better quality will contain more female parasitoids than poorer patches, as has been found in many field studies (Hassell 1978). A parasitoid foraging in a patch in which its host encounter rate is lower than the average encounter rate in the environment will move, at no cost, to a patch where its rate of fitness gain will be optimal and equal to the fitness gained by all its competitors. Therefore, the IFD is an evolutionary stable strategy (Sutherland 1996).

As such a theoretical model is based on highly unrealistic assumptions, it should only be considered a null model to which other realistic factors are added (Sutherland 1996). For example, competition between foragers is purely exploitative in the IFD. Interference competition is usually observed in insect parasitoids, however. IFD models incorporating interference produce results, especially in terms of spatial density dependence, that differ from the classic IFD model that predict host mortality to be spatially density independent (Sutherland 1983; Lessells 1985).

Adding patch depletion to the IFD provides another set of interesting predictions. Several theoretical models were developed in this way (Sutherland 1996), but the models of Cook and Hubbard (1977) and Comins and Hassell (1979) are particularly useful because, like the MVT, they predict the optimal time females should remain on host patches. These predictions are graphically illustrated in Fig. 2. When females enter a habitat containing host patches of different quality, they should first forage in the patch of higher quality in which they will achieve the highest host encounter rate. As a consequence, the patch will be depleted until it reaches a quality equal to the second best patch in the habitat. As this point, according to the IFD, parasitoids will redistribute themselves so that the two best patches will be depleted in parallel until their quality is equal to the third best patch, and so on. Hence, the classic

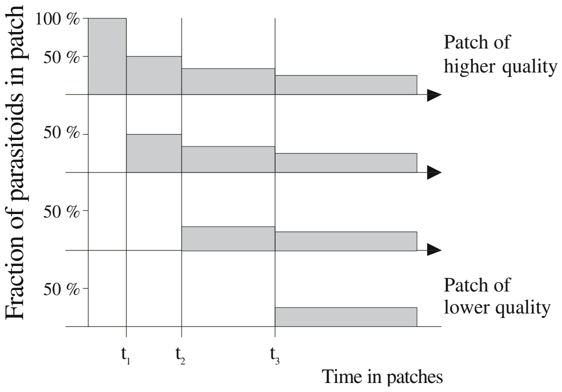

Fig. 2 A graphical representation of possible predictions of the Cook and Hubbard (1977) and Comins and Hassell (1979) models. In this figure, four patches of different qualities are present in the habitat, and female parasitoids should all initially forage on the best patch, depleting it up to the time t_1. At this time, the quality of the exploited patch equals the quality of the second best patch, and females will redistribute themselves so that the two best patches will be exploited simultaneously. The two patches will be depleted up to time t_2, in which females will again redistribute themselves equally over the three best patches, and so on (adapted from Godfray 1994)

IFD model can be considered as a snapshot, at any given instant, of such a time-varying process (Lessells 1995).

Using a series of simulation models, Bernstein et al. (1988) relaxed the assumption that parasitoids should "know" the quality of all patches in the habitat. Rather, these authors considered that animals, by sampling their environment, progressively learn the quality of the host patches to be exploited. In a non- or slowly depleting environment, results show that foragers' distribution rapidly approaches the IFD. Thus, having an innate knowledge of the quality of all host patches in the habitat is not a prerequisite for female parasitoids to achieve an ideal free distribution.

When an increasing cost of traveling between patches is included, the distribution of foraging animals follows the predictions of the IFD less and less (Bernstein et al. 1991). In some insect parasitoids, however, the time needed to travel between patches remains very low, so the IFD should be a good model to predict optimal foraging times in these animals (van Alphen and Vet 1986). Finally, the IFD assumes that all foragers are equal, despite strong differences in competitive ability, even sometimes genetically determined, as has been shown in some parasitoids (Wajnberg et al. 2004). The consequences of adding a difference in competitive ability between foragers in an IFD model are still being discussed (Sutherland 1996; van der Meer 1997).

What proximate behavioral mechanisms parasitoid females use to behave optimally?

What has been observed experimentally?

Tables 1, 2, 3, 4, and 5 give a detailed summary of all experimental studies conducted on insect parasitoids testing the effects of: (1) patch characteristics, (2) female condition, (3) previous visits to host patches, (4) abiotic conditions, and (5) other miscellaneous factors. As can be seen, many different factors were tested. A large amount of experimental work has tested the effect of increasing the number of hosts available on the patches (see Table 1b and c). Except for a couple of exceptions, female parasitoids stay longer on patches of better quality, a phenomenon known as "parasitoid aggregation" or "non-random search" (Hassell 1978). Such an effect is in agreement with the predictions of both the Marginal Value Theorem and the Ideal Free Distribution. The MVT also predicts that female parasitoids should spend more time on host patches when their waiting (i.e., travel) time between patches is high. Despite its importance in understanding the reproductive behavior of insect parasitoids, only a few studies have tested such a prediction (Cronin and Strong 1999). In all of these studies, travel time was "simulated" by holding female wasps captive for different lengths of time between successive patch visits, instead of letting them freely move between patches. Despite weaknesses in this experimental protocol and except for the results of Visser et al. (1992b) on *Leptopilina heterotoma*, results are in agreement with the MVT: the longer females have to wait before reaching a patch, the longer they stay on the patch (see Table 3e).

Only two studies have tested the third prediction of the MVT, i.e., that patches of different quality should be reduced to the same level of profitability upon leaving. This prediction has been confirmed for *Trichogramma brassicae* (Wajnberg et al. 2000), but not for *Anaphes victus* (Boivin et al. 2004). Finally, Visser et al. (1992b) showed that freshly captured *L. heterotoma* females spent, on average, less time on host patches compared to females reared in the laboratory. This result is likely due to freshly collected females estimating their habitat as being more profitable, compared to females reared in the laboratory. Thus, laboratory results should be treated with caution if accurate information on the history of the strains used is not provided.

The results in Tables 1, 2, 3, 4, and 5 provide a rich set of information leading to a better understanding of the proximate factors influencing patch time allocation strategies of insect parasitoids. Almost all of these factors could now be included in patch time allocation optimization models. Optimal foraging theorists, however, tend to ignore the behavioral mechanisms required to implement the solution of their models (Green and Ayal 1998). Parasitoid females cannot be expected to calculate optimal behaviors in the way suggested by optimization models (Houston 1987). They would be more likely expected to use proximate behavioral rules that should be both simple and robust, so as to be efficient in different environments. Females acquire information about the different features of their habitat while foraging and optimize their patch residence time accordingly (van Alphen et al. 2003). But what patch-leaving decision rules, shaped by natural selection, lead parasitoid females to be optimal foragers?

Simple rules of thumb

In the early literature, at least three simple patch-leaving rules, so-called rules of thumb, were successively described: (1) Gibb's (1962) fixed number rule proposed that female wasps should leave a patch when a fixed number of hosts had been discovered and attacked, (2) Krebs' (1973) fixed time rule suggested that females should always spend a fixed amount of time in each patch before leaving, and (3) Hassell and May's (1974) and Murdoch and Oaten's (1975) fixed giving-up time (GUT) rule assumed that females should forage on a patch as long as the time of the last host attack does not exceed some predefined fixed time. Some other rules, deriving from these ones, were also sometimes proposed [see Krebs (1973), for a useful review].

