ORIGINAL PAPER

Patch departure rules in Bumblebees: evidence of a decremental motivational mechanism

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Received: 20 July 2006 / Revised: 12 March 2007 / Accepted: 11 April 2007 / Published online: 22 May 2007 © Springer-Verlag 2007

Abstract The patch living rules of a pollinator, the bumblebee Bombus terrestris L., are studied here in the framework of motivational models widely used for parasitoids: The rewarding events found during the foraging process are supposed to increase or decrease suddenly the tendency of the insect to stay in the current patch and therefore to adjust the patch residence time to the patch profitability. The foraging behaviour of these pollinators was observed in two environment types to determine their patch-leaving decisions. The rich environment was composed of male-fertile flowers, offering pollen and nectar, and the poor one of male-sterile flowers, offering little nectar and no pollen. The experimental design consisted of a patch system in which inflorescences were evenly arranged in two rows (1 m distance). Residence times of foragers inside inflorescences and rows were analysed by a Cox proportional hazards model, taking into account recent and past experience acquired during the foraging bout. Most of the results showed a decremental motivational mechanism, that is, a reduction in the residence time on the inflorescence or in the row related to exploitation of flowers within inflorescences and inflorescences within rows These results indicate that bumblebees tend to leave the patch using departure rules similar to those found in parasitoids. The results also provide information on the memory,

Communicated by M. Giurfa

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J.-S. Pierre (\boxtimes) UMR BiO3P, INRA, Domaine de la Motte, P.O. Box 35327, 35653 Le Rheu, France e-mail: jean-sebastien.pierre@rennes.inra.fr learning and evaluating capabilities of bumblebees especially when rich and poor environments were compared. The patch-leaving mechanism suggested by this study is consistent with the central place foraging theory.

Keywords Decremental motivation model · Cox regression model · Residence time · Optimal foraging · Bumblebees (*Bombus terrestris*)

Introduction

Bumblebees ensure the pollination of wild and cropped plants, which makes their movement within and between plants of great biological and agronomic importance. Given that flowers are generally clustered in inflorescences, themselves grouped in the field (rows in cultivated plants), the analysis of bumblebee foraging behaviour in relation to the optimal residence time in a feeding patch (inflorescence or row) is of particular interest. This is a classical component of the optimal foraging theory since Charnov's (1976) pioneer work (Krebs and Davies 1992; Cézilly and Benhamou 1996). The functional approach of optimality, considered as pertaining to the ultimate causes, was later complemented by a more proximal approach, which addressed the precise departure mechanisms from patches. Many authors (for a review, see Van Alphen et al. 2003) have proposed that animals follow rules for leaving a patch, for example, a fixed number of captured prey, a fixed time spent in a patch or a maximum elapsed time between two prey meetings ("giving up" time).

In the literature, determination of rules for patch leaving has been based on female parasitoids (23 references cited by Van Alphen et al. 2003) with few studies using pollinators (Pyke 1982; Hodges 1985a, b; Kadmon and

Shmida 1992). Parasitoid wasps lay their eggs in the bodies of their hosts, which strongly links their foraging success in finding available hosts and their fitness (Mangel 1989). In a well known article devoted to a pyralid moth larvae parasite (Nemeritis=Venturia canescens), Waage (1979) proposed a new kind of mechanistic model based on the latent variable: motivation. In this model, the forager is expected to enter the patch with an initial level of motivation (Fig. 1). In the absence of any event, this level decreases monotonously. If a valuable food or host item is found, the motivation level rises suddenly after an incremental mechanism. The final decision to leave the patch occurs when the motivation to stay falls below a given threshold. The combination of these elements (motivation level, food encounter) determines the residence time within a patch. On the other hand, a decremental mechanism was suggested for Venturia canescens (Driessen et al. 1995; Driessen and Bernstein 1999). In this model, each encounter with a host decreases suddenly the tendency to stay. More recently, it has been shown in parasitoids that incremental and decremental mechanisms can be combined (Pierre et al. 2003).

