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Genetic variability in the area searched by a parasitic wasp: analysis from automatic video tracking of the walking path

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Abstract

The ability of foraging hymenopterous parasitoid females to discover their hosts, and thus to be efficient agents in biological control programs, is likely to be related to the surface they are able to prospect per unit of time. However, this behavioural trait has never been accurately estimated, and its implication in female efficiency has never been really demonstrated. This paper provides an algorithmic method that can be used to estimate this trait from an automatic recording of the females' walking path. Using stochastic procedures simulating walking tracks, this trait is shown to be strongly related to the number of hosts that parasitoid females are able to attack per unit of time. This trait was estimated for individual females of *Trichogramma brassicae* Bezdenko (Hymenoptera; Trichogrammatidae). On average, females of this species are able to prospect about 28 $mm^2 s^{-1}$. Finally, the genetic variation in this trait was studied using the iso-female line method. A significant genetic variability was observed. It provides the basic information that is necessary to start a genetic selection of mass-reared *Trichogramma* in order to improve their efficiency in controlling target pests in biological control programs. The functional and evolutionary implications of these results are discussed.

Keywords: Area searched; Genetic variability; *Trichogramma*; Automatic video tracking; Stochastic simulation

1. Introduction

The surface prospected by a parasitoid (or predator) looking for hosts (or prey) has always been considered to be an important feature of host–parasitoid (or predator–prey) associations. Early in the 1930s, the so-called 'Area of Discovery' (in which all hosts or prey are found) was already one of the few important behavioural features included in models developed to understand host–parasite (or predator–prey) dynamics (Nicholson, 1933; Nicholson and Bailey, 1935; Hassell, 1976, 1978; Begon and Mortimer, 1981). In such simple models, the area searched was considered to be constant for a given parasitoid (or predator) and this parameter, which has a strong influence on the dynamics of the system, has unceasingly been considered in the continuous development of more realistic models (Hassell and May, 1973; Beddington et al., 1975; Hassell, 1978; Hassell and Comins, 1978).

For most insect parasitoids, the last step of host-finding behaviour is predominantly performed by walking (Vinson, 1984; Wajnberg, 1994). It corresponds to the behaviour adopted by a foraging female that has just landed on a leaf surface on which potential hosts are living. The study of the surface searched by parasitoid females who are looking for hosts is thus aimed at understanding the strategy adopted to prospect this particular environment. Since this strategy is directly linked to the ability of finding hosts to lay eggs and, therefore, to the production of offspring, we can expect that the surface prospected per unit of time would be a behavioural trait strongly influenced by natural selection (Boulétreau, 1986; van Alphen and Vet, 1986; Bell, 1990, 1991).

The study of this trait in parasitoid species that are used for biological control programs could provide very useful results. Even though it has never been clearly demonstrated, females that are able to prospect a bigger surface per unit of time are expected to present a higher

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host attack rate, and thus to be better biocontrol agents. For this reason, both experimental and theoretical studies that aim to quantify the quality of biological control agents, are now including behavioural traits involved in host-searching ability (Bigler et al., 1988; Bigler, 1994; Bruins et al., 1994; Godfray, 1994; Wajnberg, 1994).

To date, several different indirect methods have been proposed for the estimation of the surface prospected by foraging animals. More specifically, from the early work of Nicholson and Bailey (1935) this trait was indirectly estimated from the number (or proportion) of hosts discovered by isolated foraging females (e.g. Edwards, 1961; Marston and Ertle, 1973; Varley et al., 1973). In fact, the estimated trait generally corresponded to the area that was actually prospected expressed as a proportion of the total available area. The estimated value may be transformed according to some knowledge of the walking velocity of foraging females, in order to get an approximate result expressed in real surface units (Marston and Ertle, 1973).

During the last decade, the use of automatic video tracking of animals' motion has become widely available (Coulon et al., 1983; Chassain et al., 1988; Varley et al., 1994; Wratten, 1994). From a video record of animal displacements, these automatic systems produce X–Y co-ordinates that generally have an accuracy of 25 points per second (Wratten, 1994). This type of analysis has been fruitfully used in order to estimate several behavioural characteristics of the host searching activity of parasitoid females. For example, Bruins et al. (1994) used such a video tracking system to estimate the distance at which hosts are perceived by the parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera; Trichogrammatidae).