The fixed GUT strategy should provide the female with a crude estimate of patch quality. On a better-quality patch, hosts will be encountered more frequently per unit of time, leading fixed GUT foragers to invest comparatively more

Table 1 A detailed summary of all experimental studies conducted on female insect parasitoids to determine the effect of different patch characteristics on patch residence times

Tested effect	Species	Result observed	Reference
a. Effect of the surface of the patch			
	Braconidae		
	Opius dimidiatus	No effect	Nelson and Roitberg (1995)
	Figitidae		
	Pseudeucoila bochei	Increase in the patch time with the surface of the patch	van Lenteren and Bakker (1978)
b. Effect of patch quality in terms of the number of hosts available			
	Aphelinidae		
	Aphytis melinus	No effect	Reeve (1987)
	Aphidiidae		
	Aphidius colemani	Increase in the patch time with the quality of the patch	van Steenis et al. (1996)
	Aphidius funebris	Increase in the patch time with the quality of the patch	Weisser (1995)
	Aphidius nigripes	Increase in the patch time with the quality of the patch	Cloutier and Bauduin (1990)
	Aphidius rhopalosiphi	Increase in the patch time with the quality of the patch	Outreman et al. (2005)
	Aphidius rosae	No effect	Völkl (1994)
	Diaeretiella rapae	No effect	Shaltiel and Ayal (1998)
	Lysiphlebus testaceipes	Increase in the patch time with the quality of the patch	Tentelier et al. (2005)
	Braconidae		
	Asobara tabida	Increase in the patch time with the quality of the patch	van Alphen and Galis (1983)
	Cotesia glomerata	Increase in the patch time with the quality of the patch	Wiskerke and Vet (1994), Vos et al. (1998)
	Cotesia plutellae	Increase in the patch time with the quality of the patch	Wang and Keller (2002)
	Cotesia rubecula	Increase in the patch time with the quality of the patch	Wiskerke and Vet (1994), Vos et al. (1998), Tenhumberg et al. (2001b)
	Dacnusa sibirica	Increase in the patch time with the quality of the patch	Sugimoto et al. (1990)
	Dapsilarthra rufiventris	Increase in the patch time with the quality of the patch	Sugimoto et al. (1987)
	Fopius arisanus	Increase in the patch time with the quality of the patch	Wang and Messing (2003)
	Eulophidae		
	Chrysocharis pentheus	Increase in the patch time with the quality of the patch	Sugimoto and Tsujimoto (1988)
	Eurytomidae		
	Eurytoma sp. Near *tibialis*	No effect	Romstöck-Völkl (1990)
	Figitidae		
	Leptopilina boulardi	Increase in the patch time with the quality of the patch	Hertlein and Thorarinsson (1987), Varaldi et al. (2005)
	Leptopilina clavipes	Increase in the patch time with the quality of the patch	Driessen and Hemerik (1992)
	Leptopilina heterotoma	Increase in the patch time with the quality of the patch	Visser et al. (1992b), Varaldi et al. (2005)
	Pseudeucoila bochei	Increase in the patch time with the quality of the patch	van Lenteren and Bakker (1978)

Table 1 (continued)

Tested effect	Species	Result observed	Reference
	Ichneumonidae		
	Diadegma semiclausum	Increase in the patch time with the quality of the patch	Wang and Keller (2002, 2005)
	Nemeritis canescens	Increase in the patch time with the quality of the patch	Hassell (1971), Hubbard and Cook (1978), Waage (1979)
	Venturia canescens	Increase in the patch time with the quality of the patch	Amat et al. (2006)
	Pteromalidae		
	Pteromalus caudiger	No effect	Romstöck-Völkl (1990)
	Scelionidae		
	Trissolcus basalis	Increase in the patch time with the quality of the patch	Field (1998)
	Trichogrammatidae		
	Trichogramma pretiosum	Increase in the patch time with the quality of the patch	Morrison and Lewis (1981)
c. Effect of patch quality in terms of the proportion of healthy hosts			
	Aphidiidae		
	Aphidius rhopalosiphi	Increase in the patch time with the quality of the patch	Outreman et al. (2001)
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time with the quality of the patch	Visser et al. (1992b)
	Ichneumonidae		
	Diadegma semiclausum	No effect	Wang and Keller (2004)
	Mymaridae		
	Anaphes victus	Increase in the patch time with the quality of the patch	Boivin et al. (2004), van Baaren et al. (2005a,b)
	Pteromalidae		
	Pachycrepoideus vindemmiae	Increase in the patch time with the quality of the patch	Goubault et al. (2005)
	Trichogrammatidae		
	Trichogramma brassicae	Increase in the patch time with the quality of the patch	Wajnberg et al. (2000)
	Trichogramma thalense	Increase in the patch time with the quality of the patch	Keasar et al. (2001)
d. Effect of patch quality in terms of the proportion of different host instars			
	Aphidiidae		
	Aphidius funebris	No effect	Weisser (1995)
e. Effect of patch quality in terms of the hosts age			
	Scelionidae		
	Gryon obesum	Increase in the patch time with the age of the hosts	Hirose et al. (2003)
f. Effect of the presence of hosts' traces (e.g., kairomones, honeydew, feeding damages)			
	Aphelinidae		
	Aphelinus asychis	Increase in the patch time with the presence of traces	Li et al. (1997)
	Encarsia formosa	Increase in the patch time with the presence of traces	van Roermund et al. (1993, 1994)
	Aphidiidae		
	Aphidius nigripes	Increase in the patch time with the presence of traces	Cloutier and Bauduin (1990)

Table 1 (continued)

Tested effect	Species	Result observed	Reference
	Braconidae		
	Asobara tabida	Increase in the patch time with the presence of traces	Galis and van Alphen (1981)
	Fopius arisanus	Increase in the patch time with the presence of traces	Wang and Messing (2003)
	Opius dimidiatus	Increase in the patch time with the presence of traces	Nelson and Roitberg (1995)
	Figitidae		
	Leptopilina clavipes	Increase in the patch time with the presence of traces	Hemerik et al. (1993)
	Leptopilina fimbriata	Increase in the patch time with the presence of traces	Vet and van der Hoeven (1984)
	Leptopilina heterotoma	Increase in the patch time with the presence of traces	van Alphen et al. (1984), Vet and van der Hoeven (1984), Dicke et al. (1985)
	Ichneumonidae		
	Diadegma semiclausum	Increase in the patch time with the presence of traces	Ohara et al. (2003), Wang and Keller (2004)
	Nemeritis canescens	Increase in the patch time with the presence of traces	Waage (1978)
	Venturia canescens	Increase in the patch time with the presence of traces	Driessen et al. (1995), Driessen and Bernstein (1999)
	Trichogrammatidae		
	Trichogramma evanescens	Increase in the patch time with the presence of traces	Gardner and van Lenteren (1986)
g. Effect of the density of hosts' traces (e.g., kairomones, honeydew) per surface unit			
	Aphidiidae		
	Diaeretiella rapae	Increase in the patch time with the density of traces	Shaltiel and Ayal (1998)
	Braconidae		
	Opius dimidiatus	Increase in the patch time with the density of traces	Nelson and Roitberg (1995)
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time with the density of traces	Dicke et al. (1985)
	Ichneumonidae		
	Nemeritis canescens	Increase in the patch time with the density of traces	Waage (1978)
h. Effect of the time since hosts' traces deposition (e.g., kairomones, honeydew)			
	Aphidiidae		
	Diaeretiella rapae	Decrease in the patch time with an increase in the time since traces deposition	Shaltiel and Ayal (1998)
i. Effect of a preceding visit of the patch by a conspecific			
	Braconidae		
	Asobara tabida	Decrease in the patch time if there was a preceding visit	Galis and van Alphen (1981)
	Fopius arisanus	Decrease in the patch time if there was a preceding visit	Wang and Messing (2003)
	Encyrtidae		
	Epidinocarsis lopezi	Decrease in the patch time if there was a preceding visit	van Dijken et al. (1992)

