

Oviposition height increases parasitism success by the robber fly *Mallophora ruficauda* (Diptera: Asilidae)

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Abstract For parasitoids, host finding is a central problem that has been solved through a variety of behavioural mechanisms. Among species in which females do not make direct contact with hosts, as is the case for many dipteran parasitoids, eggs must be laid in an appropriate part of the host habitat. The asilid fly *Mallophora ruficauda* lays eggs in clusters on tall vegetation. Upon eclosion, pollen-sized larvae fall and parasitize soil-dwelling scarab beetle larvae. We hypothesized that wind dissemination of *M. ruficauda* larvae is important in the host-finding process and that females lay eggs at heights that maximize parasitism of its concealed host. Through numerical and analytical models resembling those used to describe seed and pollen wind dispersal, we estimated an optimal oviposition height in the 1.25- to 1.50-m range above the ground. Our models take

into account host distribution, plant availability and the range over which parasitic larvae search for hosts. Supporting our findings, we found that the results of the models match heights at which egg clusters of *M. ruficauda* are found in the field. Generally, work on facilitation of host finding using plants focuses on plants as indicators of host presence. We present a case where plants are used in a different way, as a means of offspring dispersal. For parasitoids that carry out host searching at immature stages rather than as adults, plants are part of a dissemination mechanism of larvae that, as with minute seeds, uses wind and a set of simple rules of physics to increase offspring success.

Keywords Asilidae · Parasitoid · Parasitism · Superparasitism · Wind dispersal · Oviposition · Fitness · Host location

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Introduction

For parasitoids—insects that develop at the expense of other insects and live freely as adults—reproductive success depends directly on the behaviour that leads to the encounter of suitable hosts. For the large majority of species, host searching is carried out by adult females that lay eggs in or on their host. Host location by this type of parasitoid has been extensively studied, largely focusing on Hymenoptera (Godfray 1994; Vet et al. 1995, 2002; Vinson 1976, 1984, 1998). However, in many dipteran parasitoids, adults lay eggs in the host environment, and it is immature

stages that are responsible for host searching and parasitism (Fournet et al. 2001; Godfray 1994). Host-finding and exploitation strategies used by these parasitoids are necessarily different (Adamo et al. 1995; Eggleton and Belshaw 1993; Feener and Brown 1997; Feener et al. 1996; Hagen 1964; Harris and Todd 1980; Vinson 1984). Analogous to seed and pollen dispersal in plants, a central problem for these parasitoids is disseminating larvae to increase encounters of hosts, which are usually concealed. In essence, successful attacks will occur when the eggs are laid at a distance from hosts such that offspring dispersal will ensure host finding by young larvae. This strategy implies that parasitoid larvae have to travel some distance from the oviposition site to the host body, in contrast with those parasitoids that do not depend on immature stages moving towards their hosts (Godfray 1994).

The family Asilidae is a group of Diptera commonly known as “robber flies” that relies for its development on the successful attack of larvae of Scarab beetles. Host larvae live buried in the soil and are thus invisible to female robber flies (Clements and Bennett 1969; Musso 1983). Asilid flies adults are predatory of other insects, and at least some species, such as the *Mallophora*, may be regarded as koinobiont ectoparasitoids during their larval stages (Castelo 2003; Castelo and Lazzari 2004; Clements and Bennett 1969; Copello 1922; Musso 1978, 1983).

Asilid females lay eggs away from their hosts, and host foraging is achieved by the larvae provided they fall within a short distance of its host (e.g. Castelo and Lazzari 2004). Several species inhabiting grasslands deposit their eggs near the top of the plants or in high positions showing marked oviposition site selection (Adamovic 1974; Alcock 1974; Dennis and Lavigne 1975; Lawson and Lavigne 1984; Linsley 1960; Reinhard 1938; Stubbs 1970). Because adults are insect predators, attempts have been made to correlate oviposition sites with prey hunting areas (Londt 1994). Other works have considered the association between robber fly oviposition site selection and plants upon which beetle larvae feed (Hardy 1929; Kershaw 1912).

In more recent work, some of us have shown that the robber fly *Mallophora ruficauda* (Diptera: Asilidae), a species common to the South American *Pampas*, tends to choose high locations for oviposition and that this height selectivity does not relate directly to plant species (Castelo and Corley 2004). Selectivity towards higher substrates in *M. ruficauda* occurs both on plants and on artificial supporting structures such as wire fences, where no plant cues are involved, including those that could be derived from damage caused by host larva in the soil. The remarkable selectivity for oviposition height displayed by *M. ruficauda* suggests that females actively chose oviposition sites and that such behaviour may relate to increased

offspring success (Castelo and Corley 2004). We conjecture that height selection relates to the fact that larvae are small and can be dispersed by the wind, a feature that may also contribute towards explaining the resulting spatial patterns of parasitism. Castelo and Capurro (2000) have shown that parasitism by *M. ruficauda* is density-dependent at large spatial scales and inversely density-dependent at smaller scales, as a consequence of a shared host-searching strategy involving adults and larvae, larval dispersal and host spatial distribution.