In this paper, we propose an algorithmic method that enables the estimation of the area searched by foraging wasps, based on an automatic analysis of their walking paths. This method resulted in a direct estimation of the area searched per unit of time. A stochastic model was then used in order to understand how this trait may be related to the ability of females to find their hosts. This model simulates the walking activity of individual females in the presence of hosts with different spatial distribution patterns. The results obtained clearly showed that this behavioural trait was positively related with wasp efficiency to find their hosts. Using the method described, this trait was estimated in isolated females of *Trichogramma brassicae* Bezdenko (Hymenoptera; Trichogrammatidae) (= *T. maidis* Pintureau and Voegelé), and its genetic (i.e. polygenic) variability was quantified in the population studied using the iso-female strain method (Parsons, 1980; Hoffmann and Parsons, 1988). The wasp that was examined in this study is an egg parasitoid of several moth species. It was chosen because it is the insect that is most intensively produced worldwide for biological control programs (Wajnberg and Hassan, 1994). A quantification of the genetic variability of the biological traits involved in its efficiency could provide information that is necessary for the improvement of this efficiency by means of genetic selection programs (Roush, 1979; Wajnberg, 1994). Moreover, this information could contribute to the better understanding of the adaptive and evolutionary mechanisms involved in host–parasitoid associations (Boulétreau, 1986).

2. Materials and methods

2.1. Estimation of the area searched by a female wasp

From an automatic analysis of the video-recorded motion of females, Bruins et al. (1994) showed that *T. brassicae* females were able to perceive their hosts (i.e. eggs of lepidopterous pests) from an average distance of 3.5 to 4 mm (i.e. 'reactive distance', Holling, 1966; Roitberg, 1985), depending on which host species they were offered. Odourless glass beads of 0.45 mm in diameter were also perceived from about the same distance, indicating that visual perception mechanisms were involved. Thus, during their walking behaviour, females are perceiving on both the right and left side a continuous strip that has a width of two reactive distances. Within this strip, all hosts will be discovered. Therefore, measuring this surface will give an estimation of the area that is actually searched per unit of time by foraging wasp females. The method used to estimate this surface, using a combination of circles and rectangles, is explained Fig. 1.

The main characteristic of this method is that each surface unit is counted only once, even if the female is crossing its own path once or several times. This method is analogous to procedures that have been used to estimate the visual scanning area for plovers (Pienkowski, 1983). It assumes that the reactive distance is constant over the whole path. However, this trait is known to vary according to a number of different factors that are related to the internal state of the animal (Bell, 1990, 1991). For example, hunger is known to often affect the distance at which resources may be detected (Holling, 1966; Jones, 1976). Thus, the method used here gives only an average estimation of the surface prospected, providing that an average reactive distance is used. According to the laws of large numbers, the use of an average value will mean that it is necessary to consider reactive distance as a random stochastic trait, which is quite acceptable in most cases.

The area searched per unit of time by females of *T. brassicae* was estimated using a reactive distance of 3.67 mm. This value corresponds to the average distance at which females of this species could visually perceive odourless glass beads of 0.45 mm of diameter (see Table

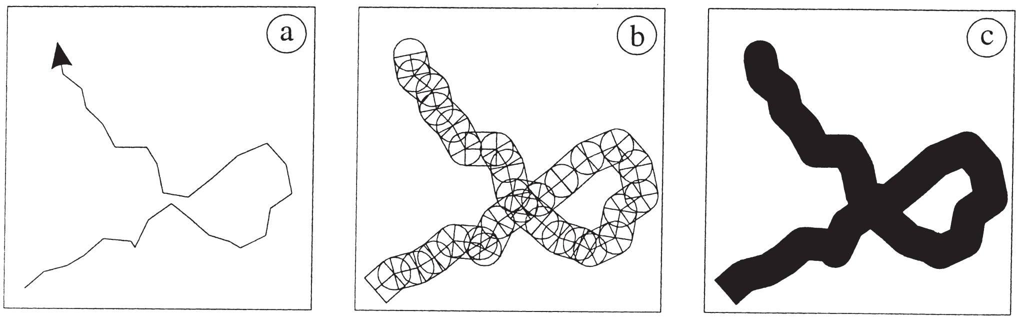

Fig. 1. Three steps used for the estimation of the area searched per unit of time by a walking female. A recorded walking path (a) is completed with a combination of circles and rectangles (b) of diameter and width equal to two reactive distances to hosts (Bruins et al., 1994). These circles and rectangles are then filled (c), and the corresponding surface is measured. The result is finally expressed in surface unit per time unit.

