

Travel duration, energetic expenditure, and patch exploitation in the parasitic wasp *Venturia canescens*

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Abstract Foraging animals usually keep track of how costly it is to reach new resource patches and adjust patch residence time and exploitation rate accordingly. There are at least two potential factors, which are not necessarily closely linked, that animals could measure to estimate costs of traveling: the time the forager needs to reach the next patch and the amount of energy it has to invest until arrival. In the parasitoid wasp *Venturia canescens*, females forage for hosts from which their offspring can develop. Two different types of this parasitoid exist. The thelytokous type lives in anthropogenic habitats where flight is not necessarily linked with foraging. The arrhenotokous type lives under field conditions and shows frequent flight activity. We tested whether the wasps would use time or energy needed to assess patch availability, by either confining them into vials or letting them travel actively in a flight mill between patch visits. Our results show that in thelytokous

lines, time is a sufficient cue influencing patch exploitation and an additional effect of the energy needed was not visible. In the arrhenotokous wasps, however, only the number of rounds flown in the mill influenced subsequent behavior, while mere time spent traveling did not.

Keywords Marginal value theorem · *Venturia canescens* · Trade-off · Timing · Travel costs · Flight mill · Patch time allocation

Introduction

Fitness trade-offs take a central place in shaping life-history evolution (e.g., Stephens and Krebs 1986; Stearns 1992; Reznick et al. 2000; Futuyma 2005). From the perspective of life-history theory, a trade-off occurs when an increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in a second trait (Roff 2007). While this has been well studied for physiological traits, it now becomes apparent that information use and learning are shaped by similar selective forces (Stephens 1989; Dall et al. 2005; Dukas 2008). Obtaining information and maintaining an adequate cognitive system is costly in terms of time (Vet et al. 1995; Eliassen et al. 2007; Raine and Chittka 2008) and energy (Mery and Kawecki 2003, 2004; Kolss and Kawecki 2008). Thus, under circumstances where the information gathered can aid in predicting, for example, future foraging success, animals are expected to invest these costs; whereas when environments are either completely predictable or unpredictable, animals are likely to use fixed, inherited strategies instead (Stephens 1993). In support of this idea, individuals within one species, but coming from contrasting environments, use similar cues to different extents or in different

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ways (e.g., Mery and Kawecki 2002; Odling-Smee and Braithwaite 2003; Vos and Vet 2004; Thiel et al. 2006; Thiel and Hoffmeister 2006), depending on the informational value of cues in a specific situation.

Many habitats are spatially structured such that resources occur in discrete and depletable patches and animals searching and exploiting such patches will usually experience diminishing returns over time as the number of resource items left in the patch decreases. Thus, after a while, it would pay to stop searching and start traveling toward the next patch (Stephens and Krebs 1986). The optimal timing of patch departures depends on the relative quality of the patch and also on the accessibility of other, new patches (Charnov 1976). It has been shown from experimental studies of animals foraging for food (Krebs et al. 1974; Cook and Cockrell 1978; Zimmerman 1981; Cassini et al. 1990; Cuthill et al. 1994; Johnson and Collier 1999; Fortin 2003), oviposition sites (Roitberg and Prokopy 1982; Takasu et al. 1997; Cronin and Strong 1999; Boivin et al. 2004; Thiel and Hoffmeister 2004; Tentelier et al. 2006; Thiel et al. 2006), or mates (Parker 1978; Alonso-Pimentel and Papaj 1996) that the more easily animals find new resource patches, the higher their leaving tendency on the already exploited one becomes.

The links between information use, foraging success, and fitness pay-off are especially close in insect parasitoids: they search for hosts (often the larvae of other insects) as a food source for their offspring. The more hosts a female is able to parasitize during her lifetime, the more offspring she is likely to have, thus a strong selection pressure on optimizing foraging strategies can be expected (Godfray 1994; Roitberg et al. 2001; van Baalen and Hemerik 2008). Besides foraging for hosts, however, parasitoids also forage for food (e.g., Wäckers and Lewis 1994; Takasu and Lewis 1995; Casas et al. 2003), because in many species feeding greatly enhances lifetime reproductive success (recently reviewed by Jervis et al. 2008; Strand and Casas 2008). This immediately leads to a behavioral trade-off, since feeding and ovipositing are mutually exclusive events. The potential costs connected with each decision differ between parasitoid species, depending on where food can be found (Bernstein and Jervis 2008; Jervis et al. 2008): some species feed from host hemolymph (Jervis and Kidd 1986; Heimpel and Collier 1996; Rivero and West 2005) or from the same substrate the host feeds upon (Eijs et al. 1998; Casas et al. 2003). The costs of switching between feeding and ovipositing are therefore relatively low and frequent changes in behavior are likely to occur (Sirot and Bernstein 1996; Tenhumberg et al. 2006). In other species, food is not connected with the occurrence of hosts (Ahmad 1936). In such cases, the wasps are only expected to search for food if the fitness gained by this long-term investment is significantly greater than the fitness gained by continued oviposi-