The optimality of either incremental or decremental mechanisms has been addressed theoretically (Iwasa et al. 1981). The fundamental difference between these mechanisms relies on the forager's knowledge of the patch quality distribution in the environment (Van Alphen et al. 2003). Incremental mechanisms are more adaptive in aggregate environments with highly variable and/or unreliable number of hosts per patch, whereas decremental mechanisms are more adapted to environments where host variability per patch is low and likely to be learnt by foragers. Moreover, this relies on the hypothesis that host distribution is constant over the generation and that there is selection for the appropriate mechanism.



Fig. 1 Waage's (1979) model. The forager is expected to enter the patch with an initial level of motivation. The decision to leave the patch occurs when the motivation falls below a threshold (*horizontal dashed line*). In the absence of any event, this level decreases monotonously (*thin line, Residence time 1*). If a valuable food or host item is found, the motivation level rises (incremental mechanism, *bold line, Residence time 2*) or decreases suddenly (decremental mechanism, *dashed line, Residence time 3*)

The statistical method of proportional hazards model (Cox 1972) was efficient in studies of parasitoids, as it successfully detected the type of mechanism of a given species (Haccou et al. 1991; Hemerik et al. 1993; Outreman et al. 2005; Wajnberg et al. 1999, 2003; Van Alphen et al. 2003). The method consists in recording the time spent by a forager in a patch and the events that occurred while foraging in the patch. The experiment is repeated for a set of foragers, and the time spent by each of them is then regressed on various variables, such as the encounters with host, prey or food items that are treated as time-dependent covariates (Therneau and Grambsch 2000).

The relative probability of leaving the patch during an infinitesimal period dt, conditionally to the presence of the forager in the patch at time t, is defined as the hazard rate.

When the encounter with a host reduces the hazard rate (as compared to the baseline hazard), it increases the mean residence time in the patch. Then, a significant effect detects an incremental effect of each encounter. On the contrary, when an encounter increases significantly the hazard rate, this indicates a decremental effect. This method is based on a stochastic model, taking into account the individual variability of the results. The influence of internal factors can be estimated, and the influence of past events can be considered. These features are well suited for the study of animals that adapt themselves to their environment by continuously re-evaluating its quality (McNamara and Houston 1985; Pierre et al. 2003). The use of censored data is possible, and nested patch structures can be taken into consideration. However, this interesting method has not yet been applied to pollinators.

The question of the departure rule was addressed many times in bumblebees. Hodges (1985a, b) demonstrated that bumblebees leave Delphinium nelsonii inflorescences immediately after probing a flower, offering a relatively small volume of nectar but often stay and visit a new flower after probing a flower with a high volume. This departure rule, based on probing time, itself based on a threshold volume rule, is distinct from a "giving-up" time departure rule. Goulson et al. (2000) suggested another rule based on two successive encounters with empty inflorescences of Trifolium repens. Biernaskie et al. (2002) showed that bumblebees visit more flowers in artificial inflorescences when flowers contain the same volume of nectar than in inflorescences providing the same average reward but with a high variance. In the same way, a simulation made by Pappers et al. (1999) showed that visit duration decreased on plants with variable nectar quantities per flower. These results suggest that encounters with poor quality flowers induce bumblebees to leave the patch (plant or inflorescence), whatever the quality of the best exploited flowers. In addition, in the Biernaskie et al. (2002) experiment, this preference was expressed only when the resource variability could be determined by

comparative sampling. In all of these experiments, a decremental mechanism based on encountering poor quality flowers in patches seemed to arise, but this was not explicitly noticed by the authors. Moreover, Ferdy and Smithson (2002) reported an effect of the forager's past experience: Bumblebees tend to visit more flowers per rewarding artificial inflorescence after having experienced unrewarding or partially empty inflorescences.

All these studies strongly suggest that incremental/ decremental mechanisms determine patch-leaving decision. However, very few studies have modelled departure mechanisms. Among them are Pleasants (1989) using Hodges' (1985a, b) data, Kadmon and Shmida (1992) and Ohashi and Yahara (2002). In these studies, no references to the models of Waage (1979) or Driessen et al. (1995; Driessen and Bernstein 1999) were cited.