Table 1 (continued)

Tested effect	Species	Result observed	Reference
	Figitidae		
	Leptopilina heterotoma	No effect	Dicke et al. (1985)
	Ichneumonidae		
	Venturia canescens	Decrease in the patch time if there was a preceding visit	Bernstein and Driessen (1996)
j. Effect of arrival of a competitor			
	Scelionidae		
	Trissolcus plautiae	Increase in the patch time	Ohno (1999)
k. Effect of the presence of conspecific competitors on the patch			
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time	Visser et al. (1990)
	Ichneumonidae		
	Nemeritis canescens	Decrease in the patch time	Hassell (1971)
	Pteromalidae		
	Pachycrepoideus vindemmiae	Decrease in the patch time	Goubault et al. (2005)
l. Effect of the presence of hyperparasitoids on the patch			
	Aphidiidae		
	Aphidius funebris	No effect	Völkl et al. (1995)
	Lysiphlebus cardui	No effect	Völkl et al. (1995)
m. Effect of the presence of healthy or infested plant odours upwind			
	Ichneumonidae		
	Diadegma semiclausum	No effect	Ohara et al. (2003)
n. Effect of the presence and intensity of chemical compounds (synomones) released by the plant in response to host attacks			
	Aphidiidae		
	Lysiphlebus testaceipes	Increase in the patch time with an increase in the intensity of synomones	Tentelier et al. (2005)

time on a better than on a poorer patch. This strategy is in agreement with both the Marginal Value Theorem and the Ideal Free Distribution, and with most of the experimental results on Table 1. A fixed-number forager will conversely stay longer on a poorer patch because the fixed number of hosts to attack will be reached sooner on a better patch, while a fixed-time forager will invest the same amount of time in all patches irrespective of quality.

Using a theoretical approach, Iwasa et al. (1981) showed that the fixed GUT rule is the best strategy when there is large variance in the number of hosts among patches. When all patches are of the same quality, the fixed number rule gives the highest average host capture rate. Finally, the fixed time rule is the optimal strategy when the number of hosts per patch follows a Poisson distribution (Green 1987).

These three fixed strategies are obviously idyllically simple and do not take into account the information acquired by females while foraging on a host patch. Thus, female parasitoids should be capable of using more elaborate, dynamic patch-leaving rules. They should incorporate information about the way hosts are encountered and attacked during patch exploitation and also about inter-patch distances, the presence of competitors, etc.

More elaborate patch-leaving rules—the Waage's (1979) model

An interesting idea is that patches contain not only hosts to attack but also information about the quality of the environment. Hence, like practical statisticians, parasitoid females are likely able, on a continuous basis, to correct prior expectations about the features of their environment through information collected during the foraging process (Giraldeau 1997; Pierre et al. 2003). Such sampling processes can be simply incorporated in mechanistic patch-leaving rules like those presented above, allowing parasitoids to more efficiently track variation in habitat quality.

In this respect, the most well-known rule was proposed by Waage (1979) who suggested that female parasitoids enter a host patch with a certain tendency to remain on it. The initial responsiveness to the patch, which corresponds to a tendency to turn sharply when the edge of the patch is reached (Waage 1978), is determined by the concentration of contact kairomones and, thus, by the number of hosts available. When no hosts are encountered, the level of responsiveness is assumed to decrease linearly over time down to a threshold value at which time the turning

Table 2 A detailed summary of all experimental studies conducted on female insect parasitoids to determine the effect of different biotic conditions on patch residence times

Tested effect	Species	Result observed	Reference
a. Effect of the age of the female			
	Aphidiidae		
	Lysiphlebus cardui	Older females stay longer on the patch	Weisser (1994)
	Braconidae		
	Asobara tabida	Older females stay longer on the patch	Thiel and Hoffmeister (2004)
	Monoctonus paulensis	Older females stay longer on the patch	Michaud and Mackauer (1995)
	Ichneumonidae		
	Nemeritis canescens	Older females stay longer on the patch	Thiel et al. (2006)
	Mymaridae		
	Anaphes victus	Older females stay longer on the patch	Wajnberg et al. (2006)
	Pteromalidae		
	Pachycrepoideus vindemmiae	Older females stay longer on the patch	Goubault et al. (2005)
b. Effect of female's egg load			
	Braconidae		
	Asobara tabida	No effect	Thiel and Hoffmeister (2004)
c. Effect of mating			
	Braconidae		
	Monoctonus paulensis	Mated females stay longer than virgin females on the patch	Michaud and Mackauer (1995)
d. Effect of laboratory rearing			
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time with an increase in the time populations are reared in the laboratory	Visser et al. (1992b)
	Ichneumonidae		
	Venturia canescens	Increase in the patch time with an increase in the time populations are reared in the laboratory	Thiel et al. (2006)
e. Effect of a previous experience with hosts on different substrates			
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time if foraging on the substrate on which the female had a previous experience	Vet and Schoonman (1988), Papaj et al. (1994)
f. Effect of oviposition experiences before entering the patch			
	Aphelinidae		
	Aphelinus asychis	Experienced females stay a lower time on patch than naive females	Li et al. (1997)
g. Effect of previous contact with hosts already attacked by a conspecific			
	Braconidae		
	Monoctonus paulensis	Increase in the patch time if previous contacts with already attacked hosts	Michaud and Mackauer (1995)
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time if previous contacts with already attacked hosts	Roitberg et al. (1992)
h. Effect of a previous experience with hosts of a different species that those encountered on the patch			
	Ichneumonidae		
	Nemeritis canescens	Decrease in the patch time compared to a previous experience with the same host	Waage (1979)
i. Effect of previous contacts with conspecific females before entering the patch			
	Figitidae		
	Leptopilina heterotoma	No effect	Visser et al. (1992b)

Table 2 (continued)

Tested effect	Species	Result observed	Reference
	Pteromalidae		
	Pachycrepoideus vindemmiae	Increase in the variance of patch residence times	Goubault et al. (2005)
	Scelionidae		
	Trissolcus plautiae	Increase in the patch residence time	Ohno (1999)
j. Effect of the time spent isolated from conspecifics			
	Scelionidae		
	Trissolcus basalis	No effect	Field (1998)
k. Effect of a previous treatment at increasing concentrations with deltamethrin			
	Aphidiidae		
	Aphidius matricariae	No effect	Desneux et al. (2004)

response is no longer elicited and the patch is left. When a host is attacked, the responsiveness is increased by a given increment. Even though this has never been accurately studied, the increment size was supposed to depend on the time elapsed since the last oviposition. The equation that gives the time T a female will remain on a host patch is:

$$T = \frac{aP + \sum I_i - r^*}{b}, \tag{1}$$

where P is the number of hosts on the patch, a is a constant relating host density to kairomone concentration, b is the decay rate of responsiveness and r^* is the responsiveness level whereupon the patch is left. The summation term represents the effect of ovipositions, the ith leading to an increment size of I_i. This equation is graphically presented in Fig. 3.