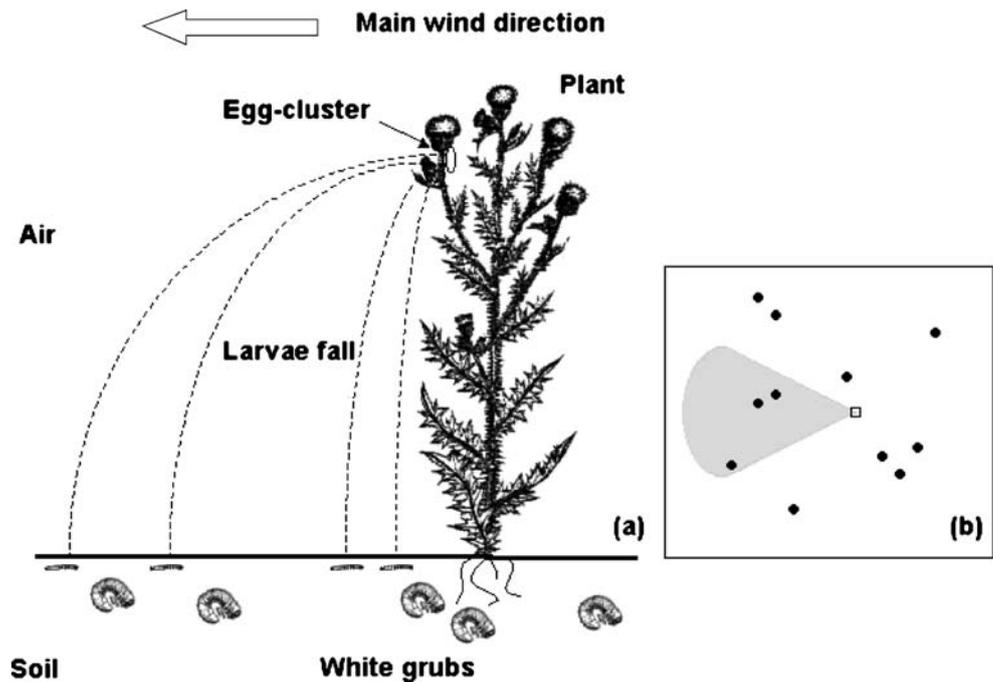
Little is known about the specific developmental requirements of the larvae of the Asilidae species. The vast majority bears predacious larvae that live subterraneously in sand or soil and feed on beetle larvae. Their oviposition strategies are varied, and in all cases, larvae reach the ground or wood, where they undergo further development (Londt 1994; Musso 1981; Musso and Garcin 1975).

In this work we aim to analyse the influence of oviposition height selectivity on parasitism using a modelling approach. We hypothesize that oviposition height selection, by favouring larval dispersal by the wind, affects parasitoid fitness. We ask whether for these parasitoids, wind dissemination of larvae is an adaptive means of parasitism and attempt to predict the distribution of plant heights selected in the field.

Biology of the robber fly-beetle larva study system

Mallophora ruficauda Wiedemann is a pestiferous robber fly common in the open grasslands of South America. Foraging adults are active during the austral summer (December to March) whenever there is good weather. During their life span, mated females deposit eggs in clusters—328 eggs per cluster on average—on elevated sites, typically tall grasses and in areas close to bee hives where their main adult prey is found (Castelo and Corley 2004; Copello 1922). *M. ruficauda* oviposits preferentially within a height range between 1.00 and 1.25 m on wire fences, and between 1.25 and 1.50 m on the available natural herbaceous vegetation, typically on *Carduus acanthoides* L. (Asteraceae) (Castelo 2003; Castelo and Corley 2004). Emerging larvae are minute (1.35 mm length, 0.32 mm wide; Castelo 2003) and drop to the soil. Once on the soil, they rapidly bury themselves and search for their hosts—third instar larvae of scarab beetles—mainly *Cyclocephala signaticollis* Burmeister (Coleoptera: Scarabaeidae) (Castelo 2003) (Fig. 1). Recent work has shown that once in the soil, the larvae move towards neighbouring hosts guided by chemical cues arising from the bodies of the white grubs (Castelo and Lazzari 2004). Host larvae are

Fig. 1 Schematic description of larval dispersal in *M. ruficauda*. **a** Larvae dispersal occurs from an egg cluster on a plant, in the main wind direction. Larvae land on the ground and colonize white grubs (their hosts). **b** The same process is shown on the soil surface. *Black circles*, white grubs; *white square*, egg cluster; *grey area*, the shadow (area that encompasses all larvae after landing on the ground)



phytophagous and live in the soil during winter (March to August) feeding on roots. Larvae of *M. ruficauda* are solitary parasitoids that feed on and finally kill their hosts when they are ready to pupate. However, probably because search by larvae occurs within a limited spatial scale, superparasitism is common (Castelo 2003; Castelo and Lazzari 2004). The life cycle of successful individuals is completed approximately 2 months later, when the adult robber flies emerge from the soil (Copello 1922; Musso 1983).

The model

This section is divided into two parts. First we derive the fitness gained by larvae that disperse with the wind from plants of given heights. Secondly, the optimal oviposition strategy for an adult female is obtained in the framework of foraging theory (Stephens and Krebs 1986). This strategy boils down to the selection of an appropriate plant height for oviposition. Given this strategy, the distribution of plants chosen by parasitoids is then deduced, based on the distribution of plants available in the field.

Fitness of the female

Here we assess the fitness gained by a female parasitoid depositing an egg cluster on a plant of given height. After the female deposits a cluster on tall grass, emerging larvae will drop to the ground. A larva may move within a limited area to locate a host that is concealed in the soil. Successful

host encounter thus depends not only on host larvae distribution but also on parasitoid larvae distribution. Where a parasitoid larva lands depends on the location and height from which it drops. The contribution to the fitness gained by the female through an oviposition event is given by the number of hosts parasitized by larvae emerging from the egg clusters.