The present article aims to evaluate the existence of incremental/decremental processes, in foraging bumblebees, analogous to those widely demonstrated in parasitoids. Bumblebees share with parasitoids the characteristic of foraging on discrete resource units of variable quality. However, the difference between bumblebees and parasitoids is that bumblebees are central place social foragers and do not forage only for their own benefit. Therefore, the link between energy gain and ultimate inclusive fitness is less tight than in parasitoids and probably not linear. A priori predictions on the type of motivational mechanism is not straightforward, and an experimental approach seems useful.

To study these hypothetical processes, we tested the foraging behaviour and patch-leaving decisions of bumblebees (*Bombus terrestris*) in two environments of different profitability.

Materials and methods

General framework

The foragers were placed in a greenhouse with access to rich or poor environments using two types of oilseed rape flowers. Both environments were tested because it was of practical interest for pollination to know how pollinators behave when plants to pollinate are more or less rewarding. Data were analysed using the Waage model and the Cox proportional hazards regression model. The results are discussed with consideration of the decision process involved and the relevance of this approach to social insects.

Plants and insects

The oilseed rape flowers used for the experiments came from a field in Le Rheu, Western France. To maximise pollen and/ or nectar rewards, flowers were protected from visitation by insects by a net (tulle) and were collected at full flowering. Two plant genotypes were used in the experiments: a malefertile genotype (cv. 'Tanto', MF) producing pollen and nectar and a male-sterile genotype (cv. 'Fu-Tanto', MS), which produced little nectar and no pollen. Low nectar production of male-sterile genotype is due to a cytoplasmic transformation that induces both sterility of anthers and reduction in nectaries (Pierre et al. 1999). Therefore, MF and MS inflorescences were considered 'rich' and 'poor' resources, respectively, for the foragers.

Bumblebees came from a French commercial breeding company (GIE La Croix[®]). The colony was received at 6 weeks of age and consisted of the queen and about 80 workers. It was immediately placed in the experimental greenhouse and deprived of excess food supply to increase foraging motivation. The experiment began 48 h later and took place for seven consecutive days. The colony was regularly monitored to prevent it from too high starvation by controlling the reserve in the honey pot reserve.

Experimental design

The experiment was carried out in an experimental thermoregulated greenhouse $(3 \times 7 \times 3 \text{ m height})$ where two rows of oilseed rape flowers were placed 1 m distant from each other. This distance was enough to induce spatial discrimination between both rows by bumblebees (Plowright and Cantin-Plante 1997). Each row was composed of 20 inflorescences maintained in vials of water. Inflorescences were 20 cm distant from each other. In oilseed rape, the inflorescence is like a bunch of about 10-15 open flowers, which are not systematically visited by the insect. The number of available flowers per inflorescence was limited to 7 by elimination of the youngest or oldest supernumerary flowers. Two treatments were laid out to test the effect of environment quality on the foraging behaviour of bumblebees: (1) a rich environment (MF) composed of two rows of MF inflorescences and (2) a poor environment (MS) composed of two rows of MS inflorescences. Bumblebees were tested in both environments every experimental day.

The hive was placed in a cage of 1 m^3 with a small door, which allowed the entry of a single bumblebee into the experimental area. Only one bumblebee was observed per trial, i.e. during a single foraging bout. At the end of the observation, the bumblebee was caught, set aside and put back in its hive at the end of the day. In this manner, the foragers were observed once a day. The same forager could have been observed on another day, but the probability was low given the colony size. If the same forager was observed in the following days, they were naïve because they could have performed only one foraging bout on the previous day, which was not sufficient to acquire overnight memory retention (Keasar et al. 1996). Nine individuals were tested

per environment type. After each individual foraging bout, the flowers were renewed to avoid scent marking by bumblebees (Goulson et al. 2000).

Data collection

Observation of a bumblebee's foraging behaviour began when it entered the experimental area. A foraging bout started when the bumblebee visited the first flower (absolute time). An observation lasted at most 30 min, but generally the foraging behaviour ended before. When a bout was ongoing at the end of the 30-min period, its length was censored. A foraging bout was considered as finished when the bumblebee rested or flew continuously for 5 min without searching for flowers.