The linear decrease in the tendency to remain on the patch during the foraging time is believed to correspond to a progressive habituation to host kairomones (Waage 1979) and/or to the perception of an increased concentration of chemical traces left by the females while searching for hosts (Bernstein and Driessen 1996). Habituation processes are usually modeled using logarithmic functions, leading Pierre et al. (2003) to propose a version of Waage's (1979) patch-leaving rule with a logarithmic decay in patch responsiveness over time. Other versions of Waage's (1979) model took into account the effect of encounters with previously parasitized hosts, leading to decrements in the tendency of females to remain on the host patch (van Alphen 1993; Pierre et al. 2003).

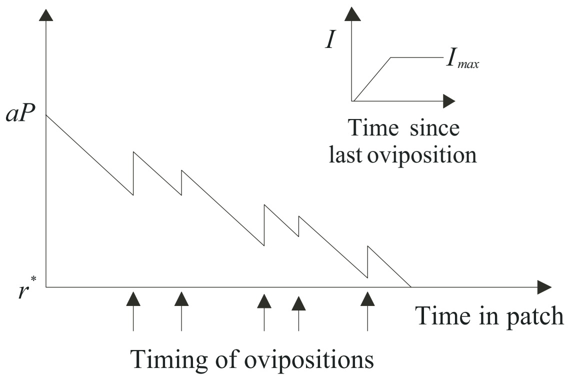

Fig. 3 A graphical representation of Waage's (1979) patch-leaving mechanistic rule. Upon entering a patch, the female wasp has an initial tendency aP to remain on it, which decreases linearly over time. Each oviposition increases this tendency, and the size of the increment depends on the time since the last oviposition (see insert). When the tendency to remain on the patch reaches the threshold r^*, the patch is left

On better-quality patches, more hosts will be encountered. Thus, increments associated with each host attack will lead females to stay longer on better than on poorer patches, which is in agreement with the theoretical predictions of both the Marginal Value Theorem and the Ideal Free Distribution. Some experimental work, however, demonstrated that patch residence time can sometimes be reduced when hosts are attacked. For example, *Cardiochiles nigriceps* immediately leaves the patch after a single oviposition (Strand and Vinson 1982). This led Driessen et al. (1995) to propose that oviposition may also have a decremental or a "count-down" effect on females' patch-leaving tendency. Iwasa et al. (1981) theoretically demonstrated that an incremental mechanism can lead to a result that closely approximates the optimal strategy when there is large variance in patch quality (i.e., a clumped host distribution). In this case, Waage's (1979) patch-leaving rule works like the fixed GUT rule of thumb, except that, in the fixed GUT rule, responsiveness is reset to its initial value after each oviposition. A decremental mechanism would be conversely adaptive when hosts are uniformly distributed or equivalently when host patches are small. In this case, the Waage's (1979) rule, despite being more flexible and more elaborated, looks like a fixed-number rule of thumb. When hosts follow a Poisson distribution, oviposition should have no effect on the tendency of females to leave the patch, and the rule becomes a fixed-time rule of thumb (Green 1987). In all cases, as information acquired while foraging is taken into account by the female, Waage's (1979) rule will work better than any other simple rules of thumb.

Table 3 A detailed summary of all experimental studies conducted on female insect parasitoids to determine the effect of previous visits to host patches on patch residence times

Tested effect	Species	Result observed	Reference
a. Effect of the quality of previous visited patch(es)			
	Aphidiidae		
	Aphidius rhopalosiphi	Increase in the patch time with an increase in the quality of the previous visited patch	Outreman et al. (2005)
	Lysiphlebus testaceipes	Increase in the patch time with a decrease in the quality of the previous visited patch	Tentelier et al. (2006)
	Figitidae		
	Leptopilina heterotoma	Increase in the patch time with a decrease in the quality of the previous visited patch	Visser et al. (1992b)
	Ichneumonidae		
	Nemeritis canescens	Increase in the patch time with an increase in the quality of the previous visited patch(es)	Waage (1979)
	Mymaridae		
	Anaphes victus	Increase in the patch time with a decrease in the quality of the previous visited patch	van Baaren et al. (2005a)
b. Effect of the time spent in the previous visited patch(es)			
	Ichneumonidae		
	Nemeritis canescens	Decrease in the patch time with an increase in the time spent on the previous visited patch(es)	Waage (1979)
c. Effect of successive visits to the same patch			
	Aphidiidae		
	Aphidius rhopalosiphi	Decrease in the patch residence time	Outreman et al. (2005)
	Braconidae		
	Dacnusa sibirica	Decrease in the patch residence time	Sugimoto et al. (1990)
	Fopius arisanus	Decrease in the patch residence time	Wang and Messing (2003)
	Encyrtidae		
	Epidinocarsis lopezi	Decrease in the patch residence time	van Dijken et al. (1992)
	Eulophidae		
	Chrysocharis pentheus	Decrease in the patch residence time	Sugimoto and Tsujimoto (1988)
	Figitidae		
	Leptopilina boulardi	No effect	Varaldi et al. (2005)
	Leptopilina heterotoma	Decrease in the patch residence time	Haccou et al. (1991)
	Leptopilina heterotoma	No effect	Varaldi et al. (2005)
	Ichneumonidae		
	Nemeritis canescens	Decrease in the patch residence time	Waage (1978, 1979)
	Venturia canescens	No effect	Bernstein and Driessen (1996)
	Scelionidae		
	Telenomus busseolae	Decrease in the patch residence time	Wajnberg et al. (1999)
d. Effect of successive visits to one or several other patch(es) of the same quality			
	Aphidiidae		
	Aphidius colemani	Decrease in the patch residence time	van Steenis et al. (1996)
	Aphidius rhopalosiphi	Decrease in the patch residence time	Outreman et al. (2001)
	Braconidae		
	Asobara tabida	Decrease in the patch residence time	Thiel and Hoffmeister (2004)
	Dapsilarthra rufiventris	No effect	Sugimoto et al. (1987)
	Eulophidae		
	Chrysocharis pentheus	No effect	Sugimoto and Tsujimoto (1988)
	Ichneumonidae		
	Nemeritis canescens	Decrease in the patch residence time	Waage (1979), Thiel et al. (2006)
	Mymaridae		
	Anaphes victus	Decrease in the patch residence time	van Baaren et al. (2005a)

Table 3 (continued)

Tested effect	Species	Result observed	Reference
	Trichogrammatidae		
	Trichogramma evanescens	Decrease in the patch residence time	Gardner and van Lenteren (1986)
e. Effect of an increase in the time interval between two successive patch visits (equivalent to an increase in travel time)			
	Aphidiidae		
	Lysiphlebus testaceipes	Increase in the patch residence time for the second visit	Tentelier et al. (2006)
	Braconidae		
	Asobara tabida	Increase in the patch residence time for the second visit	Thiel and Hoffmeister (2004)
	Dapsilarthra rufiventris	Increase in the patch residence time for the second visit	Sugimoto et al. (1987)
	Figitidae		
	Leptopilina heterotoma	No effect	Visser et al. (1992b)
	Mymaridae		
	Anaphes victus	Increase in the patch residence time for the second visit	Boivin et al. (2004)