tion behavior (Sirot and Bernstein 1996; Tenhumberg et al. 2006). These differences also provide a great opportunity to study how information use affects the trade-off between host and food search. A parasitoid species that is especially suitable for this is the ichneumonid *Venturia canescens* (Gravenhorst), because it occurs in two distinct types, a parthenogenetic (thelytokous) and a sexual (arrhenotokous) one (Schneider et al. 2002). Wasps of the two types strive preferentially in different habitats, which favor flying behavior to different extents: whilst the arrhenotokous strain largely predominates in field conditions (Schneider et al. 2002; Amat 2004), only the thelytokous strain can be found in anthropogenic habitats such as mills or granaries. In the field, *V. canescens* attacks larvae of various pyralid moths (Lepidoptera: Pyralidae) in desiccated fruits hanging from the fruit-bearing trees, e.g., figs, dates, medlar, carob, almonds or walnuts (Salt 1976; Driessen and Bernstein 1999). Host larvae are more or less homogeneously distributed across fruits as one fruit generally harbors only one or two hosts (Driessen and Bernstein 1999). The tree species may occur solitary, in small stands, or in orchards (Driessen and Bernstein 1999; Schneider et al. 2003) and parasitoids have to fly frequently during host search (Desouhant et al. 2003). While some of the fruits are suitable food sources for the parasitoid (e.g., figs or carob pods), others cannot be utilized (e.g., almond or walnut husks); however honeydew and nectar provide additional resources (Casas et al. 2003; Desouhant et al. 2005). Inside the storage buildings, where the thelytokous populations of *V. canescens* thrive exclusively, the wasps attack host larvae feeding on stored products (Beling 1932; Ahmad 1936; Waage 1979). There is virtually no food available inside these buildings and commuting behavior between host patches and feeding sites outside has been suggested (Beling 1932; C. Bernstein, unpublished observation).

Thelytokous and arrhenotokous wasps differ in allocation of energy reserves to reproduction vs. metabolic maintenance and dispersal, which is most likely caused by the aforementioned differences in their habitats (Pelosse et al. 2007). The arrhenotokous field populations emerge with more metabolic resources, especially glycogen that can be used for flying and metabolic maintenance, than thelytokous ones. The thelytokous wasps in turn have higher initial egg loads and greater capacity to mature eggs throughout their lifetimes, which clearly indicates the existence of a trade-off (Pelosse et al. 2007). This trade-off between usages of energy for reproduction vs. somatic maintenance and dispersal very likely influences the foraging decisions of *V. canescens* females, since newly emerged arrhenotokous females leave patches of identical quality sooner than their thelytokous counterparts, presumably to engage in food search (Pelosse et al. 2007). When thelytokous and arrhenotokous wasps were compared in a flight mill study (J. Lukáš, C. Bernstein,

H. Gu, S. Dorn, unpublished data), arrhenotokous wasps flew faster on average and performed fewer flights to cover the same distance. It is therefore quite likely that the arrhenotokous field populations would also take their energy budget into account when it comes to assessment of patch availability in the habitat. In a previous study, thelytokous wasps reduced their patch residence times when the time interval between patch visits was low, even though they only passively waited for the next patch to appear, whereas the arrhenotokous ones did not show this response (Thiel et al. 2006). We therefore assume that thelytokous females, which usually do not fly during host search, are most likely optimizing their reproductive success by maximizing their oviposition rate, while the arrhenotokous ones, under natural conditions, might be constrained by the necessity of frequently refueling their energy reserves, due to the necessity of frequent flying. We thus hypothesize that in the arrhenotokous wasps, energy spent between patches indicates patch availability in the habitat, whereas in the thelytokous wasps, time is the important cue. This idea was tested by comparing the searching behavior and patch-leaving decisions of arrhenotokous and thelytokous *V. canescens* females that had passively traveled between patches in a small vial with those that had been flying in a flight mill for similar periods of time.

Material and methods

Insect cultures

Three thelytokous and two arrhenotokous populations of *V. canescens* were available for experiments. The thelytokous populations originated from areas close to the cities of Valence and Antibes in France and from the area of San Juan de Alicante, Spain. The arrhenotokous populations came from Valence and Antibes, France. The parasitoids had been initially collected from the field habitat with baits, as described in Schneider et al. (2002). They were maintained in a room with natural light conditions at a temperature of $25 \pm 3^\circ\text{C}$, using the flour moth *Ephesia kuehniella* (Zeller) as a host.

Newly emerged female wasps were removed from the rearing boxes within 2 h and put separately into plastic vials. They were provided with honey and agar for nourishment; for the arrhenotokous females two males

were also added for 24 h to allow mating. The day after emergence, females were assigned to one of three treatments at random (Table 1). The different lines of wasps (arrhenotokous and thelytokous from all locations) were reared and tested during the same period of time.