In the absence of data to fit the parasitoid larvae distribution on the ground, we use a model that has already been tested for plant and tree seeds (Andersen 1991). As for seeds, the main agent of dispersal of parasitic larvae is the wind. Models of wind-mediated dispersal have been mainly formulated in the context of plant ecology and can also be applied to the passive dispersal of any organism dispersed by air currents, including minute insects and acari (Bullock and Clarke 2000; Greene and Johnson 1989, 1996; Nathan and Katul 2005; Nathan et al. 2001a,b, 2002; Nurminiemi et al. 1998; Nuttle 2005; Okubo and Levin 1989). This analogy is discussed in more detail in Appendix A.

On the ground, the distribution of the parasitoid larvae originating from a single cluster is called a “shadow”, i.e. a sector that originates at the base of the plant of release with a bisecting line that points in the main direction of the wind (Clark et al. 1999; Nathan et al. 2001a; Wagner et al. 2004). The shadow borders are determined by two parameters: angle and radius (i.e. bisecting line length). Typically, a falling particle reaches a constant terminal falling velocity—constant rate of a particle falling in still air (see Appendix A)—after the liberation from a point at some elevation (Guries and Nordheim 1984; Nathan et al. 1996). The horizontal distance travelled by a particle transported

by the wind is a function of the terminal velocity, release height and wind velocity during the particle flight (Andersen 1991; Grenne and Johnson 1989, 1997; Johnson et al. 1981; Katul et al. 2005; Nathan and Katul 2005; Okubo and Levin 1989; Pennanen et al. 2004; Schippers and Jongejans 2005; Sharpe and Fields 1982). We use a basic mechanistic model that allows calculating the radius as a linear function of the height of release (h), the maximum horizontal wind speed during larval flight (U) and the terminal velocity (T) (see Eq. 2, and Greene and Johnson 1989, 1996; Nathan et al. 2001a). Furthermore, as a first approximation, the parasitoid larvae are assumed to be uniformly distributed within the shadow. Note that, in agreement with various models of seed dispersal (Andersen 1991; Okubo and Levin 1989) that are compared with field data, the mean (often equal to the mode) of the parasitoid larvae (or seeds) spatial distribution model depends linearly on the height of release.

We assume random host distribution at the scale of the shadow in our initial model. With low mobility, host larvae are assumed to be confined to a small area that is set equal to the unit area in this model. A parasitic larva that lands directly above this area finds the single host lying below (if there is one) with probability of one. Additional parameters are the host density (the probability that there is a host in a given unit area) p and, finally, the number of larvae emerging from a single egg cluster, Q . The number of host parasitized by the Q larvae is the number of hosts present in the piece of ground delimited by the shadow, weighted by the probability that each host is found by at least one larva (see Eq. 5). Similarly, the number of host superparasitized is given by the probability that each host is parasitized by at least two larvae (see Eq. 6).

From Eq. 2 and parameter values given in Table 1 for *M. ruficauda*, we can assume that the linear extent (i.e. the bisecting line) of the shadow is about 30 m. Castelo (2003)

showed that at this scale the host distribution was aggregated. Therefore we also explore the consequences of non-random host distribution at the scale of the shadow. Aggregation may be the result of a variety of biological situations, most likely a heterogeneous host distribution, but there may also be some heterogeneity in the searching behaviour of parasitoid larvae that could manifest itself as a non-random distribution of attacked host. As a simple means of incorporating the effects of aggregation, the negative binomial distribution substitutes the Poisson distribution that was used to model random host distribution (see Appendix A). The negative binomial is characterised by two parameters: the mean of the distribution and the shape parameter k , which characterizes the degree of clumping of host distribution (see Eq. 7).

We then further explore the dependence of fitness (number of host parasitized by the Q larvae emerging after a single oviposition event) on plant height by performing numerical simulations (see Appendix B). This allows us to study an additional host distribution for which no exact analytical methods are available. The simulation model relies on the same assumptions as the analytical model except that hosts are patchily distributed and can be randomly distributed within each patch. The only difference with the negative binomial distribution used in the analytical model is that hosts are now in patches that are separated by empty spaces and are of given shape. We study different situations by varying patch size and number while keeping the average number of hosts constant. Results from both analytical and numerical models are compared.

Oviposition strategy of the parasitic female

We consider a time-limited parasitoid that risks dying with unladen eggs. An oviposition strategy of searching exclu-

Table 1 Main variables and parameters used in the simulation model of the larval dispersal in *M. ruficauda*

Symbol	Parameter (units)	Comments	Value (range ^d)
H	Egg cluster height in the substrate (m)	Plant height. Empirically determined ^c	0–4
T	Terminal velocity of the larva (m/s)	Constant velocity reached by the smaller biological particles during their falling against gravity ^a	0.3 [0.1, 0.5]
U	Wind velocity (m/s)	Mean wind velocity measured in the field in the study area at 2 m above the soil ^b	3.0 (\approx 15 km/h) [0, 3]
θ	Wind angle span ($^\circ$)	Angle that determines the dispersal surface of the larvae in the soil	45 [0, 180]
Q	Number of eggs per egg cluster	Empirically determined ^c	328 [56, 729]
τ	Handling time over travelling time	Empirical observations	1200 [5, 5000]
P	Host density	Arbitrary	0.5

^a The terminal velocity value was taken from the *Panicum meliaceum* L. seed that is approximately 0.3 m/s. This species seed has a weight and shape similar to *M. ruficauda* larvae (Xie and Zhang 2001).