The Waage's (1979) model has been increasingly used as a central reference for understanding the proximate behavioral mechanisms used by female parasitoids to adjust their patch residence times under different environmental conditions. Several problems or inconsistencies of this model, however, have been discovered. Among others, this model assumes that, upon entering a patch, female parasitoids obtain information about its quality not only through kairomone concentration but also through oviposition (Driessen and Bernstein 1999). This model also does not enable females to use other important information, such as the presence and number of competitors simultaneously depleting the patch (van Alphen et al. 2003; Wajnberg et al. 2004). From a statistical point of view, except for the timing of oviposition which is a realization of a random process, the Waage's (1979) model is essentially deterministic. Therefore, Waage's model parameters cannot be estimated from experimental data. For example, suppose that hypothetical data is collected by measuring the patch residence time of females attacking either zero or exactly one host. For these two sets of females, the Waage's (1979) model (see Eq. 1) will be:

$$\begin{cases} T_0 = \frac{aP - r^*}{b} \\ T_1 = \frac{aP + I - r^*}{b} \end{cases} \qquad (2)$$

Even if we deliberately assume that the patch is left when the level of responsiveness falls to zero (i.e., $r^*=0$), we still have two independent equations for estimating three parameters: aP (considered as a single parameter), b, and I. Incorporating additional observations with two or more host attacks will not add any additional independent equations. Thus, as this has been pointed out by Waage (1978) himself, the initial responsiveness level aP cannot be independently estimated from its rate of decay with time b (Pierre et al., unpublished data). Only increments or decrements associated with each oviposition can be accurately estimated from experimental data using appropriate statistical tools.

A statistical tool to identify the patch-leaving rules: the Cox regression model

Quantifying patch-leaving decision rules from experimental data has repeatedly been considered a difficult task (Haccou et al. 1991; Hemerik et al. 1993), and specific statistical methods should be used. The chief trait measured is the time female parasitoids spend on a host patch; a variable well known to be non-normally distributed. In this case, so-called survival analyses can be used (Collett 1994; Kalbfleisch and Prentice 2002). The corresponding statistical models, which have been used for decades in the medical and social sciences (Moya-Laraño and Wise 2000), have been transposed to ecological problems by Haccou and Hemerik (1985) and Haccou et al. (1991). These models can properly incorporate so-called censored data. Censored data may occur, for example, when the observation period ends before the observed female leaves the host patch (see Bressers et al. 1991 and Haccou and Meelis 1992, for a discussion on this). Censored observations should not be discarded as the estimated average patch residence time will be biased toward shorter values, and the mechanisms determining patch residence time will not be accurately estimated. Survival analysis models can also incorporate fixed or so-called time-dependent explanatory variables (e.g., temperature or the number of times a behavior is displayed by the female). In the latter case, the value can change during the course of the observations. In this context, several statistical models can

Table 4 A detailed summary of all experimental studies conducted on female insect parasitoids to determine the effect of abiotic conditions on patch residence times

Tested effect	Species	Result observed	Reference
a. Effect of the time of the day at the start of the observation			
	Scelionidae		
	Trissolcus basalis	No effect	Field (1998)
b. Effect of temperature			
	Aphelinidae		
	Encarsia formosa	No effect	van Roermund et al. (1993, 1994)
c. Effect of the photoperiod during development			
	Figitidae		
	Leptopilina heterotoma	Short days (fall) lead to in increase in the patch residence time	Roitberg et al. (1992)
d. Effect of a cold storage during development			
	Mymaridae		
	Anaphes victus	Decrease in the patch time with an increase in cold storage duration	van Baaren et al. (2005b)
e. Effect of a decrease in temperature before the observation			
	Ichneumonidae		
	Venturia canescens	Increase in the patch residence time compared to no change in temperature	Amat et al. (2006)
f. Effect of a dropping in barometric pressure during the observation			
	Figitidae		
	Leptopilina heterotoma	Increase in the patch residence time compared to a steady barometric pressure	Roitberg et al. (1993)

be used to identify the patch-leaving mechanisms used by the females, from observational data. Some models are fully parametric and based on restrictive assumptions (see Collett 1994; Kalbfleisch and Prentice 2002). The proportional hazards model (also called Cox's regression model) is usually used instead (Cox 1972). It is semi-parametric, with regards to the distribution of the residual values.

Typical experiments conducted to collect data from which patch-leaving rules can be estimated are based on observing a female parasitoid foraging on a host patch. Using an event recorder running on a desktop computer, the observer can accurately record when a patch is entered and exited, the data of which are then used to compute total residence time. Timings of other behaviors like host attacks or rejections, grooming, resting, handling hosts, etc. can also be simultaneously assessed. In most studies, times of non-search behaviors like grooming and host handling are included in the total patch time (e.g., Wajnberg et al. 1999, 2003). In others, only active search components are taken into account (e.g., Nelson and Roitberg 1995; van Steenis et al. 1996). During the observation, the female can leave the patch and walk or fly a short distance away for a short excursion before returning to the hosts. Thus, an arbitrary time threshold should be used for such excursions above which the patch is considered to be left. Depending on the species studied, this arbitrary threshold can range from 1 s (Wajnberg et al. 1999) to 1 h (van Roermund et al. 1993, 1994). Some authors have examined whether different values for this threshold lead to a qualitative change in the results (e.g., Waage 1979; Wajnberg et al. 1999).

Opposed to standard regression models, Cox's regression model does not express patch times as a function of one or more explanatory variables. It is rather expressed in terms of the hazard rate, which is the probability per unit of time that a female leaves the patch, given that she is still on it. Thus, this represents the tendency for a female to leave a patch. There are simple relationships between patch times and patch-leaving tendency, however (Collett 1994; Kalbfleisch and Prentice 2002). In survival analysis terminology, entering the patch corresponds to a renewal point and leaving the patch corresponds to a failure. Unlike Waage's (1979) model, Cox's regression model is essentially stochastic, allowing for variation in patch residence times. Hence, as pointed out by Tenhumberg et al. (2001a), Cox's regression model can be viewed as a state-dependent rule of thumb, where the state of the animal is represented by a set of explanatory variables that significantly influence its tendency to leave a patch.