Experimental design

An experimental patch consisted of a 10 mm-deep Petri dish, 34 mm in diameter, filled with semolina and four fifth instar larvae of the pyralid moth *E. kuehniella*. The searching behavior of the parasitoid is triggered by substances (so-called kairomones) that the hosts deposit while feeding (Corbet 1973; Waage 1979); hosts were therefore placed within the semolina 2 days before the patch was actually used. Immediately before starting a trial, a patch was embedded into clean semolina in a larger arena (21 cm diameter) so that the patch was sunk flush with the surrounding clean semolina.

The main idea of the experiments was to compare the behavior of parasitoids that had traveled in a flight mill (flight treatment, FLY), and thus had spent a relatively large amount of energy, with those that had merely waited inside small vials until they were released onto the next patch (waiting treatment, WAIT). A day after the females had emerged, those assigned to the treatments FLY and WAIT were chilled for a few seconds until they stopped moving and a short stick made of copper wire was glued on their back (using cyanoacrylate-containing power glue). A third group of wasps (Control treatment, CON) was not treated with glue and cooling (Table 1).

After a recovery period of another 1–2 days, the females from all three treatments (who had had unrestricted access to honey and water) were given a first host-containing patch. The few wasps that failed to show proper searching behavior were discarded, as well as those that later failed to fly in the mill. Wasps that had lost their stick during the recovery period were treated according to the WAIT treatment, irrespective of whether they had been assigned to WAIT or FLY before.

Experiments were conducted in a climate room at $24\text{--}25^\circ\text{C}$ and 30–60% humidity. The parasitoids were allowed to search their first patch, which contained four hosts, until they decided to leave either by walking or flying away from the arena. They were carefully caught from the plastic cage surrounding the arena and either kept in a glass vial or tethered to the mill,

Table 1 Description of the experimental treatments

Treatment	Chilled and glued	Searching 1st patch with stick on the thorax	Flight during traveling
CON	No	No	No
WAIT	Yes	21 % Yes; 79 % No	No
FLY	Yes	Yes	Yes

where the number of rounds they flew was recorded. A description of the mill used is provided by Schumacher et al. (1997). The length of the time interval a female was supposed to travel had been determined in advance in a randomized fashion and ranged from 5 min to 7 h. Four to 10 min before the end of the traveling period, all wasps were transferred into honey-containing glass vials, where they could feed ad lib. After that, the females were released on the second host-containing patch and their behavior was recorded.

Event recording and statistical analysis

Wasps were observed continuously during their first and second patch visit and their behavior was recorded using the event recording program *The Observer*® (Noldus, Wageningen). Successful oviposition can be easily recognized in *V. canescens* by a characteristic “cocking” behavior of the searching female (Rogers 1972), even when larvae are concealed within the substrate. Patch residence time was defined according to previous experiments (e.g., Driessen and Bernstein 1999; Thiel et al. 2006) as the time between the first entrance to the patch until the last departure of the patch, including short off-patch excursions. A patch visit was considered terminated when the wasp had left the arena either by walking or flying off.

Generalized linear models (GLM, Nelder and Wedderburn 1972, Crawley 2005) were fitted to the data by using the procedure GENMOD (SAS Institute Inc 1999). The use of GLM was the most powerful approach for our data, since appropriate error distributions and link functions can be defined also for data sets not following a normal distribution (Nelder and Wedderburn 1972). Details for the method of model selection in GLM analysis are well explained by Crawley (2005). A GLM consists of a linear predictor η_i , which is described by the following function:

$$\eta_i = \sum_{j=1}^p \beta_j x_{ij} \quad \text{with } (i = 1, 2, \dots, N);$$

where β_j is the impact of factor x_{ij} (for $j=1, 2, \dots, p$).

The individual data points μ_i are transformed by a link function to become η_i (e.g., by identity link, $\eta_i = \mu_i$, power (-1) link, $\eta_i = \mu_i^{-1}$ or log link, $\eta_i = \ln \mu_i$).

A Gamma distribution with log link function was used to analyze patch residence times during first patch visit. Data of visits on the second patch, however, was not always adequately described by a gamma distribution of the error. In those cases, which are all indicated in the results section, the residence times were first log-transformed and then analyzed with a normal distribution and either log or identity link function. A Poisson distribution with a log link function was used to test for effects on the number of

cocking movements (number of ovipositions) performed. Explanatory variables were selected by backward elimination of non-significant effects from the full type-3 model (SAS Institute Inc. 1999).

Results

Two arrhenotokous (Valence and Antibes) and three thelytokous populations (Valence, Antibes, and San Juan) have been analyzed in the experimental study. This is not a full factorial design. Effects of “reproductive mode” and “place of origin” would not be disentangled if arrhenotokous and thelytokous populations were pooled in one analysis. Therefore, wasps from the two reproductive modes were analyzed separately.