The foraging behaviour was recorded continuously using an event recorder "The Observer" (Basic version 3.0 for Windows, Noldus Information Technology, Wageningen, The Netherlands). The beginning and the end of each behavioural item were recorded with an accuracy of 0.1 sec.

Data were considered at three levels of observation as follows: movement onto or off of a flower, inflorescence and row. Foraging items also included exploitation or rejection of the patch; however, because of the hierarchical structure of the resource, the criteria differed at each level. To move onto and off, a flower corresponded to an exploitation of a flower. An inflorescence was considered as being exploited when at least one flower, among the seven, was exploited by the forager. When a bumblebee landed twice on the same inflorescence, the second landing was counted as a new exploitation. A flower or an inflorescence was noted as rejected when it was obvious that the bumblebee approached it at a distance less than 1 cm but did not land. Throughout the text, the term "visit" corresponds to both exploitation and/or rejection. A row was qualified as "exploited" when at least one inflorescence was exploited.

Cox's proportional hazards model

General model

A thorough description of the proportional hazards model (Cox 1972) can be found in Collett (2003). This model is formulated in terms of hazard rate, which is defined as the ratio of instantaneous "mortality" rate on the survival rate at time t. In the present context, this represents the probability per unit time that a bumblebee leaves the visited patch (respectively, at the row or the inflorescence level) given that it is still in the patch (Haccou and Meelis 1992). The model assumes that the patch-leaving tendency is the product of the basic tendency to leave the patch (i.e. the baseline hazard) and of a factor representing the joint effect of all the

exogeneous variables taken into account (i.e. the covariates). The model may be written as:

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

in which h(t; z) is the hazard rate, $h_0(t)$ the baseline hazard, t the time elapsed since the bumblebee entered in the current patch and β_i the regression coefficients that give the relative contributions of the p covariates $z_i(t)$. A quantitative measure of the effect of any particular variable is given by the expression exp ($\Sigma\beta_i z_i$), the hazard ratio. If the hazard ratio is less than one, the bumblebee's patch-leaving tendency is reduced, while a hazard ratio greater than one increases this tendency.

Covariates tested in our models

Haccou et al. (1991) pointed out that consideration of all observable behavioural events that occur during the foraging behaviour is unfeasible because this set would be obviously too large. Furthermore, when many factors and covariates are involved in a linear model, the parsimony principle recommends keeping as few as possible. Thus, the selection of covariates was an important step in the analysis. The covariates and factors were classified in two groups: firstly, covariates related to the experience gained within the current patch (present experience) and secondly, related to the events that occurred before entry into the patch (past experience). The covariate "number of visits to the current inflorescence" was classified in the "within patch experience" but depends also on the past experience as it records the number of times where the inflorescence was visited since the bumblebee release to the current moment. Precise details about all the covariates initially included in the model are given in Table 1 (inflorescence) and Table 2 (row). In the tables, the "numeric" type indicates the quantitative covariates, and the "factor" type indicates a qualitative set of distinct levels. Covariates are considered as time dependent when the precise time of occurrence of an event is taken into account. For instance, each visit to a flower is considered time dependent, as the precise moment of the visit is considered. Time-dependent covariates are recorded as follows: The total time spent in the patch (row or inflorescence) is split in the file into as many lines as recorded events plus one. The time recorded in the first line corresponds to the delay between the entry in the patch and the first event. In the second line, it corresponds to the delay between the first and the second event and so on until the departure from the patch. The value of the covariate is 0 for the first line, 1 for the second and so on. In addition, a censor variable is set to the "censored" value for all lines except the last, which is set to

Table 1 Analysis at the inflorescence level

Covariate	Туре	Time dependent
Bumblebee effect (labelled from 1 to 18)	Factor	No
Experience within a patch		
Exploitation of a flower in the current inflorescence	Numeric	Yes
Number of visits to the current inflorescence	Numeric	No
Experience preceding a patch visit		
Total number of inflorescences approached by the bumblebee	Numeric	No
Total number of inflorescences exploited by the bumblebee	Numeric	No
Total number of flowers exploited by the bumblebee	Numeric	Yes
Number of flowers exploited in the last exploited inflorescence	Numeric	No
Action on the last encountered inflorescence (exploitation or rejection)	Factor	No

Variables of interest used in the Cox proportional hazards model.