The hazard rate function is assumed to be the product of a basic tendency to leave the patch (baseline hazard), which is reset after each renewal point, and a so-called hazard ratio, which gives the combined effect of all the explanatory variables. The general form of the model is:

$$h(t) = h_0(t) \exp\left\{\sum_{i=1}^{p} \beta_i z_i\right\} \quad (3)$$

Table 5 A detailed summary of all experimental studies conducted on female insect parasitoids to determine different miscellaneous effects on patch residence times

Tested effect	Species	Result observed	Reference
a. Effect of the hosts distribution			
	Ichneumonidae		
	Diadegma semiclausum	Increase in the patch time if hosts show an aggregative distributed	Wang and Keller (2005)
b. Effect of the presence of another patch on the same plant			
	Aphidiidae		
	Aphidius colemani	No effect	van Steenis et al. (1996)
	Braconidae		
	Fopius arisanus	Decrease in the patch residence time	Wang and Messing (2003)
c. Effect of the architecture of the plant bearing the patch			
	Aphidiidae		
	Aphidius funebris	No effect	Weisser (1995)
f. Effect of the distance to the next patch to visit			
	Ichneumonidae		
	Diadegma semiclausum	Increase in the patch residence time with an increase in the distance to the next patch	Wang and Keller (2003)
e. Effect of behavioral defence mechanisms of the attacked hosts			
	Ichneumonidae		
	Diadegma semiclausum	Increase in the patch residence time	Wang and Keller (2003, 2004, 2005)
f. Effect of the leaf side of the plant bearing the hosts			
	Aphelinidae		
	Encarsia formosa	No effect	van Roermund et al. (1993, 1994)

where $h(t)$ is the hazard rate function describing the females' patch-leaving tendency, $h_0(t)$ is the baseline hazard function, t is the time since the last renewal point, and β_i are the coefficients that provide the relative contribution of p covariates. These coefficients can be interpreted through the hazard ratio, which is the exponential term. When the combined effect of the covariates results in a hazard ratio greater than 1, it is interpreted as having an increasing tendency for leaving the patch. A hazard ratio less than 1 is interpreted in the opposite way. Covariates can be time-dependent or fixed. The baseline hazard function, which is not necessarily monotonous, is the hazard rate function when all covariates equal zero. It is left unspecified. The name "proportional hazards model" stems from the assumption that the hazard rates are proportional for different values of a fixed explanatory variable (Collett 1994; Kalbfleisch and Prentice 2002). There are statistical and graphical methods available to test this important assumption (Andersen 1982; Collett 1994).

One important feature of this statistical model is that it is flexible, enabling one to statistically test the effect of any explanatory variable that is a priori believed to influence the patch-leaving tendency of female parasitoids. Thus, the model can be a tool for assessing, using experimental data, which factors in the analysis affect the females' leaving tendency (Haccou et al. 1991). In particular, when the variables are the number of ovipositions and host rejections, fitting the model will estimate the importance, variance, and, thus, statistical significance of the incremental or decremental effects as defined in the Waage's (1979) model. By explicitly taking into account stochasticity in patch residence times, Pierre et al. (unpublished data) showed that the link between the increments/decrements of Waage's (1979) rule and the β estimates of the Cox's regression model is monotonically decreasing: the higher the increments, the smaller the β estimates, leading to lower hazard ratios. In contrast to an implicit assumption made by all authors and apart from such a decreasing link, there is no other straightforward relationship between the Waage's (1979) patch-leaving rule and Cox's regression model (Pierre et al., unpublished data).

There are two different ways of fitting a Cox's regression model to experimental data. Haccou and Hemerik (1985), Haccou et al. (1991), Hemerik et al. (1993), and following works all used a so-called renewal process in which entering the patch and ovipositing in a host both correspond to renewal points, in both cases leading to a reset in the baseline hazard function. In this case, every oviposition is considered a censored event as it is not known when the parasitoid female would have left the patch if the host had not been attacked. In Wajnberg et al. (1999, 2000, 2003, 2004) and related works, the baseline hazard function is conversely reset only when a female enters a patch. Hence, in the renewal process, the variable modeled is the time since the last oviposition (i.e., the GUT), whereas in the other case, it is the total patch residence time. These two ways of fitting a Cox's regression model to experimental data should lead, at least qualitatively, to the same results. The influence, if any, of every oviposition on patch-leaving tendency in a Cox's regression model is indeed assumed to be constant from the moment it occurs to the end of the patch residence time (see Eq. 3). Thus, such an influence should be detectable during inter-oviposition times and should affect every corresponding GUT, after the oviposition occurs, causing it to appear significant whatever the fitting method. There are, however, two key technical differences between the two approaches: (1) in the renewal process, all explanatory variables are fixed, whereas those describing female intra-patch experience are considered to be time-dependent in the other case and (2) censored data is important when using a renewal process, whereas there is almost no censoring in the other case. Having fixed or time-dependent variables should not lead to differences when the two fitting procedures are compared. The presence of censored data, however, potentially lowers the quality of the parameter estimates and the power of statistical tests performed. On the other hand, a renewal process is more flexible, enabling fitting of Cox's regression model under less restrictive conditions.

I compared the two fitting procedures on the same data sets (i.e., those of Wajnberg et al. 1999, 2000). The results and the adequacy of the fitted models, assessed with residual plots, were qualitatively equivalent. As the trait of interest is more often the total patch residence time than the GUT, the fitting procedure, using only one renewal point when the patch is entered and time-dependent explanatory variables, is more straightforward.

Observed patch-leaving mechanisms in different parasitoids

Using the aforementioned statistical tools, several works investigated whether different parasitoid species use an incremental, a decremental, or no mechanism for each encounter/oviposition or host rejection on their patch-leaving tendency. The list of species studied, with the observed effects, is provided in Tables 6 and 7, respectively.

In all of these experimental works, an observed incremental effect likely resulted from females increasing their turning tendency along with a reduction in walking speed (Yano 1978; Gardner and van Lenteren 1986). Such an arrestment response, which leads to an increased tendency to remain on the patch, has also been shown in insects after feeding (e.g., Carter and Dixon 1982) or during mate finding (Schal et al. 1983). On the contrary, a decremental mechanism should correspond to the opposite effect: an increase in walking speed with a decrease in turning tendency (Stillman and Sutherland 1990).

The fact that some species use an incremental mechanism, others a decremental rule, and others do not modify their patch-leaving tendency when a host is encountered and/or attacked is most likely related to the distribution of available hosts in the habitat. As shown previously, Iwasa et al. (1981) demonstrated that an incremental mechanism would be adaptive when there is large heterogeneity in patch quality. A decremental mechanism would be conversely better when hosts are uniformly distributed over patches. Finally, no effect should be found when hosts follow a Poisson distribution. Unfortunately, in most cases, accurate information is not available about the ecology and distribution of all potential hosts attacked by the species listed in Table 6, and such an explanation cannot be easily verified (Driessen and Bernstein 1999; Wajnberg et al. 2003). Nevertheless, several simulation models, parameterized for specific situations in which the ecology and distribution of hosts were known, demonstrated that the patch-leaving rule adopted by females were those that enabled them to behave optimally, for example, in accordance to the predictions of the Marginal Value Theorem (Driessen and Bernstein 1999; Wajnberg et al. 2000).

All the species listed in Table 6 use a patch-leaving mechanism that is assumed to be adaptive. This assumes, however, that behavioral mechanisms have been progressively settled by natural selection and that there is or was, in all populations, genetic variation on which selection could act (Wajnberg 2004). Such intra-population genetic variation in patch-leaving rules has been observed and quantified on some parasitoid species (Wajnberg et al. 1999, 2004). Several other factors are also known to influence, in a dynamic way, the patch-leaving rules adopted by female wasps when a host is encountered and/or successfully attacked. For example, Outreman et al. (2005) showed that, on average, *Aphidius rhopalosiphi* females use an incremental mechanism each time a host is encountered/attacked (see Table 6). As females depleted their egg load, however, they progressively switched to a decremental mechanism. Such a switching rule is particularly effective for this species as it will lead females to leave a heavily exploited patch and experience a reduced level of superparasitism (Outreman et al. 2005). Significant variation between different populations of the same species was also observed (e.g., Wajnberg et al. 2003). Thus, in opposition to what is usually stated, the patch-leaving mechanisms listed in Table 6 are not strictly species-specific and important intra-specific variation has been observed. Finally, different experimental protocols could lead to different results for the same species (van Baaren et al. 2005b). This indicates that laboratory results should always be treated with caution.