^b From Czajkowski and Rosenfeld (1992)

^c From Castelo and Corley (2004)

^d Range of values used in the simulation and in the model

sively for the highest plants would put the female at risk of running out of time to lay the potential number of egg clusters since few plants of the chosen height may be available. Such strategy would maximize fitness by egg cluster, by exploring a larger area and avoiding superparasitism, as a result of higher larvae dissemination (i.e. a higher probability of a given larva to fall within a host patch, see Appendix A). Our model rather uses rate maximization (fitness gain over time) in the framework of foraging theory and was adapted from the classical “prey model” (Stephens and Krebs 1986). A female is assumed to move through space in search for prey items that are plants for oviposition in our case. Prey quality corresponds to the height of the plant. This approach would maximize the fitness gain of the animal over his life span.

The female parasitoid encounters plants of several different types. Plants are divided into n types ordered by increasing height and indexed by i : $i=1$ for plants of height 0 to h , $i=2$ for plant heights in $[h; 2h]$, ..., $i=n$ for plant heights in $[H-h; H]$, where H is the maximum height encountered in the field and h is an appropriately chosen range of height.

By ranking plants in an increasing order of height, we have ranked plants by parasitic fitness in the sense that fitness increases with height, i.e. the higher the plant, the larger the number of host parasitized (see Fig. 2). Note that by ranking plants in this way we reverse the notation usually used in the prey model (Stephens and Krebs 1986).

Other parameters are r_i , the proportion of plants of type i , and τ , the handling time (the time to land on the plant and to lay eggs) over travelling time (the time spent searching for a new plant).

The parasitoid female is assumed to be omniscient, to separate searching and handling activities as it encounters

plants sequentially, and to be able to identify plant type. Females fly above the mean canopy height, encountering plants as they come across them in the grassland, and decide whether to accept a given plant for oviposition or leave it and move on to another. Handling occurs when it has chosen a plant and proceeds to lay an egg cluster, assumed to be attached to the top range of the plant.

The detailed application of the prey model to our system is explained in Appendix C. The optimal strategy is obtained as follows: the smallest number j for which

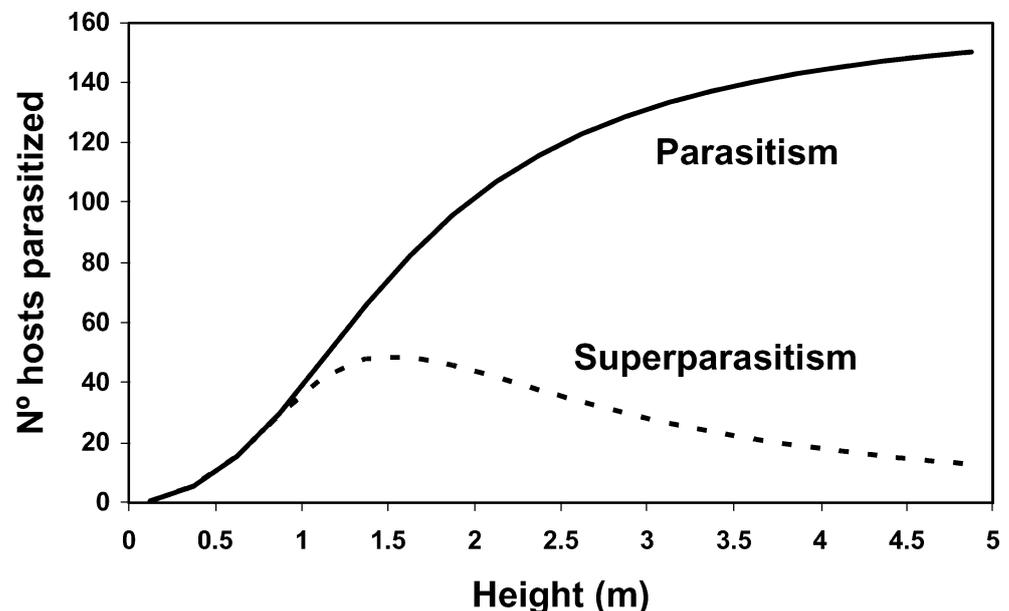
$$f_j > \frac{\tau \sum_{i=j+1}^n r_i f_i}{1 + \tau \sum_{i=j+1}^n r_i} \quad (1)$$

is true is computed, leading to a threshold $i^*=j$ below which plants are rejected (which translates into a threshold plant height below which plants are rejected). The analysis of this condition leads to the conclusion that each plant type is either always or never selected (no partial preferences) and whether a plant type is chosen depends on its fitness gain but not its density, and on both the fitness gain and density of higher plants (i.e. lower i).

Female parasitoid often alters their egg-laying strategy depending on internal state, mainly their position in the egg-limitation time-limitation continuum (Fletcher et al. 1994; Mangel 1989; Roitberg et al. 1992, 1993; Sirot et al. 1997). Here we have only considered time-limited females. Future work would consider the conditions for egg limitation in *M. ruficauda*, both from the theoretical and experimental points of view.

The model is applied to the *M. ruficauda* system where the rate of encounter of plants of each type is obtained from the height distribution of plants observed in the field. This

Fig. 2 Theoretical number of parasitized (fitness) and superparasitized hosts according to oviposition height. The figure shows that the higher the oviposition height, a higher parasitism and a lower superparasitism are achieved



distribution is bell-shaped with few, very low or very high plants (Castelo and Corley 2004). The mode of this distribution (i.e. plants that are encountered most often in the field) lies at a value that is denoted i_r . This distribution has to be truncated at i^* , which corresponds to a threshold below which no plants are selected. This gives the distribution of plants that should be chosen by the parasitoid.