"uncensored." This type of coding was suggested by Therneau and Grambsch (2000) and is currently implemented in the *coxph* function of the *R* (R Development Core Team 2006) language.

Statistical analysis

The effect of each variable and the overall significance of the fitted model were assessed by likelihood ratio tests (Collett 2003). Following Wajnberg et al. (1999), this test was used

Table 2 Analysis at the row level

Covariate	Туре	Time dependent
Bumblebee effect (labelled from 1 to 18)	Factor	No
Experience within a patch		
Number of inflorescences exploited in the current row	Numeric	No
Number of inflorescences rejected in the current row	Numeric	No
Number of visits to the current row	Numeric	No
Experience preceding a patch visit		
Total number of inflorescences yet exploited by the bumblebee	Numeric	No
Total number of inflorescences yet rejected by the bumblebee	Numeric	No
Number of inflorescences exploited in the previously exploited row	Numeric	No
Number of inflorescences rejected in the previously exploited row	Numeric	No

Variables of interest used in the Cox proportional hazards model.

iteratively to identify the parameters having a significant influence on the forager's patch-leaving tendency. First order interaction between two factors (qualitative covariate) or between a factor and a quantitative covariate were considered in the model. Higher order interactions were not included to avoid overparameterisation. All computations were done with the S-plus statistical software (MathSoft©; Becker et al. 1988). Results are given as mean±standard error.

Results

Eighteen individuals (nine per environment) were observed. Data of two foragers among the 18 were censored, leading to an overall censor rate of 11.1%. Four hundred and twenty seven bouts on inflorescences were observed, from which eight were censored (censor rate, 1.9%). We recorded 44 bouts on rows, among which eight were censored (censor rate, 18.2%). Censoring events were more frequent for rows than for inflorescences. Therefore, greater statistical power was expected at the inflorescence level rather than the row level.

The residence times were studied at the inflorescence and row levels. To facilitate comprehension of results, an increase or a decrease in the leaving tendency $[\exp (\beta)]$ was translated into a reduction or an increase in the mean residence time $[1/\exp (\beta)]$, respectively. An indicative calculation based upon the hypothesis of an exponential distribution of the residence time indicated that, when the risk hazard is multiplied by $\exp (\beta)$, the mean residence time is divided by the same value, that is, multiplied by $1/\exp(\beta)$. The covariates, mentioned in Tables 3 (analysis at the inflorescence level) and 4 (analysis at the row level) and numbered, respectively, from 1 to 9 and 1 to 7, were those determined to be significant after model selection.

Results at the Inflorescence level

In both environments, the 'bumblebee' factor had a significant effect on the time spent in each inflorescence (Table 3), which indicated that bumblebees individually differed in their foraging behaviour. Bumblebees were then considered as clusters of foraging bouts on inflorescences or random blocks. No significant interaction was found between this factor and any other.

In the rich MF environment (Table 3, lines 1–3), all the factors selected by the model had a decremental effect on the patch residence time. The moment when exploitation of a flower began since the visit to the current inflorescence (line 1) significantly increased the leaving tendency by a factor 1.32 (reduction in the residence time by a factor 0.76). Each return to an already exploited inflorescence (line 2) highly enhanced the patch-leaving tendency by a