2 in Bruins et al., 1994). A series of computations has revealed that the use of a different reactive distance would only lead to a change of scale, and would not qualitatively affect all the simulation and experimental results presented here.

2.2. Insects and experimental set-up

The area searched per unit of time was estimated using isolated *T. brassicae* females which belonged to a population which was collected several years ago from parasitised *Ostrinia nubilalis* Hübner (Lepidoptera; Pyralidae) eggs in Alsace (France). This population probably originated from the Moldavian population which was released in this area for biological control against the European corn borer. Its electrophoretic patterns for esterases are the same as those described by Pintureau and Babault (1981). This strain was also the one used by Bruins et al. (1994). It has been maintained under laboratory conditions, for more than 100 generations, on the eggs of one of its factitious hosts, *Ephestia kuehniella* Zeller (Lepidoptera; Pyralidae), at 25°C, LD 12:12.

Searching behaviour by foraging animals can be influenced by both external (i.e. presence, quality and distribution of resources, presence of other foraging individuals) and internal (i.e. hunger, experience) environmental factors (see Bell, 1990 for a general review on this topic). Therefore, in order to estimate this trait in conditions that were as standardised as possible, experiments were performed on mated, naive, honey-fed, less than 24 h old females, without hosts. Each female was released in an open arena (a Petri dish of 9 cm in diameter) and its walking activity was video-recorded with the same equipment and under the same conditions as those used in Bruins et al. (1994) (i.e. 7000 lux, at 23 ± 1°C and 70% R.H.). The walking activity near the border of the arena was not taken into account when computing the trait, so that the estimate was obtained, as much as was possible, from undisturbed animals (see Bigler et al., 1988).

From the video records obtained, an automatic tracking computer device was used to transform each walking path into X–Y co-ordinates with an accuracy of 25 points per second (Coulon et al., 1983; Varley et al., 1994). The method described in Fig. 1 was then used to estimate the area searched per unit of time by each of the recorded females.

Twenty seven mated females, taken at random from the mass-reared population, were used to establish 27 iso-female lines (i.e. families). Experiments were performed on the next generation. On average, 5.96 (± 0.45) daughters were measured per family. The walking activity of the analysed females was recorded during 25.92 (± 1.23) seconds. The statistical test of the variation observed between families provides a way to quantify the genetic variation in the trait studied (i.e. iso-female line method, Parsons, 1980; Falconer, 1981; Hoffmann and Parsons, 1988). The area searched per unit of time by a walking female can be considered to be normally distributed. Therefore, the statistical comparison of the different families was based on standard parametric methods (i.e. Analysis of Variance).

3. Results

3.1. What is the meaning of this behavioural trait?

A series of simulations were performed using the stochastic model described by Yano (1978) and Bruins et al. (1994). This model simulates the walking behaviour of isolated females in the presence of hosts that have a fixed density and spatial distribution. Briefly, this model generates a walking path by drawing, at each step, an angular direction from a normal distribution with the direction at the previous step as mean, and with a fixed standard deviation. The walking velocity is linearly and positively related to the distance to the last host attacked, up to a fixed maximal value. Finally, when the distance to an unattacked host is lower or equal to a fixed reactive distance, the female moves straight to it and attacks it and the procedure used to generate random angular directions is reset (see Bruins et al., 1994 for a more detailed description). This model was also used to generate walking paths without hosts. In this case, the walking velocity was fixed to its maximal value, and the path was generated by drawing an angular direction at each step as described above. According to Yano (1978), such a procedure, in the presence of hosts, leads to the generation of rather tortuous paths (low linear speed and high angular speed). Without hosts, however, the generated paths are more or less following a straight line (high linear speed and low angular speed), which correspond to the walking behaviour of insects between patches of resources (Bell, 1990). Paths were generated using different linear velocities and for each path, the prospected surface per unit of time was estimated according to the method described in Fig. 1. Fig. 2 gives an example of the results obtained.