Although the parasitoid oviposition strategy remains unchanged (it is given by the threshold i^*), one of two situations might arise depending on whether i^* is lower or higher than i_r (the mode of the plant distribution). In the first case, the plants chosen by the parasitic female follow a distribution whose maximum frequency coincides with i_r . In the second case ($i^* > i_r$), the selected plants follow a distribution whose maximum frequency is higher than i_r . In other words, the first case is close to the situation where plants are chosen at random because only lower and rarer values are eliminated from the truncated distribution. In the latter case, selectivity of taller plants should be observable. For convenience, the first case will be referred to as random search and the second as height selectivity.

This analysis relies on the value of i^* , which in turn depends on handling time (i.e. on τ) and on fitness gained by egg clutch (function f). Note that the right-hand side term of (Eq. 1) is an increasing decelerating function of τ , so for shorter τ , i^* decreases as τ increases. However, when τ (the handling time in terms of units of travelling time) is very short, there is no optimal plant height since the condition (Eq. 1) is never fulfilled. Note that for long handling times the threshold i^* is hardly sensitive to τ , and the shorter the handling time is or the longer the travelling time is, the lower the chosen plant height should be.

Using the software Maple, the value of i^* was determined for various random combinations of the parameters values.

Empirical data used in the model

The model requires that plants be grouped in ranges and that eggs be laid at the top section of each plant. Castelo and Corley (2004) report that among 784 plants the minimum plant height lies at 0.44 m (below this value, there are no appropriate plants used by the robber flies for oviposition; Londt 1994). The highest plant censused was 2.80 m. The total height of plants was measured and grouped in 0.25-m ranges (Castelo and Corley 2004), and plants were ranked by height. Therefore in order to apply the model to this system, the plant types are set as follows: $i=1$ for plants in [0; 0.25], $i=2$ for [0.25; 0.50], $i=12$ for [2.75 m; 3.00 m], etc. In a sample of 784 plants, between 0.99 and 1.65 m height on average [five species: *Carduus acanthoides* L. (Asteraceae), *Cichorium intybus* L. (Compositae), *Ammi majus* L. (Umbelliferae), *Tagetes minuta* L.

(Compositae), *Solidago chilensis* Meyen (Asteraceae) and “unspecified dried plants”], 64 carried one or more egg clusters (three species: *C. acanthoides*, *C. intybus* and *T. minuta*); 84.4% of the 64 plants carried one to four clusters, but a small number of them had many (e.g. one plant carried 28 egg clusters). A total of 250 egg clusters were censused (Castelo and Corley 2004).

Among these, 86% were attached to the top 0.25-m range of the plant, in good agreement with our assumption. This percentage comes to 95.3% in the subset of the 64 highest clusters (cases where there are several clusters attached to a single plant).

Egg masses are very light (≈ 10 to 15 mg, Castelo M., unpublished data) as a consequence, the main constraint for a plant being used as a support of an egg mass is that it could support the weight of the female (293 ± 6.25 mg, Castelo M., unpublished data) while egg laying. Visual inspection suggests that all available plants are equally suitable as support for an egg mass.

Castelo and Corley (2004) plotted the distribution of “available” plant heights in 0.25-m ranges. They considered that a plant of, for instance, 0.40 m is to be counted both in [0; 0.25] and [0.25; 0.50] ranges (i.e. a female could lay a cluster in the lower or upper section of the plant). Comparing this distribution to the “used” distribution of heights of the 250 egg clusters, the authors found a high selectivity towards higher sites on plants.

Here we take a different perspective than that of Castelo and Corley (2004) by assuming that the parasitic female strategy is to choose plants according to their total height and then to attach the egg cluster at the top segment of the plant. We discuss below the occurrence of deviations from this strategy, that is, clusters that are not attached to the top range of the plant. The point here is that there are no reasons to put the egg cluster at middle height of the plant when it could be placed higher and benefit from a higher parasitism rate and lower superparasitism rates.

The value of the mean wind velocity for the Pampas region, where *M. ruficauda* lives, is between 10 and 22 km/h (Czajkowski and Rosenfeld 1992).