Treatment	Covariates	β	$SE(\beta)$	exp(β)	χ^2 (df)	P value	Effect on leaving tendency	Effect on residence time
Rich	Bumblebee effect				41.6 (8)	< 0.001		
environment (MF)	1—Exploitation of a flower in the current inflorescence	0.275	0.0627	1.32	19.5 (1)	< 0.001	↑	Ļ
	2—Number of visits to the current inflorescence	1.056	0.1527	2.87	38.1 (1)	< 0.001	↑	Ļ
	(—Last encountered inflorescence exploited)	0.000	0.0000	1.00	20.1 (2)	< 0.001	REF	REF
	3—Last encountered inflorescence Rejected	0.365	0.0898	1.44			↑	Ļ
	Overall significance of the model				130.1 (12)	< 0.001		
Poor	Bumblebee effect				48.8 (8)	< 0.001		
environment (MS)	4—Exploitation of a flower in the current inflorescence	0.173	0.0501	1.19	12.3 (1)	< 0.001	Î	Ļ
	5—Number of visits to the current inflorescence	0.499	0.1023	1.65	21.4 (1)	< 0.001	↑	Ļ
	(-Last encountered inflorescence exploited)	0.000	0.0000	1.00	33.3 (1)	< 0.05	REF	REF
	6—Last encountered inflorescence Rejected	0.456	0.093	1.58			↑	\downarrow
	7—Number of flowers exploited in the last exploited inflorescence	-0.059	0.0274	0.94	5.2 (1)	< 0.001	\downarrow	↑
	8—Total number of rejected inflorescences since the beginning of the trial	-0.125	0.0334	0.88	15.2 (1)	< 0.001	\downarrow	↑
	9—Total number of flowers exploited since the beginning of the trial	0.017	0.0045	1.02	15.8 (1)	< 0.001	↑	\downarrow
	Overall significance of the model				155.6 (15)	< 0.001		

Table 3 Cox analysis at the inflorescence level

Estimated regression coefficients (β), standard errors (SE) and hazard ratios exp(β) of covariates that have a significant effect (P<0.05) on the tendency of *Bombus terrestris* to leave inflorescences of oilseed rape according to the environment (rich or poor). The χ^2 corresponds to the asymptotic likelihood ratio tests. Downward arrows indicate a decreasing effect; upward arrows indicate an increasing effect of the covariate (1 to 9) on the patch-leaving tendency or the residence time. REF indicates the reference level for the qualitative factors. The rich environment was composed of two rows of male-sterile inflorescences (MF), and the poor environment was composed of two rows of male-sterile inflorescences (MS).

factor 2.87 (reduction in the residence time by 0.35), suggesting that the insects were able to discriminate between fresh and depleted inflorescences. The rejection of the previous inflorescence (line 3) also increased the leaving tendency (reduction in the residence time by 0.69) as compared to its acceptation and exploitation (taken as reference in the Cox Model).

In the poor MS environment (Table 3, lines 4–9), similar results were observed. The strongest effects were registered when the previous experience was considered (lines 5 and 6). The exploitation of one flower (line 4) and the number of flowers visited (exploited and/or rejected; line 5) also had a decremental effect, respectively, increasing the leaving tendency by a factor 1.19 and 1.65 (reduction in the residence time by 0.84 and 0.60). Another decremental effect was observed when the last encountered inflorescence was rejected (line 6) as compared to the opposite situation when the last encountered inflorescence was actually exploited (reduction in the residence time by 0.63). In

ted (reduction in the

addition, the total number of flowers exploited since the beginning of the trial (line 9) slightly increased the leaving tendency from inflorescences by a factor 1.02 (reduction in the residence time by 0.98). On the contrary, the number of flowers exploited in the previous inflorescence (line 7) as well as the total number of rejected inflorescences since the beginning of the trial (line 8) slightly decreased the leaving tendency by a factor 0.94 and 0.88, respectively (increase in residence time by 1.06 and 1.14). This was the only incremental effect registered at the inflorescence level.

Results at the row level

At the row level, the bumblebee individual effect was significant for both environments.

In the rich MF environment (Table 4, lines 1-3), the number of inflorescences exploited in the previous row (line 1) increased the leaving tendency from the current row by a factor 1.29 (reduction in the residence time by 0.78). The