Without hosts, when paths were more or less linear, there was a clear linear relationship between the females' walking velocity and the area searched per unit of time. The slope of the relationship was proportional to the path width (i.e. reactive distance). However, when hosts were present and the paths were more tortuous, there was still a significant relationship ($p < 0.01$), but it remains an important residual variation in the area searched per unit of time that cannot be explained by a variation in the females' walking speed. In order to analyse this residual variability, other simulations were performed, in the presence of hosts, with a fixed linear walking velocity and under three different host spatial distributions. Fixing the linear walking speed will thus lead to variation in the area searched that cannot be explained by variation in the walking velocity. The corresponding results will thus reveal the importance of the area searched as a new parameter quantifying females' host searching behaviour. In this case, for all simulated paths, both the area searched and the number of hosts encountered per unit of time were estimated. The number of hosts encountered gives an estimation of the females' host-searching efficiency. Fig. 3 gives an example of the results obtained.

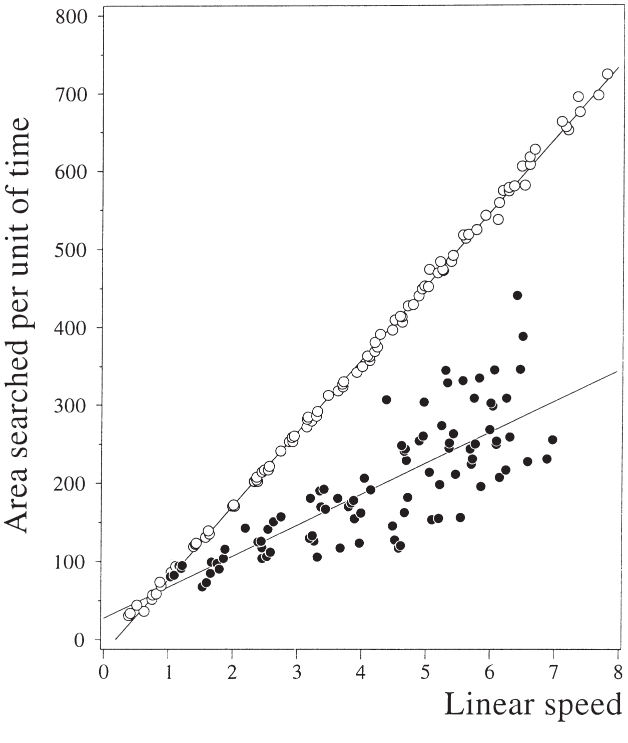

Fig. 2. Relationship between area searched per unit of time (computed as explained in Fig. 1) and linear speed of females' displacement, estimated from simulated walking paths in the presence (black circles) or absence (white circles) of hosts. Each point is a path simulated with the same set of parameters (except for linear speed) as those indicated on Fig. 1 in Bruins et al. (1994). Simulations in the presence of hosts were performed using 500 randomly distributed hosts. Similar results were obtained with different host densities and spatial distributions. Axes were graduated with arbitrary units.

Regardless of the host spatial distribution, there was a strongly significant, positive relationship between surface prospected by foraging females per unit of time and their ability to discover their hosts. Such a strong relationship clearly suggests that, without taking into account differences in linear walking speed, the behavioural trait studied here is likely to be involved in the parasitoid females' efficiency to find their hosts. Thus, this trait might be positively related with the wasps' ability to control phytophagous pests in biological control programs. Despite the fact that the statistical conclusion remains the same, relationships shown in Fig. 3 seem to be stronger for more regularly distributed hosts. On aggregated hosts, only mobile foraging females would remain unaffected by resource dispersion, while the others would have a lower ability to locate clumped hosts. This phenomenon was experimentally demonstrated on lepidopteran larvae that were looking for their host plants (Cain et al., 1985).