Results

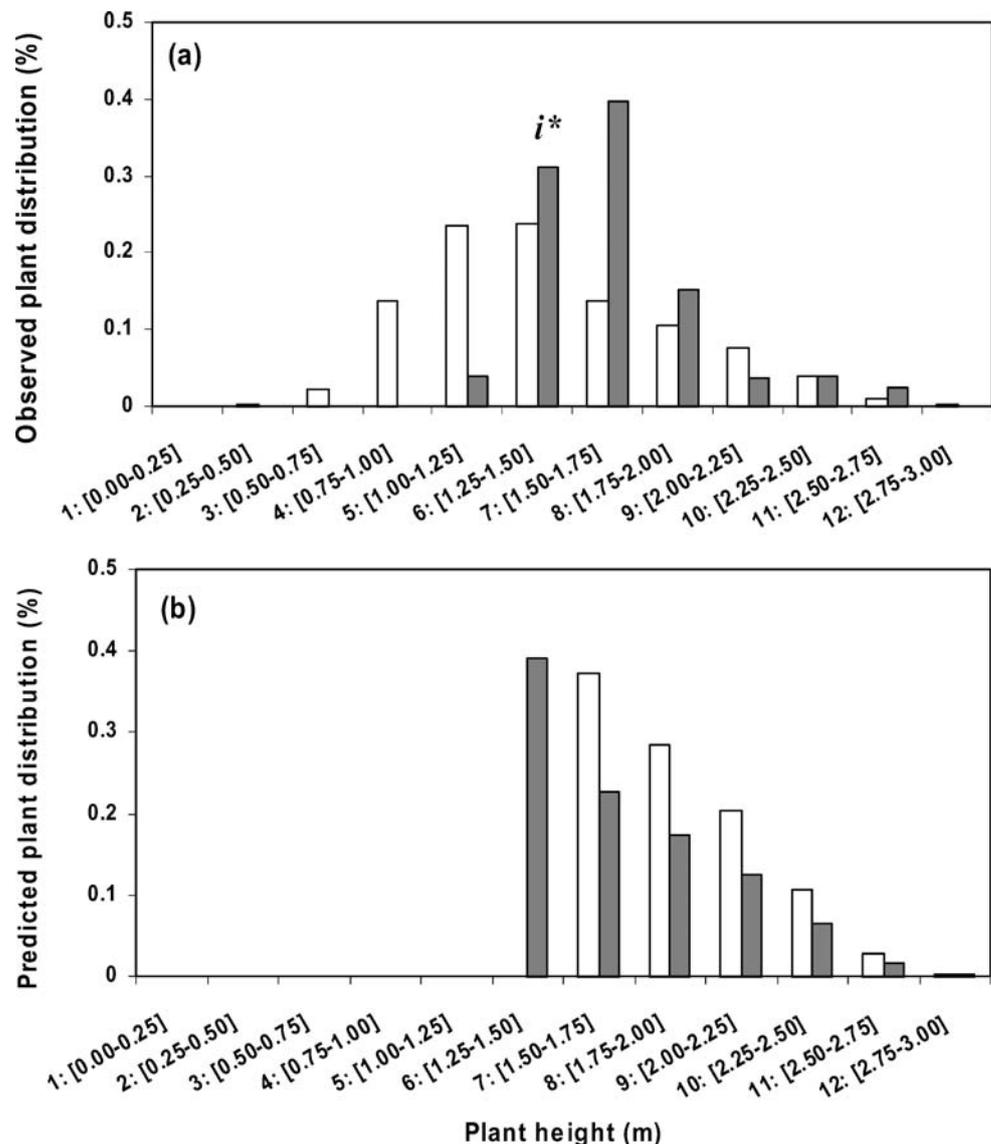
The model is applied to *M. ruficauda* oviposition behaviour in two steps. We first look at the shape of the relationship between fitness and plant height. In particular, we compare several host distributions with different degrees and types of aggregation. Secondly, we examine the conditions for plant selectivity in *M. ruficauda* and compare our predictions with field data reported in Castelo and Corley (2004). We then proceed to study the sensitivity of the optimal solution to the values of each parameter.

Fitness of the parasitic female as a function of height

Firstly, we consider that hosts are randomly distributed and plot $f(h)$, the number of host parasitized, as a function of plant height. Figure 2 shows that according to the model, the higher the egg clutch is placed (increasing h), the more hosts are parasitized, with the benefit of increased height flattening out for tall plants. Superparasitism initially increases with oviposition height, but it decreases when the point of release is high enough because the probability that two larvae will land at the same point decreases.

Figure 2 is plotted with parameter values given in Table 1. This plot depends on the value given to a combination of parameters (see Eqs. 3 and 4). The larger the value of this combination, the smaller the number of host parasitized for a given height h . More precisely, a large value of this combination is obtained for large egg clusters, low wind speed or low wind angle span, and favours higher plants.

Fig. 3 Plant height distributions for oviposition by *M. ruficauda*. **a** Available and selected plant height distributions in the field (from Castelo and Corley 2004). Heights are given as intervals of 0.25 m. *Full bars* represent selected plants and *open bars* the available ones. **b** Predicted selected plant distribution for two values of i^* corresponding to short or long handling time (τ , seconds). *Full bars* are for $i^*=6$ and *open bars* are for $i^*=7$. Comparison of Figs. 3b (selected plants) and 4 ($i^*=6$) shows that the model prediction is qualitatively close to the observed data. Heights are given as intervals of 0.25 m

Plant height selectivity and parasitism in *M. ruficauda*

We now explore the consequences of plant height selectivity by *M. ruficauda*. The model assumes that height selectivity ensures a successful host location for larvae issued from an egg cluster and dispersed by wind. This model can now be used to predict the distribution of plant height selected by females and the results compared with the observed selected plant height distribution (Castelo and Corley 2004).

The distribution of heights of plants that carry one or more egg clusters, hereafter called the *selected plant distribution*, may be derived from both the model and field data and the results compared. The model gives the theoretical distribution, based on the calculation of fitness and on the rate of encounter of plants or *available plant distribution* (see Fig. 3a). The time unit was set as the approximate time it takes to travel from one plant to the

neighbouring plant (on the order of a few seconds). Figure 3a shows that the mode of the plant height distribution (i_r) lies in [1.00; 1.50] range (i.e. $i_r=5$ or 6). From Eq. 5 with the parameter values of Table 1 (see Fig. 2) and the data plotted in Fig. 3a, inequality (Eq. 1) allows the optimal strategy and then the selected plant distribution to be calculated. The observed selected plant distribution is also plotted in Fig. 3a. This graph is built upon the heights of 250 clusters attached to the 64 plants carrying one or more clusters (i.e. the same plant may appear several times in the distribution since the same plant may be selected by several females). The plants that were chosen for oviposition in the field were those markedly higher than their neighbours in the grassland, thereby exposing the developing larvae to the wind (Castelo 2003).