Patch 1

Searching with a stick glued on their backs might be a serious handicap for the females and behavior of insects is often influenced by previous contact with anesthesia (Nicolas and Sillans 1989; Barron 2000). Therefore, it was important to check how the treatment would influence the wasp’s searching behavior. Since females from the CON treatment had not been chilled and glued, and because some of the wasps from WAIT had lost their stick already when searching their first patch (Table 1), we can disentangle the effects that chill and glue on the one side and the stick on the back on the other side have had on wasp behavior.

192 wasps were analyzed in this test, 105 thelytokous and 87 arrhenotokous ones.+

Thelytokous It turned out that the residence time on the first patch was influenced significantly by the treatment the wasps had been assigned to ($\chi^2_{df=2, n=105} = 14.35; p < 0.001$). This result, however, seemed to depend only on the chill/glue effects and not on the stick itself (Fig. 1), since wasps that had been anesthetized but lost their stick stayed significantly shorter than wasps that had never been in contact with an ice-cold plate and glue ($\chi^2_{1, 73} = 4.98; p = 0.026$). On the other hand, there was no difference between those that had lost the stick and those searching the patch with the stick still on their back ($\chi^2_{1, 66} = 2.47; p = 0.12$). A female’s place of origin showed no effect significant at the alpha=0.05 level ($\chi^2_{2, 105} = 5.25; p = 0.073$), even though it can be seen that differences between the Spanish San Juan wasps and the French Antibes and Valence wasps were relatively large (Fig. 1). When the number of cocking movements during the first patch visit was considered (see electronic supplementary material S1), we found again a significant effect of the handicap status ($\chi^2_{2, 105} = 16.68; p < 0.001$), with the wasps that had never been glued laying

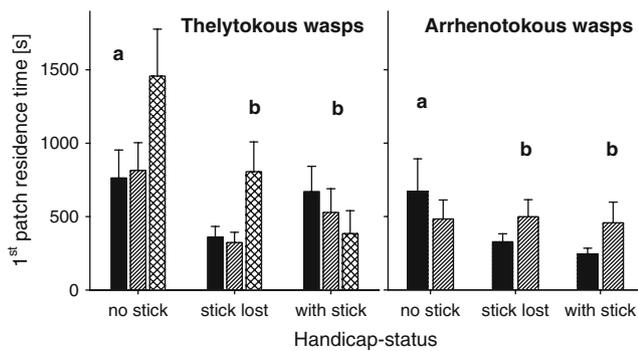


Fig. 1 Average patch residence times of thelytokous and arrhenotokous females on the first patch visited. The females differed in their handicap status, i.e., they had never been anesthetized and glued (*no stick*, CON); they had been glued but lost the stick during the recovery period and thus, searched the patch without a stick (*stick lost*, WAIT); or they still had the stick glued on their thorax when searching the first patch (*with stick*, either WAIT or FLY). Wasps from Valence are represented by *black bars*, those from Antibes by *striped bars* and those from San Juan by *crossed bars*. *Small bars* indicate the standard errors; different letters indicate significant differences

more eggs than those that had been chilled and glued but lost the stick ($\chi^2_{1,73}=11.51$; $p<0.001$), but with no difference between those that had lost the stick and those searching the patch with the stick still on their thorax ($\chi^2_{1,66}=0.00$; $p=0.99$). A female's place of origin also had a significant effect ($\chi^2_{2,105}=18.41$; $p<0.001$), with females from San Juan laying the most and females from Valence laying the least eggs (see electronic supplementary material S1).

Arrhenotokous As in the thelytokous wasps, the residence time on the first patch (Fig. 1) was influenced significantly by the handicap status ($\chi^2_{df=2,n=87}=7.34$; $p=0.026$) and wasps that had been anesthetized but lost their stick stayed significantly shorter than wasps that had never been chilled and glued ($\chi^2_{1,64}=6.75$; $p=0.009$), while there was no difference between those that had lost the stick and those searching the patch with the stick attached to their thorax ($\chi^2_{1,58}=0.29$; $p=0.59$). A female's place of origin did not have a significant effect ($\chi^2_{1,87}=1.68$; $p=0.20$). When the number of cocking movements during the first patch visit was

considered (see electronic supplementary material S1), we found no significant effect of the handicap status ($\chi^2_{2,87}=5.82$; $p=0.053$), with the wasps that had never been glued laying more eggs than those that had been glued and lost the stick ($\chi^2_{1,64}=4.13$; $p=0.042$), but with no difference between those that had lost the stick and those that searched the patch with the stick on their thorax ($\chi^2_{1,58}=0.19$; $p=0.66$). A female's place of origin did not have a significant effect ($\chi^2_{1,87}=1.71$; $p=0.19$).