Table 4 Cox analysis at the row level

Treatment	Covariates	β	$\begin{array}{c} \text{SE} \\ (\beta) \end{array}$	ехр (β)	χ^2 (df)	P value	Effect on leaving tendency	Effect on residence time
Rich	Bumblebee effect				28.2 (8)	< 0.001		
environment (MF)	1—Number of inflorescences exploited in the previous row	0.254	0.112	1.29	5.9 (1)	< 0.05	↑	Ļ
	2—Number of inflorescences rejected in the previous row	-0.772	0.313	0.46	7.8 (1)	< 0.01	Ļ	Î
	3—Total number of inflorescences exploited since the beginning of the trial	0.424	0.146	1.52	21.4 (1)	< 0.001	↑	Ļ
	Overall significance of the model				45.3 (11)	< 0.001		
Poor	Bumblebee effect				37.7 (8)	< 0.001		
environment (MS)	4—Rejection of an inflorescence in the current row	0.971	0.427	2.64	14.2 (1)	< 0.05	↑	Ļ
	5—Number of inflorescences exploited in the previous row	0.462	0.170	1.59	12.1 (1)	< 0.001	↑	Ļ
	6—Number of inflorescences rejected in the previous row	-1.760	0.712	0.17	14.4 (1)	< 0.05	\downarrow	Ŷ
	7—Total number of inflorescences exploited since the beginning of the trial	0.380	0.158	1.46	9.9 (1)	< 0.01	↑	\downarrow
	Overall significance of the model				54.6 (12)	< 0.001		

Estimated regression coefficients (β), standard errors (SE) and hazard ratios exp(β) of covariates that have a significant effect (P<0.05) on the tendency of *Bombus terrestris* to leave a row of 20 oilseed rape inflorescences according to the environment (rich or poor). χ^2 corresponds to the likelihood ratio tests. Downward arrows indicate a decreasing effect; upward arrows indicate an increasing effect of the covariate (1 to 7) on the row-leaving tendency or the residence time. The rich environment was composed of two rows of male-fertile inflorescences (MF), and the poor environment was composed of two rows of male-sterile inflorescences (MS).

total number of inflorescences exploited since the beginning of the trial (line 3) was also significant, increasing the leaving tendency by 1.52 (reduction in the residence time by 0.68). However, on the contrary, the number of inflorescences rejected on the previously visited row (line 2) highly decreased the leaving tendency from the currently visited row by a factor 0.46 (increase in the residence time by 2.17), which corresponded to an incremental effect.

In the poor MS environment (Table 4, lines 4–7), a high decremental effect of the rejection of an inflorescence in the current row (line 4) multiplied the patch-leaving tendency by 2.64 (reduction in the residence time by 0.38). The effects of the other covariates were similar to those found in the rich environment. Decremental effects were also found for the number of inflorescence exploited in the previous row (line 5, reduction in the residence time by 0.62) and of the number of inflorescences exploited since the beginning of the trial (line 7, reduction in the residence time by 0.68). As in the rich environment, the rejection of several flowers in the previous row (line 6) had an incremental effect (increase in the residence time by 5.88).

Discussion

The results were clear at the inflorescence level, which was considered to be a small scale patch. Each flower exploitation resulted in an increase in the tendency to leave the patch, which reduced the average time spent in the patch. This corresponds to a decremental process described in parasitoids in the literature (Driessen and Bernstein 1999). At a higher level, when rows were considered as large-scale patches, we also observed a decremental effect of the exploitation of an inflorescence (small scale patch). In the latter case, the tendency to leave the row was also modified by the experience acquired in the previous row and since the beginning of the trial. This indicated a memorisation of the whole foraging bout.

These results are consistent both with theoretical predictions arising from different theoretical frames and with former results found in the literature on bumblebees.

Firstly, decremental effects are expected in the central place foraging theory (Orians and Pearson 1979; Houston and McNamara 1985). Each successful exploitation of a flower or an inflorescence increases the load either of the nectar in the crop or of the pollen in the corbiculae. This hastens the return to the hive, and the effect should be greater in a rich rather than a poor environment. This is confirmed at the inflorescence level where the effect of the exploitation of a flower is 1.6 times greater in the rich than in the poor environment (Table 3, lines 1 and 4). In bumblebees, similar conclusions obtained by a different method were also reached by Cresswell (1999) and

Goulson et al. (2000). In this experiment, a decremental effect was also found when considering the number of flowers already visited in the current inflorescence. This can be interpreted better in the marginal value theorem (Charnov 1976): The number of exploited flowers indicates the patch depletion and the fall of the reward rate below a critical threshold. Pyke (1982) found the same kind of effects in *Bombus flavifrons* and *appositus* on *Aconitum columbianum* and also concluded that their observations supported a Charnov-like rule.