The selected plant distribution can be derived for various conditions. Since there are only three parameters in this model (including a combination of several parameters), a relatively extensive exploration of parameter ranges could be performed.

The effect of time limitation

Mallophora ruficauda females are likely to be time limited, and travelling time and handling time are both costly. In the field, rainy and cold days occur unexpectedly during any summer, killing active adults, which could increase time limitation. It takes females approximately 20 min to lay an egg cluster which varies in size from 56 to 729 eggs (Castelo and Corley 2004), and travelling time is in the order of few seconds (Castelo M., personal observation).

We randomly picked parameter values from ranges given in Table 1. Since in most cases i^* is equal or larger than i_r , inequality (Eq. 1) implies that the selective strategy should be observed. In other words, the most common strategy was not the “random search” strategy but the selection of oviposition sites according to height. The predicted distribution of selected plants is plotted in Fig. 3b for $i^*=6$ and for $i^*=7$ (see below).

Default values given in Table 1 yield $i^*=6$ (for all τ larger than 45). Comparing Fig. 3a (selected plants) with Fig. 3b ($i^*=6$) shows that the model prediction is statistically close to the observed data (Kolmogorov–Smirnov, goodness-of-fit test, $D_{\max}=0.169$, $N=12$, $p>0.20$). Indeed, the model predicts a distribution that shares several features with field data; notably, it peaks at height interval [1.25; 1.50] and is asymmetrical around the peak, in favour of higher plants. The plot based on the data rises less sharply from the left to the peak of the distribution than the plot based on the model. The precise threshold at which the distribution rises depends on parameter values; including some variability in these values (clutch size or wind speed for instance, and the state

of the animal) would create variability in the critical i^* value, reducing the differences between model and data.

The effect of larval wind dispersal

With wind as the dispersing agent, both wind speed and directionality may play a role (Andersen 1991, Wagner et al. 2004), as well as the velocity reached by a small and light particle such as the larvae while falling to the ground (Greene and Johnson 1989; Okubo and Levin 1989). In the model, these parameters are combined into one: $\theta (U/T)^2$ (see Eq. 4). Using values selected at random in ranges given in Table 1, small wind angle, low wind speed and large terminal velocity all favour plant height selectivity. Random search, on the other hand, is predicted only for extreme values of the parameter ranges, combined with a low handling time. For instance, when U/T varies from 1 to 25 and other parameters are fixed as in Table 1, the height threshold given by i^* decreases from 7 to 5. Random search, on the other hand, is predicted only for extreme values of the parameter ranges. When $U/T=30$, which is the maximum value investigated for this ratio (see Table 1), $i^*=4$, a value equal or lower than i_r , suggesting a strategy closer to random search.

The effect of parasitoid egg load

In most parasitoid species, females produce many eggs independent of parasitism opportunities (Heimpel et al. 1998). Notwithstanding this, the egg cluster size is a model parameter that plays a role in plant height selectivity in our model. The larger the cluster size Q , the higher the point of release should be, in order to maximize host parasitism (see Eqs. 3 and 5). This is confirmed by an analysis of plant height selectivity, i.e. using successive values for Q in the range given in Table 1, where larger egg cluster sizes shift selectivity towards higher plants (see e.g. Table 2). This result is in agreement with a recent experiment that investigated the relation between cluster size and cluster height (Castelo and Corley 2004).

The effect of host distribution

Hosts may be rare or abundant, and they may homogeneously or heterogeneously spread. Host density p affects parasitism success (Eq. 4), but according to our model does not influence plant height selectivity. This can be seen in inequality (Eq. 1) that gives the optimal strategy since p can be eliminated from both sides of this inequality. The best strategy in terms of plant height does not depend on host density.

Finally, host spatial distribution may also influence plant height strategy. In the previous section, we assumed that

host distribution was random. However, past work has shown that white grubs, *M. ruficauda* hosts, are aggregated in the field (Castelo 2003; Castelo and Capurro 2000). To explore the consequences of host aggregation on parasitism, we then consider two models: first, by introducing a negative binomial distribution for the encounter rate between hosts and parasitoids (Fig. 4a) and second, by simulating host patches of various sizes (Fig. 4b and Appendix B). Castelo (2003) has shown that in field conditions, the degree of aggregation as measured by k was most likely to lie within [0.086; 2.213] interval (recall that when k tends to infinity the Poisson distribution is restored). We thus use the two extreme values in this interval in Fig. 4a. Both models show that for a given height of release, the more aggregated the host distribution is, the more variable and smaller the number of hosts parasitized (fitness) will be (Fig. 4a,b). Next, fitness has to be injected in the condition for plant height selectivity [see (Eq. 1)] in order to evaluate i^* and to compare it to i_r . Calculating i^* for various parameter values shows a low impact of host aggregation level: stronger aggregation level leading to a somewhat higher selected plants (i.e. higher i^*). For instance, when decreasing aggregation from $k=0.08$