Patch 2: general analysis

In the arrhenotokous wasps, residence times on the second patch were influenced by all factors tested, even though *place*-related interactions were not significant (Table 2; electronic supplementary material S2); the strong increase of residence times in the flight treatment being the most striking effect (Fig. 2). In the thelytokous wasps, residence times on the second patch increased with increasing travel time and were also influenced by experimental treatment (Table 2) with wasps from WAIT staying the shortest and those from CON the longest (Fig. 2). The lack of significance in the interaction of those two indicated that the slope of the travel time response curve was similar in all treatments, while the significant interaction term *place*×*treatment* showed that the effect of experimental treatment differed between populations originating from different places (see electronic supplementary material S2).

An analysis of the number of cocking movements of the arrhenotokous wasps gave a slightly different picture (Fig. 3, electronic supplementary material S3). Experimental treatment had a strong impact (Table 3), with wasps from WAIT laying the lowest number of eggs. The effect of the time spent traveling, however, did not differ between treatments. The significant interaction term *place*×*ln(traveltime)* indicated that wasps from Antibes laid generally more eggs with increasing travel time, while those from Valence did not (see electronic supplementary material S3).

Table 2 Variables tested (full model) for their effects on patch residence times during the second patch visit

Variable	Thelytokous wasps ($n=105$)			Arrhenotokous wasps ($n=87$)		
	<i>df</i>	χ^2	<i>p</i>	<i>df</i>	χ^2	<i>p</i>
place	2	3.63	0.16	1	0.79	0.37
ln(traveltime)	1	4.42	0.036	1	7.21	0.007
treatment	2	30.71	<0.0001	2	9.31	0.010
place×ln(traveltime)	2	2.45	0.29	1	1.52	0.22
treatment×ln(traveltime)	2	0.44	0.80	2	8.28	0.016
place×treatment	4	12.75	0.013	2	4.89	0.087
place×treatment×ln(traveltime)	4	3.33	0.5	2	5.44	0.066

Those in italics remained in the final model

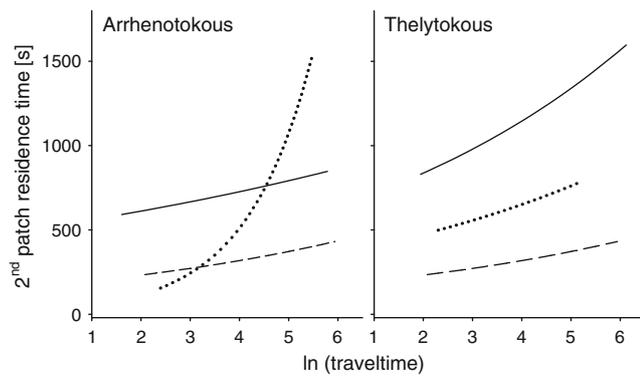


Fig. 2 Average patch residence times as predicted by the GLM analysis for arrhenotokous (*left*) and thelytokous (*right*) wasps on the second patch visited, averaged for all *place*-related effects for the sake of simplicity. The different treatments are indicated as follows: *Solid line* CON, *dashed line* WAIT, *dotted line* FLY

The number of cocking movements in the thelytokous wasps was, similar to the residence times, highly influenced by experimental treatment (Table 3), with wasps from WAIT laying the least and those from CON laying the most eggs (Fig. 3). The number of cocking movements increased with increasing travel time length, though this effect was not significant. The number of cockings was also dependent on the place the population originated from (Table 3, electronic supplementary material S3).

Patch 2: the effect of flying

The major goal of our study was to distinguish between the effects of the time spent waiting between patch visits and the amount of energy spent during traveling. Therefore, we analyzed which parameter, the travel time or the number of rounds flown, would affect patch residence time and number of ovipositions in those females that had spent their time traveling in the flight mill.

It turned out that the number of rounds a female flew (see electronic supplementary material S4), analyzed with a normal distribution and log link function, was strongly dependent on her travel time (i.e. the time she had spent in the mill) for the arrhenotokous ($\chi^2_{1,30}=15.37$; $p<0.001$) as well as the thelytokous wasps ($\chi^2_{1,28}=7.06$; $p=0.008$). The place of origin was also important in both reproductive modes (arrhenotokous, $\chi^2_{1,30}=9.64$; $p=0.002$; thelytokous, $\chi^2_{2,28}=6.98$; $p=0.03$; electronic supplementary material S4), while the interaction term $\text{rep.mode} \times \text{place}$ did not provide any additional explanatory value (arrhenotokous, $\chi^2_{1,30}=0.29$; $p=0.59$; thelytokous, $\chi^2_{2,28}=1.37$; $p=0.50$), i.e., the relationship between the number of rounds a female flew and the time she had spent in the mill was not significantly different between the places of origin.

A combined analysis of thelytokous and arrhenotokous wasps showed that the number of rounds flown was not

different between the two modes ($\chi^2_{1,58}=0.49$; $p=0.49$) and neither was the interaction term $\text{rep.mode} \times \ln(\text{traveltime})$ ($\chi^2_{1,58}=0.44$; $p=0.51$). Only the time spent traveling ($\chi^2_{1,58}=24.1$; $p<0.001$) and the place the population had originated from ($\chi^2_{1,58}=17.7$; $p<0.001$) had an effect on the distance covered.