Fewer studies have examined the effect of rejecting a healthy or already parasitized host (see Table 7). Except for *Opius dimidiatus* (Nelson and Roitberg 1995), rejecting a host leads to a decreased tendency of or has no significant influence on the female to remain on the host patch. Rejection of a host is generally assumed to inform the foraging female about the decreasing value of the patch and/or simply leads to a decrease in its motivation to continue searching (van Alphen and Vet 1986). In both cases, the result will be a reduction in patch residence time, a mechanism that is repeatedly assumed to be adaptive (van Alphen and Vet 1986; van Lenteren 1991; van Alphen 1993).

Table 6 A detailed summary of all experimental studies conducted to determine the effect of each encounter/oviposition with/in a healthy and/or parasitized host on the patch-leaving tendency of female parasitoids

Effect of each oviposition	Species	Encounter or oviposition	Healthy or parasitized	Reference
a. Incremental				
	Aphelinidae			
	Encarsia formosa	Oviposition	Healthy	van Roermund et al. (1993, 1994)
	Aphidiidae			
	Aphidius rhopalosiphi	Oviposition	Likely both	Outreman et al. (2005)
	Lysiphlebus testaceipes	Oviposition	Likely both	Tentelier et al. (2005)
	Braconidae			
	Asobara tabida	Encounter	Healthy	van Alphen and Galis (1983)
	Cotesia glomerata	Oviposition	Both	Vos et al. (1998)
	Dacnusa sibirica	Encounter	Likely both	Sugimoto et al. (1990)
	Dapsilarthra rufiventris	Encounter	Likely both	Sugimoto et al. (1987)
	Opius dimidiatus	Oviposition	Healthy	Nelson and Roitberg (1995)
	Eulophidae			
	Chrysocharis pentheus	Encounter	Likely both	Sugimoto and Tsujimoto (1988)
	Figitidae			
	Leptopilina clavipes	Oviposition	Healthy	Hemerik et al. (1993)
	Leptopilina heterotoma	Oviposition	Likely both	Haccou et al. (1991), Varaldi et al. (2005)
	Pseudeucoila bochei	Encounter	Likely both	van Lenteren and Bakker (1978)
	Ichneumonidae			
	Nemeritis canescens	Oviposition	Likely healthy	Waage (1978, 1979)
	Mymaridae			
	Anaphes victus	Oviposition	Healthy	van Baaren et al. (2005a,b)
	Trichogrammatidae			
	Trichogramma brassicae	Oviposition	Healthy	Wajnberg et al. (2000)
	Trichogramma evanescens	Oviposition	Healthy	Gardner and van Lenteren (1986)
b. Decremental				
	Aphidiidae			
	Aphidius colemani	Encounter	Likely both	van Steenis et al. (1996)
	Diaeretiella rapae	Oviposition	Likely healthy	Shaltiel and Ayal (1998)
	Braconidae			
	Cardiochiles nigriceps	Oviposition	Likely healthy	Strand and Vinson (1982)
	Eulophidae			
	Sympiesis sericeicornis	Oviposition	Not specified	Casas et al. (1993)
	Ichneumonidae			
	Diadegma semiclausum	Oviposition	Likely both	Wang and Keller (2003, 2004, 2005)
	Venturia canescens	Oviposition	Likely both	Driessen and Bernstein (1999), Driessen et al. (1995)
	Mymaridae			
	Anaphes victus	Oviposition	Both healthy or parasitized	Boivin et al. (2004), Wajnberg et al. (2006)
	Scelionidae			
	Telenomus busseolae	Oviposition	Likely both	Wajnberg et al. (1999)
	Trichogrammatidae			
	Trichogramma chilonis	Oviposition	Healthy	Wajnberg et al. (2003)
	Trichogramma oleae	Oviposition	Healthy	Wajnberg et al. (2003)
	Trichogramma principium	Oviposition	Healthy	Wajnberg et al. (2003)
	Trichogramma semblidis	Oviposition	Healthy	Wajnberg et al. (2003)
	Trichogramma vogelei	Oviposition	Healthy	Wajnberg et al. (2003)

Table 6 (continued)

Effect of each oviposition	Species	Encounter or oviposition	Healthy or parasitized	Reference
c. No effect				
	Aphelinidae			
	Encarsia formosa	Oviposition	Parasitized	van Roermund et al. (1993, 1994)
	Braconidae			
	Asobara tabida	Encounter	Parasitized	van Alphen and Galis (1983)
	Figitidae			
	Leptopilina boulardi	Oviposition	Not specified	Varaldi et al. (2005)
	Ichneumonidae			
	Venturia canescens	Oviposition	Both healthy or parasitized	Amat et al. (2006)
	Scelionidae			
	Trissolcus basalis	Oviposition	Both healthy or parasitized	Wajnberg et al. (2004)
	Trichogrammatidae			
	Trichogramma brassicae	Oviposition	Parasitized	Wajnberg et al. (2000)
	Trichogramma bourarachae	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma buesi	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma cacoeciae	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma chilonis	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma dendrolimi	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma evanescens	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma exiguum	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma oleae	Oviposition	Parasitized	Wajnberg et al. (2003)
	Trichogramma principium	Oviposition	Parasitized	Wajnberg et al. (2003)
	Trichogramma semblidis	Oviposition	Parasitized	Wajnberg et al. (2003)
	Trichogramma vogelei	Oviposition	Parasitized	Wajnberg et al. (2003)
	Trichogrammatoidea bactrae	Oviposition	Both healthy or parasitized	Wajnberg et al. (2003)

Only statistically significant results are presented

Such results are also likely to depend on the characteristics of the environment in which the female parasitoids are foraging. Wang and Keller (2004, 2005), working on *Diadegma semiclausum*, found different mechanisms associated with host rejections (see Table 7). The difference was thought to result from the two experiments being conducted in environments containing different numbers of previously parasitized hosts. Moreover, for each host rejection, significant variation was observed between different populations of the same species (Wajnberg et al. 2003). This variation indicates that female patch-leaving mechanisms are flexible, enabling females to adapt their foraging strategies to local environmental conditions.

As can be seen in Tables 6 and 7, there is now a large number of species for which the effect of encountering/attacking or rejecting a host on females' patch-leaving tendency has been quantified. This data could be used to perform a phylogenetically based comparative analysis to accurately understand the evolutionary responses of parasitoids to environmental constraints (Wanntorp 1983; Harvey and Pagel 1991; Martins 1996). Such a comparative analysis has recently been conducted on the Trichogrammatidae family (Wajnberg et al. 2003). A positive correlation was found among the species compared between the patch-leaving rules associated to each oviposition and to each host rejection, and this positive correlation remained statistically significant when phylogenetic comparative statistical methods were employed. Females belonging to species that showed a strong decremental effect associated with each successful oviposition were also those that showed a strong decremental effect associated with each host rejection. This positive correlation cannot be explained by the fact that species are related phylogenetically. Thus, this correlation has adaptive meaning which is likely related to the ecology and distribution of the potential hosts that can be attacked.