Secondly, in bumblebees, the evolution through time of the tendency to stay in the patch can be interpreted as it was by Waage (1979) and his followers. Iwasa et al. (1981) suggested that incremental or decremental effects corresponded to sudden jumps of an internal Bayesian estimator of the remaining resource in the patch. They showed that the estimator is incremented when a new resource item is found if the distribution of resources within the patches is a negative binomial. In this case, the discovery of new items indicates a patch of large size and prompts longer stays. Alternatively, the estimator may be decremented if the distribution of resources is more or less uniform. For the pollinator, each new exploitation of a resource item means an increase in patch depletion and which prompts it to leave the patch to find another one to restore the energetic gain rate. Driessen et al. (1995; Driessen and Bernstein 1999) predicted by a model and assessed with an experimental design the existence of such a decremental process in the drosophilid parasitoid Venturia canescens. Our observations in bumblebees are also consistent with the Bayesian model of Iwasa (1982) predicting that the decision process should be decremental when the variance between patches is low. In the present experiment, the variance of resources between inflorescences and between rows was actually very low.

Thirdly, the results may also be interpreted in a cognitive framework. The time spent in an inflorescence was influenced by the past experience of the foragers. The rejection of the previously visited inflorescence increased the leaving tendency when compared to cases where the inflorescence was accepted. This suggests that foragers had a negative perception of their recently tested environment. Similar conclusions were reached by Goulson et al. (2001), investigating bees' behaviour with a different approach. The effect of past experience also appeared at the row level. The residence time in the currently exploited row was shortened when many inflorescences were exploited in the previous row. This effect is probably physiological, reflecting the loading of the crop or corbiculae of the bumblebee. This is related to the first point of our discussion: the central place forager nature of these insects.

Some events of the past experience have an incremental effect on the residence time. For instance, the repeated

rejection of flowers increased the time spent in the current inflorescence. Similarly, at the row level, the number of inflorescences rejected was positively related to the residence time, especially in the poor environment. Bumblebees are able to assess the quality of a flower by inspection in flight. A rejection indicates that the flower is empty. The observed persistence in searching resources in an inflorescence and in the row of poor quality could indicate that inter-patch travels or unloaded return flights to the nest are costly.

In conclusion, the motivational mechanisms proposed by Waage (1979) and his successors as patch-leaving decision rule for parasitoids appears to adequately explain the foraging behaviour of bumblebees. They share with parasitoids the characteristic of foraging on discrete units-the flowers-that are countable and generally clumped in patches. For bumblebees and generally speaking for pollinators, these resources are often organised in nested clusters for natural or agronomic reasons. Flowers are grouped into inflorescences, and inflorescences are clumped in patches in natural habitats, in rows and plots in agricultural landscapes. This study indicates that grouping may be important in the foraging process. Bumblebees are social insects, which makes them central place foragers. They should use more likely a decremental rule than parasitoids. Although not investigated in the literature, the decremental rule fits well with the general hypothesis of a decrease in the patch residence time during foraging bouts in that kind of foragers (Orians and Pearson 1979). In the case of parasitoids, the incremental rule is expected when the number of hosts is highly variable between patches, whereas the decremental rule is expected when this number is rather constant (Iwasa et al. 1981; Driessen and Bernstein 1999; Van Alphen et al. 2003).

The results presented here were determined by survival analysis (Cox proportional hazards model) that proved to be as well adapted to the study of patch residence time in bumblebees as in the case of parasitoids (Van Alphen et al. 2003). The strength of the method lies on its capacity to assess the effects of a series of factors, events and covariates on the patch residence time. It is suggested that more investigation using this method could be conducted on the foraging behaviour of pollinators.

Acknowledgement The authors thank Jean-Pierre Masson for useful discussions concerning the statistical analysis used in this manuscript. They also thank Franck Poirier and Samuel Monvoisin for technical support and Randy Kutcher for reviewing the English. They are indebted to the two anonymous referees of a previous version for their careful revision and useful comments. This work complied with the current laws in France and received financial support from the GIS L Bio, "Projet Pollinisation," Région Bretagne et Pays de Loire, France.

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