3.2. *Genetic variability of area searched in* T. brassicae *females*

A total of 161 females were measured at the daughter generation. The results show that on average these females prospected a surface of 28.47 (± 0.87) $mm^2\ s^{-1}$ (i.e. about 1 cm^2 every 4 s).

The genetic analysis of the phenotypic variability observed in this trait, based upon the statistical comparison between the 27 iso-female lines studied, is presented in Fig. 4.

There is strong, significant variation in this trait, between the different families compared ($F_{(26,\,134)} = 1.98$;

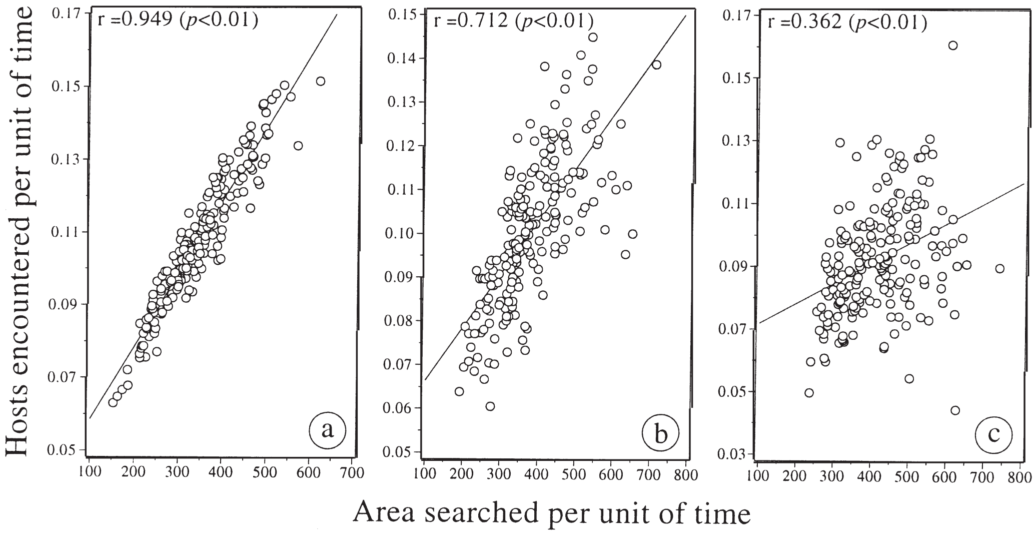

Fig. 3. Relationship between area searched per unit of time and the number of hosts found per unit of time, estimated from simulated walking paths with a fixed linear walking velocity. Each point is a simulated walking path. In all cases, simulations were performed using 300 hosts showing either a regular (a), random (b) or aggregated (c) spatial distribution. Similar results were obtained with different host densities, and were not dependent on the value of the linear speed used.

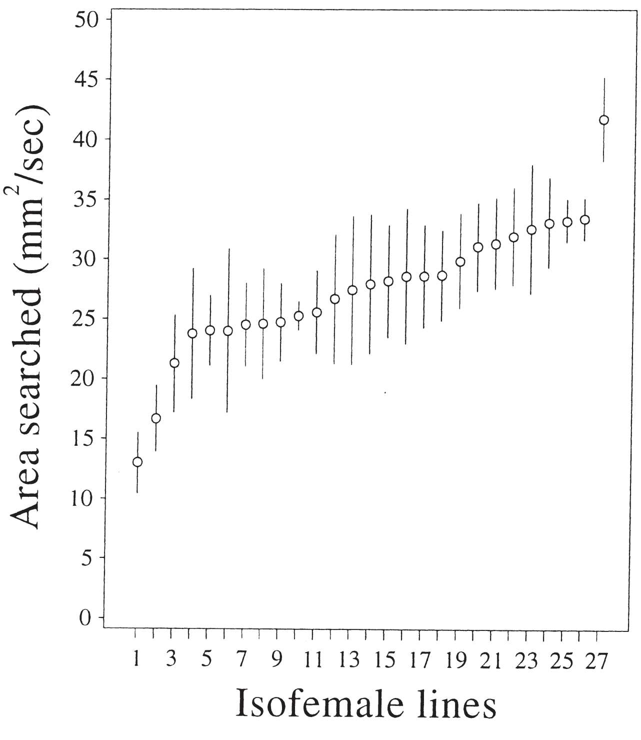

Fig. 4. Average (± s.e.) area searched per unit of time estimated on 27 iso-female lines of *T. brassicae* females. Lines are ordered according to increasing average values of the trait studied. The inter-lines variation is highly significant (ANOVA: $F_{(26,\ 134)} = 1.98$; $p < 0.01$).