The effect of the time spent traveling and the number of rounds flown during traveling was analyzed in such a way that both explanatory variables were present in the full model and the one with most explanatory power was selected by backward elimination.

The patch residence times were first log-transformed and then analyzed with identity link function for the arrhenotokous wasps and with log link function in the thelytokous wasps. This way, we fitted the models that best described the data sets. However, using the link functions vice versa gave very similar results: the number of rounds a wasp had been flying influenced the residence time in arrhenotokous females (Table 4; Fig. 4), whereas the residence time of thelytokous females was influenced by the place of origin and the time spent traveling, but not by the number of rounds flown in the mill (Table 4; Fig 4).

When analyzing the number of cocking movements performed, none of the variables had any significant explanatory power in either arrhenotokous or thelytokous wasps (Table 5).

Discussion

For properly understanding parasitoid foraging behavior, it is important to study them not only during a single patch visit but to watch behavioral changes that may occur during sequential visits (Bernstein et al. 1991; van Alphen et al. 2003). Energy dynamics, especially, are important factors

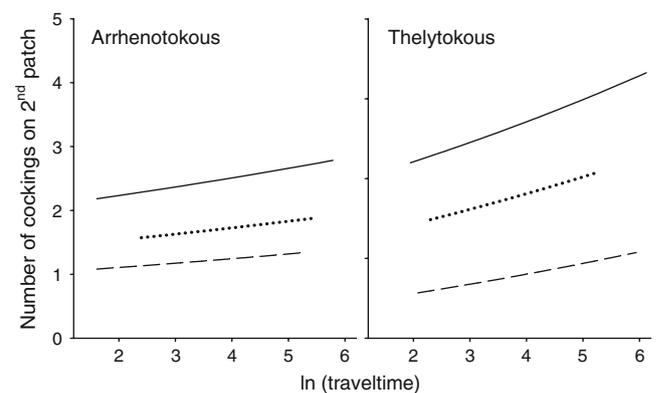


Fig. 3 Average number of cocking movements as predicted by the GLM analysis for arrhenotokous (*left*) and thelytokous (*right*) wasps on the second patch visited, averaged for all *place*-related effects for the sake of simplicity. The different treatments are indicated as follows: *solid line* CON, *dashed line* WAIT, *dotted line* FLY

Table 3 Variables tested (full model) for their effects on the number of cocking movements (ovipositions) during the second patch visit

Variable	Thelytokous wasps (<i>n</i> =105)			Arrhenotokous wasps (<i>n</i> =87)		
	<i>df</i>	χ^2	<i>p</i>	<i>df</i>	χ^2	<i>p</i>
place	2	8.00	0.018	1	2.09	0.15
ln(traveltime)	1	3.53	0.060	1	0.09	0.76
treatment	2	17.26	0.0002	2	10.43	0.005
place×ln(traveltime)	2	2.02	0.36	1	3.95	0.047
treatment×ln(traveltime)	2	0.15	0.93	2	1.69	0.43
place×treatment	4	12.47	0.014	2	0.85	0.66
place×treatment×ln(traveltime)	4	2.36	0.67	2	0.84	0.66

Those in italics remained in the final model

that may influence parasitization behavior of parasitoids in the field (Wäckers and Lewis 1994; Takasu and Lewis 1995; Casas et al. 2003; Strand and Casas 2008). On the other hand, it has been suggested from theoretical studies that the energy spent during traveling should not have a large impact on the patch residence times of parasitoids that are constrained in their reproductive success mainly by the time they have available for oviposition (Mangel 1993). This reasoning is supported by the theory of optimal information use (Stephens 1993). It is also underlying many theoretical models of parasitoid foraging behavior, even though it has never been explicitly tested. We therefore examined the patch residence time after travel periods of various lengths, during which wasps had either been confined in small vials or traveled actively in a flight mill, for five different lines of the parasitoid *V. canescens*. These lines differed in their reproductive mode (arrhenotokous or thelytokous) and/or in their place of origin (Valence, France, Antibes, France, San Juan, Spain). Wasps, especially from the arrhenotokous lines, seem to be frequent flyers during foraging (J. Lukáš, C. Bernstein, H. Gu, S. Dorn, unpublished data; Pelosse et al. 2007) and we had therefore expected that they might use energy spent during traveling as a proxy for patch availability in their habitat, whereas thelytokous wasps, which do not have to fly when foraging for hosts, might use time.