Finally, Cox's regression model was recently used to test the effect of conspecific female presence on female patch-leaving tendency (Wajnberg et al. 2004; Goubault et al. 2005). In all cases, females increase their tendency to leave, a result that is in agreement with the predictions of the Ideal Free Distribution when interference between females is taken into account (Wajnberg et al. 2004).

A unified stochastic patch-leaving mechanism

We have seen that the Waage's (1979) patch-leaving model, despite being a central reference, has problems or inconsistencies that cannot be solved. Only increments/decrements for the tendency to leave the patch can be statistically estimated using a Cox's regression model.

Table 7 A detailed summary of all experimental studies conducted to determine the effect of rejecting a healthy and/or parasitized host on the patch-leaving tendency of female parasitoids

Effect of each host rejection	Species	Healthy or parasitized	Reference
a. Incremental			
	Braconidae		
	Opius dimidiatus	Parasitized	Nelson and Roitberg (1995)
b. Decremental			
	Braconidae		
	Aphidius rhopalosiphi	Likely both	Outreman et al. (2005)
	Figitidae		
	Leptopilina clavipes	Parasitized	Hemerik et al. (1993)
	Leptopilina heterotoma	Parasitized	van Lenteren (1991), van Alphen and Vet (1986), Varaldi et al. (2005)
	Ichneumonidae		
	Diadegma semiclausum	Parasitized	Wang and Keller (2004)
	Mymaridae		
	Anaphes victus	Both healthy or parasitized	Boivin et al. (2004), van Baaren et al. (2005a,b), Wajnberg et al. (2006)
	Scelionidae		
	Telenomus busseolae	Not specified	Wajnberg et al. (1999)
	Trissolcus basalis	Healthy	Wajnberg et al. (2004)
	Trichogrammatidae		
	Trichogramma buesi	Parasitized	Wajnberg et al. (2003)
	Trichogramma brassicae	Both healthy or parasitized	Wajnberg et al. (2000)
	Trichogramma chilonis	Parasitized	Wajnberg et al. (2003)
	Trichogramma evanescens	Parasitized	Wajnberg et al. (2003)
	Trichogramma oleae	Parasitized	Wajnberg et al. (2003)
	Trichogramma principium	Parasitized	Wajnberg et al. (2003)
	Trichogramma semblidis	Parasitized	Wajnberg et al. (2003)
	Trichogramma vogelei	Parasitized	Wajnberg et al. (2003)
c. No effect			
	Aphelinidae		
	Encarsia formosa	parasitized	van Roermund et al. (1993, 1994)
	Figitidae		
	Leptopilina boulardi	Parasitized	Varaldi et al. (2005)
	Ichneumonidae		
	Diadegma semiclausum	parasitized	Wang and Keller (2005)
	Scelionidae		
	Trissolcus basalis	parasitized	Wajnberg et al. (2004)
	Trichogrammatidae		
	Trichogramma bourarachae	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma buesi	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma cacoeciae	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma chilonis	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma dendrolimi	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma evanescens	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma exiguum	Both healthy or parasitized	Wajnberg et al. (2003)
	Trichogramma oleae	Healthy	Wajnberg et al. (2003)
	Trichogramma principium	Healthy	Wajnberg et al. (2003)
	Trichogramma semblidis	Healthy	Wajnberg et al. (2003)
	Trichogramma vogelei	Healthy	Wajnberg et al. (2003)
	Trichogrammatoidea bactrae	Both healthy or parasitized	Wajnberg et al. (2003)

Only statistically significant results are presented

There is a need for a more flexible patch-leaving rule that would be strictly linked to observational data and that will lead to a more unified approach between the deterministic Waage's (1979) patch-leaving rule and its statistical counterpart, the Cox's regression model. Such a unified approach has been proposed by Pierre et al. (unpublished data) who developed a stochastic version of the Waage's (1979) patch-leaving mechanism.

In this patch-leaving rule, females enter a host patch with an initial constant hazard rate α_0. Thus, if a host is not encountered, the probability of leaving the patch continuously increases. Hence, in opposition to the Waage's (1979) model, patch residence times are not fixed but follow an exponential distribution with an average value of $1/\alpha_0$. Each time a host is encountered and attacked, the hazard rate is increased or decreased by a quantity α_i that can differ for every host attack. Host attacks are assumed to follow a Poisson process with a constant rate λ, a restrictive hypothesis which assumes that patches are very large or that there is no host depletion. Such a restrictive assumption can be relaxed in numerical applications. Using such simple assumptions, Pierre et al. (unpublished data) computed the statistical distribution of the expected patch residence times. They also proposed both a parametric and a semi-parametric way to estimate, from experimental data, the different parameters α_i (and their variance–covariance matrix) corresponding to the initial hazard rate α_0 and the effect of each host attack.

Contrary to the Waage's (1979) model, this model does not include an initial tendency to leave the patch nor a decay rate in this tendency. On the other hand, the corresponding statistical approach, which is based on estimating increments/decrements, remains consistent with the use of a Cox's regression model.

Conclusion and future directions

As a general rule, the spatial structure of the environment strongly affects the foraging decisions of animals, especially of insect parasitoids (Hassell and Southwood 1978). In this review, I have focused specifically on the spatial distribution of hosts attacked by female parasitoids, and we have seen that, in response to such spatial structure, female wasps have developed elaborate mechanistic behavioral rules that lead them to adopt patch residence times that are, in most of the cases, in agreement with the predictions of theoretical optimization models. Patch time allocation in insect parasitoids has always been considered to be an important behavioral component of host–parasitoid dynamics (Hassell and Southwood 1978; van Alphen 1988; Basset et al. 2002). Hence, patch time allocation is also likely important in estimating the efficacy of biological control programs in which insect parasitoids are released to control phytophagous pests. In the majority of cases, field crop pests are patchily distributed. As a result, an accurate understanding of the mechanisms involved in female wasp patch time allocation should lead to the optimal selection and use of parasitoid species (Waage 1990) for an efficient pest control program.

There are several avenues of research that should be developed concerning both ultimate predictions and proximate behavioral mechanisms adopted by females. From a theoretical point of view, there is a need to develop a tight association between the Marginal Value Theorem (MVT) and the Ideal Free distribution (IFD), and this does not only concern the foraging strategy of insect parasitoids. The MVT considers a single female while the IFD looks at the distribution of groups of foragers in a patchy environment. As pointed out by Godfray (1994), these two theories were developed largely independently, even though female parasitoids experience ingredients of both models (e.g., patch depletion, travel times between patches, competition, etc.) when they are foraging for hosts.

The patch-leaving rules used by females are now very well understood and several factors affecting such rules were examined. There remains a number of factors to be accurately analyzed, however, like the presence of competing females on the patch (Sjerps and Haccou 1994; Haccou et al. 2003; Wajnberg et al. 2004; Goubault et al. 2005; Hamelin et al. 2006a,b) or the effect of previous experience and learning ability. For this, theoretical predictions, likely based on game theory and dynamic programming, remain to be developed. Specific statistical tools are also required to more accurately link the stochastic features of experimental data with optimal foraging theory predictions (Tenhumberg et al. 2001a). Finally, most, if not all, of the information available regarding how parasitoid females optimally adjust their patch residence time was acquired using laboratory experiments. Field work is desperately required if we want to elucidate the detailed mechanisms used by female parasitoids to optimize their time-foraging strategies in different environments.

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