$p < 0.01$). Thus, this result shows that the ability of *T. brassicae* females to prospect a given area is a family feature, which strongly suggests that this behavioural characteristic is under a genetic variability in the population studied. Within the same population, some females have a genotype that leads them to prospect less than 6 $mm^2\ s^{-1}$ (minimal observed value: 5.46), while others can prospect up to 11 times more (maximal value observed: 67.19 $mm^2\ s^{-1}$).

4. Discussion

The present study proposes an algorithmic method that can be used to estimate, from an automatic video tracking of females' walking activity, the surface they are able to prospect per unit of time. According to the simulation results presented here, this behavioural trait appears to be linearly correlated with the linear velocity of females when they are walking on a straight line. However, such a behaviour is usually not observed on real females, especially when they are foraging in the presence of hosts (Yano, 1978; Bell, 1991). Under the assumption of a fixed walking speed, results obtained from a simulation analysis showed that, regardless of the host spatial distribution, the area searched was strongly related to the ability of wasp females to find their hosts. Thus, without taking into account variation in the linear walking velocity of the foraging females, the area searched still appears to be an important parameter that might be related to the efficiency of the parasitoid as a biological control agent. Of course, the model developed here to simulate the walking activity of wasp females is only a simplified representation of their real foraging behaviour. More accurately, this model does not take into account the time needed to attack each host encountered (i.e. handling time) and its associated variations (Wajnberg, 1989). It thus considers that all hosts available are of the same quality, which is usually not the case. Moreover, the model simulates the behaviour of isolated females only, and thus neither direct nor indirect interference between females are taken into account (Visser and Driessen, 1991). However, the model has the advantage of being easy to formulate and to understand and the result obtained can provide, at least qualitatively, information regarding the importance of the behavioural parameters that are analysed.

The area searched per unit of time was estimated for isolated *T. brassicae* females using the algorithm provided. On average, females of this species were able to prospect about 28 $mm^2 s^{-1}$. A female landing on a leaf of 100 cm^2 would thus need, on average, approximately 6 min to cover the entire surface.

Since this trait appears to be related to the ability of wasp females to find their hosts, a genetic selection, in order to increase its average value in a population, might also increase their efficiency to control a target pest, in field release programs. For this reason, the genetic variability of this trait was quantified in the *T. brassicae* population analysed, using the iso-female line method (Parsons, 1980; Hoffmann and Parsons, 1988). Despite the fact that all experiments were performed under standardised conditions, an important phenotypic variation was observed. At least in part, this variability appears to be a family feature which suggests significant genetic control. Within the population studied, some females have a genotype which enables them to prospect a large surface per unit of time, whereas others are restricted in their host-searching behaviour to small areas.

In order to quantify the behavioural trait under conditions as standardised as possible, the walking females that were analysed were recorded without hosts. In this case, females were expected to walk more or less in a straight line (Bell, 1990). The average straightness of the walking path (i.e. the ratio of the distance between the first and the last points of the recorded path divided by the total path length (Bell, 1991; Pizzol and Wajnberg, 1995)) was only 0.333 (± 0.008), suggesting that females were walking in a rather tortuous manner. Despite this, and in accordance with the simulation results shown in Fig. 2, it remains possible that the genetic variability observed in the surface prospected by *Trichogramma* females per unit of time could be an indirect consequence of genetic variation in the females' walking speed. Therefore, this trait was estimated for each measured female and an average value of 3.117 (± 0.069) $mm\ s^{-1}$ was observed, which corresponds to the value observed by other authors on the same species or on related species (Chassain, 1988; Bigler et al., 1988; Limburg and Pak, 1991; Pompanon et al., 1994; Pizzol and Wajnberg, 1995). As a matter of fact, significant variation among the 27 families compared was observed in this trait ($F_{(26,\ 134)} = 2.19$; $p < 0.01$), suggesting that the variation in the walking velocity was also under a genetic control in the *T. brassicae* population studied. This type of intra-population genetic variation was also observed for *T. dendrolimi* Matsumura and *T. evanescens* Westwood (Limburg and Pak, 1991) and for *T. cacoeciae* Marchal (Pompanon et al., 1994). Inter-population genetic variation was also observed for *T. brassicae* (Chassain, 1988; Pizzol and Wajnberg, 1995).