Indeed, we found that the thelytokous wasps are generally influenced in their foraging behavior by the time spent traveling (Tables 2, 3; Figs. 2, 3), but not by the amount of

energy spent: in two of the three populations (Antibes and San Juan), the response curves are almost overlapping in the FLY and WAIT treatments (see electronic supplementary material S2, S3). In the third population (Valence), the response curves of FLY and WAIT are only quantitatively, but not qualitatively, different. Additionally, for all thelytokous populations, the time spent in the flight mill turned out to be a much better predictor for the subsequent patch residence time than the number of rounds the wasp flew before (Table 4; Fig. 4), even though a correlation between these two variables exists (see electronic supplementary material S4). Moreover, even only passively waiting for the next patch showed a significant effect of the travel time in these wasps (Treatment CON in Figs. 2, 3, electronic supplementary material S2, S3); as has also been described by Thiel et al. (2006). For the arrhenotokous wasps however, almost the opposite was the case. These wasps only showed a strong travel response on subsequent patch residence time in the FLY treatment (Fig. 2), but only weak ones in the other two, with the effects of travel time even being contradictory in direction between the two lines in the CON treatment (see electronic supplementary material S2). This is in line with results from previous studies (Thiel et al. 2006; A. Thiel and C. Bernstein, unpublished data from flight mill pilot studies) where, in the arrhenotokous females, an effect of the previous travel time interval on subsequent patch residence time was absent when wasps passively waited for the next patch. Moreover, the number of rounds flown was a much better predictor of subsequent residence time than the length of the

Table 4 Variables tested (full model) for their effects on patch residence times after having flown in the mill

Variable	Thelytokous wasps (<i>n</i> =28)			Arrhenotokous wasps (<i>n</i> =30)		
	<i>df</i>	χ^2	<i>p</i>	<i>df</i>	χ^2	<i>p</i>
place	2	9.84	0.007	1	0.05	0.82
ln(traveltime)	1	3.67	0.055	1	1.02	0.31
ln(rounds)	1	0.36	0.55	1	9.32	0.002
place×ln(traveltime)	2	1.29	0.53	1	0.08	0.78
place × ln(rounds)	2	3.15	0.21	1	1.61	0.20

Those in italics remained in the final model

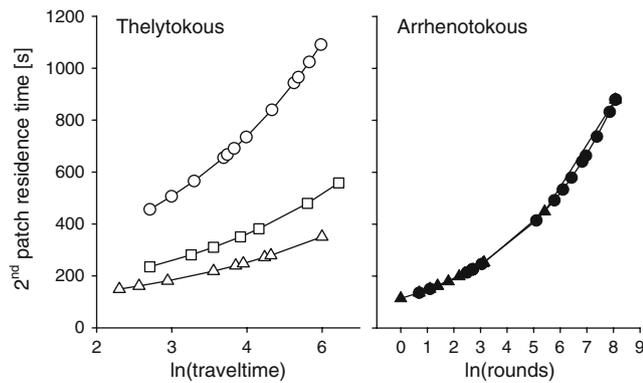


Fig. 4 Patch residence times as predicted by the GLM analysis for thelytokous (*left*) and arrhenotokous (*right*) wasps on the second patch visited in the FLY treatment. Residence times for the wasps from the different location were different for the thelytokous but not the arrhenotokous wasps. In thelytokous wasps, the number of rounds flown did not have a significant effect, only the time spent traveling. In the arrhenotokous wasps, it was the other way around. Places of wasp origin are indicated by different symbols: *triangles* Antibes, *squares* San Juan, *circles* Valence

travel time interval (Table 4; Fig. 4). These differences between the two wasp types are remarkable, and it is very likely that the two different habitat types the wasps of the different reproductive modes preferentially inhabit are responsible for the effects flight activity has on patch exploitation: arrhenotokous females exclusively live under field conditions (Schneider et al. 2002; Amat 2004), where they have to search for hosts (and food) in fruits hanging in the trees (Salt 1976; Driessen and Bernstein 1999, Desouhant et al. 2005). Flight is essential for traveling between fruits and fruit-trees and they are thus expected to be frequent flyers. Having to fly between patch visits leads to increasing energetic cost (Harrison and Roberts 2000) and thus it might be crucial for the arrhenotokous females to keep track of their energy levels, and also to initiate another feeding bout in time. Thelytokous females, on the other hand, find their hosts primarily (but not exclusively) inside grain storage buildings, bakeries, and the like (Schneider et al. 2002; Amat 2004). In the indoor habitat, the reproductive success of parasitoids would depend more on oviposition capacity than on frequent dispersal. Since food is virtually absent in these

buildings, the wasps have to leave in search for food sources somewhere else. Leaving does involve the high energetic costs for flying plus the uncertainty to find a food source in time plus the probability that the wasp may get killed before she can return to the host patches, making it quite unlikely that thelytokous wasps would show regular commuting between host and food sites. Moreover, a study by Harvey et al. (2001) clearly showed that the number of offspring produced by a thelytokous *V. canescens* female during the first 2 days of her life does not at all depend on food availability but only on host availability. When lifetime reproductive success was measured (Harvey et al. 2001), females that had had access to food either every second day or never did not differ in their lifetime reproductive success. Only under constant food access did the food significantly increase a female’s longevity and her reproductive success, however, ad libitum feeding is a possibility that is most unlikely to exist in the storage building environment. In summary, thelytokous females are less likely to run out of energy while foraging for hosts but if they do so, there is almost no possibility for them to refill, so they might as well ignore energy costs. Additionally, the time spent to reach the next patch might be a more reliable predictor of patch availability for the thelytokous wasps than their energetic expenditure, since traveling will not necessarily be linked with energy expenditure if wasps only occasionally fly. The ability to respond to the most reliable cues and ignoring others is considered to be adaptive and has been shown to occur in many other animal species as well (Stephens 1989; Vet et al. 1990; Mangel 1993; Potting et al. 1997; Vos et al. 1998; Thiel and Hoffmeister 2006).

The effects mentioned however became mainly apparent in the patch residence times of the females tested and are not visible in the number of ovipositions achieved per visit. This is probably due to the low number of ovipositions performed in general during the experiment (Fig. 3, electronic supplementary material S1), where the differences between the shortest and the longest travel times in the CON treatment were mirrored by an increase of less than one or less than two cocking movements in arrhenotokous and thelytokous females, respectively. Such a low number of ovipositions is not unusual, however, for

Table 5 Variables tested (full model) for their effects on number of cocking movements (ovipositions) after having flown in the mill

Variable	Thelytokous wasps (n=28)			Arrhenotokous wasps (n=30)		
	df	χ^2	p	df	χ^2	p
place	2	0.31	0.86	1	0.02	0.89
ln(traveltime)	1	2.04	0.15	1	0.06	0.80
ln(rounds)	2	2.61	0.11	1	1.83	0.16
place × ln(traveltime)	2	0.98	0.61	1	0.43	0.51
place × ln(rounds)	2	1.71	0.43	1	0.17	0.68

Those in italics remained in the final model

a wasp species where each oviposition has a decremental effect on the female's residence time (Driessen et al. 1995). In more natural situations, reduced residence times will probably better translate into reduced numbers of ovipositions, because hosts may be out of the parasitoid's reach, or empty patches that still contain host odor or patches with already parasitized hosts can be found.

Another indicator for the importance of the ecological circumstances on wasp behavior might be that there were differences found between wasp populations originating from different localities: the amount of energy spent during traveling did not influence the behavior of thelytokous wasp from Antibes or San Juan in a qualitative or quantitative way, since wasps from the WAIT and the FLY treatment did not differ in their travel time response (see electronic supplementary material S2 and S3). The thelytokous wasps from Valence, however, spent significantly more time on a patch in the FLY treatment compared to WAIT. This result is in agreement with a pilot study to this experiment, carried out at the UCB Lyon, in which only wasps of the Valence area had been used (A. Thiel and C. Bernstein, unpublished). The arrhenotokous wasps from Valence also showed a strong response to the number of rounds flown in this experiment (Fig. 4), as well as in the pilot study (A. Thiel and C. Bernstein, unpublished). In the Antibes habitat however, even the arrhenotokous wasps showed an effect of time spent traveling, in addition to the energy spent (see electronic supplementary material S2 and S3). Thus, it might be that the different places favor the use of either cue to different extents, but since we do not know at the moment which differences that could be, nor are we able to exclude alternative explanations, this question remains unanswered at the moment.

It is also very interesting to see how much wasp behavior has been influenced by the experimental treatment, i.e., by having been anesthetized and glued. Even after having had 2 days for recovery, the residence times and numbers of ovipositions performed in the WAIT treatment are strikingly shorter than in the CON treatment. However, the differences between CON and WAIT were always only quantitatively, i.e., the slope of the response curve was not different (Figs. 2 and 3; the opposite directions shown in the electronic supplementary material S2, S3 seem to result from the strong impact of single data points). Therefore, the differences between WAIT and FLY, and especially the steep slope found in the arrhenotokous wasps in the FLY treatment (Fig. 2) have to result from the flight activity of the wasps and not from the treatment of chilling and gluing (Table 1). The statistical tests of wasp searching behavior on the first patch also revealed that patch residence times and numbers of ovipositions had been significantly influenced by the treatment with anesthesia and glue but not by the presence or absence

of the stick on a wasp's thorax (Fig. 1, electronic supplementary material S1).

In conclusion, our study shows that physiological and behavioral trade-offs, e.g., the trade-off between searching for food vs. searching for hosts, may well be reflected in cognitive trade-offs in a way that animals respond either to one cue or another, depending on the power of the cue to predict future foraging success. In the thelytokous *V. canescens* in general, the only obvious effect is the time cost of traveling, as it has been predicted for time-limited foragers from some theoretical studies, and which has long been implicitly assumed in others. If, however, flight is an essential component of the parasitoid's searching behavior, as is the case for the arrhenotokous *V. canescens* wasps, it seems that energy expenditure is the foremost cue determining the costs of traveling.

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