The genetic variability observed in the surface prospected per unit of time, which appears to be related to variation in the females' walking speed (the correlation between the two traits, estimated on all the observed data, was 0.911 ($p < 0.01$)), could also be a consequence of variation in the females' body size. Indeed, it is possible that smaller females would exhibit slower motions, leading to both a lower walking speed and a lower surface prospected per unit of time. Schmidt (1994) has shown that the walking speed of *T. minutum* Riley, while examining *Manduca sexta* (L.) (Lep.; Sphingidae) eggs, was independent of wasp size. However, on non-host substrates, which is the case in the present study, walking velocity was shown to be proportional to body size through variation in stride length (Schmidt and Smith, 1989).

Regardless of the origin of the variation observed in the surface prospected per unit of time, the existence of the corresponding genetic variation is likely to be related to the fact that *Trichogramma* females are known to be polyphagous and will therefore experience different types of hosts with different spatial distribution patterns (Wajnberg and Hassan, 1994). Thus, a genetic variation could be maintained in the population, since females are likely to be under the pressure of opposite environmental constraints. Moreover, the genetic variability observed in this study may provide the basic information that is necessary to start genetic selection of mass-reared *Trichogramma*, in order to improve their efficiency in biological control programs. A breeding selection of this kind, which aims to increase the average value of the behavioural trait in the population, is currently in progress and should provide a way to verify, through comparative field release programs, the importance of this trait in efficient pest control.

It is important to note that the trait defined and estimated in the present study, provides a new quantitative parameter that can be used to describe the activity of a walking animal. Indeed, about 20 quantitative parameters are available for describing animal motions (Bell, 1991; Varley et al., 1994), some of them have been computed on each path co-ordinate (e.g. linear and angular speed, etc.), while others over the entire track (e.g. total walking distance, index of straightness, etc.). Among these different descriptive parameters, Kitching and Zalucki (1982) have suggested that only six were very important for the description of the movement path of an animal: (1) the average and (2) the variance of the linear speed, (3) the mean and (4) the variance of the angle turned at each step, (5) the initial angle of bearing, and (6) the proportion of time spent moving. At least on the experimental data recorded in this study, the trait defined here appeared to be positively related to the standard parameters usually used to described walking paths. With the angular speed, the correlation was 0.386 ($p < 0.01$); with the average straightness, it was 0.258 ($p < 0.01$); and with the proportion of time spent moving, it was 0.896 ($p < 0.01$). Only with the average number of stops per second, the correlation was non-significant ($r = 0.095$). Thus, the new descriptive parameter appears to give a global, synthetic quantification of a behaviour related to the main features of wasp females walking activity. Furthermore, according to the simulations presented, the new descriptive parameter gives an additional information: without taking into account variation in linear walking velocity, this new trait has been shown to be related to the ability of a foraging animal to discover new resources (in this case hosts, see Fig. 3). At present, new computer developments are being performed out in order to estimate, using the same type of algorithm, the volume prospected per unit of time (expressed in $cm^3 s^{-1}$) by a female that is flying in a 3-D environment (Riley et al., 1990; Dahmen and Zeil, 1984).

The searching activity of a foraging female has been shown to change according to both conditioning and/or experience (Bell, 1990) and to variation in abiotic (e.g. temperature, humidity, etc.) and/or biotic (e.g. resource density and availability, etc.) features of the environment (Bell, 1990, 1991). Thus, experiments are now being performed in order to estimate the changes in the behavioural trait that was studied here, in response to differences in these different sources of variation. Finally, different *Trichogramma* species will also be compared. The corresponding results will hopefully provide important information for the selection of correct species for biological control programs (Hassan, 1994).

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