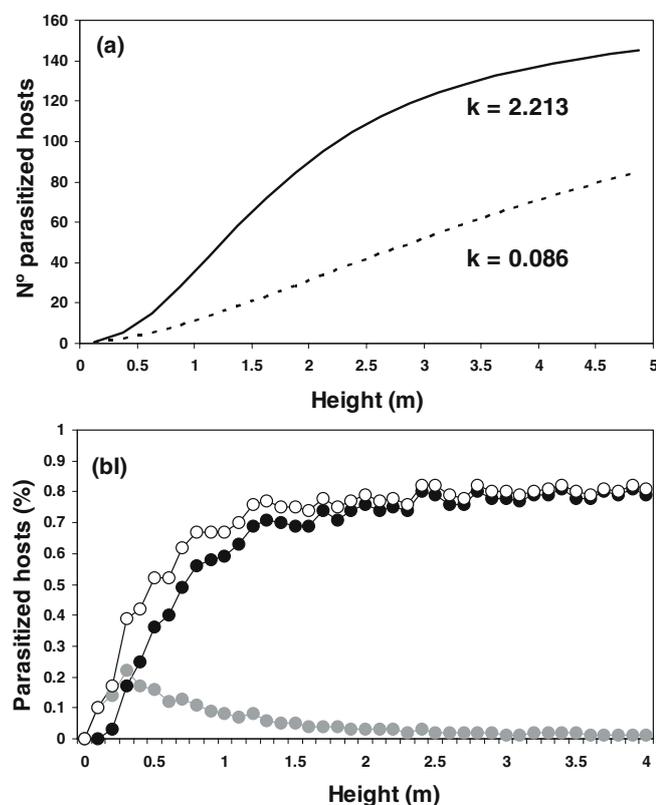


Fig. 4 Theoretical number of hosts parasitized (fitness) by oviposition height where the hosts are aggregated: (a) by introducing a negative binomial distribution for the rate of encounter between hosts and parasitoids, and (b) by performing three simulations, each one with patches of hosts of a given size, but maintaining equal host density (number of white grubs per unit area) within the grid among

Table 2 Height threshold when clutch size is varied and other parameter values are fixed as in Table 1

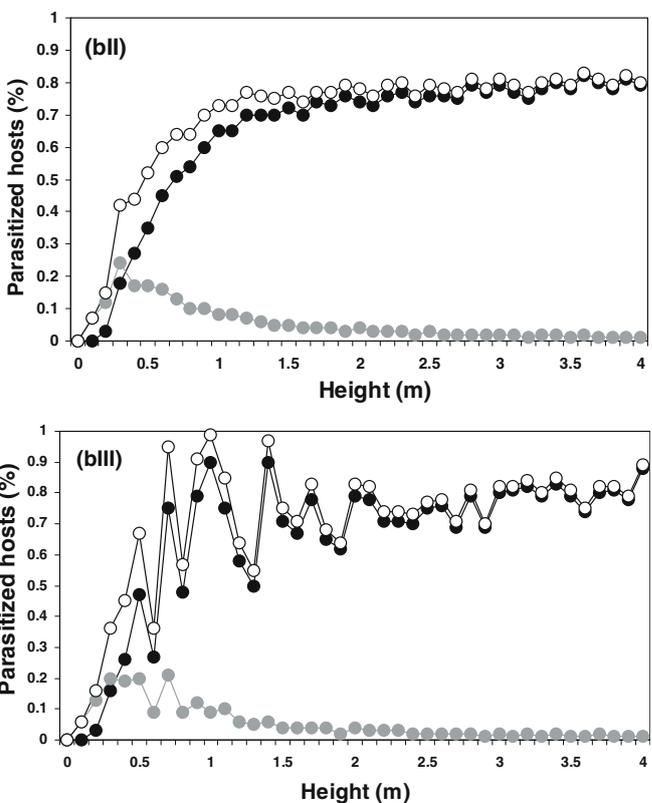
Q	1	56	328	729
I^*	2	5	6	7
Height	[0.25, 0.50]	[1.00, 1.25]	[1.25, 1.50]	[1.50, 1.75]

to $k=100$ (other parameters as in Table 1), i^* decreases from 7 to 6.

Discussion

In this paper we have explored whether wind dissemination of larvae could be an adaptive mechanism of parasitization for species in which adults do not attack hosts directly. Wind dissemination of minute, pollen-like larvae is achieved by appropriately selecting tall plants on which to oviposit.

Our results show that oviposition height may favour parasitism by species that, bearing very small larvae, must attack hidden hosts. When larvae are small enough to be wind dispersed, increasing oviposition height leads to an



runs (1,600 hosts on average). *Black circles* represent simple parasitism, *grey circles* superparasitism and *open circles* total parasitism. *I* small patches (128 patches of 5×5 cells), *II* medium patches (32 patches of 10×10 cells), *III* big patches (2 patches of 40×40 cells). The k values are taken from field conditions (Castelo 2003)

increase in parasitism rates and a decrease in superparasitism. The significant increase in fitness is limited, however, to a maximum height and by the degree of host aggregation. The use of a version of the classical “diet model” (Stephens and Krebs 1986) leads to a predicted distribution of selected plants that closely resembles the actual distribution recorded under field conditions (Castelo and Corley 2004).

The available information suggests that all robber fly species that attack concealed hosts select tall plants as oviposition sites. For instance, *Erax aestuans* Snow deposits egg clusters on the top of the dried heads of the fruiting spikes of some plant species (Reinhard 1938), *M. bromleyi* Curran lays egg masses on dead twigs of *Prosopis* and *Acacia* spp. at 1.32–1.98 m above the ground (Linsley 1960) and *M. faurix* Osten Sacken oviposits at 1.00–2.00 m at the tip of dried weed stems (Alcock 1974). Other species such as *Megaphorus guildiana* Williston, *Mallophorina pulchra* Pritchard, *Neoaratus abludo* Daniels and *Dysmachus hradskyi* Adamovic all lay eggs high on several prairie plant species (Adamovic 1974; Dennis and Lavigne 1975; Lawson and Lavigne 1984). Recent work studying oviposition site selection by the South American Asilid *M. ruficauda* shows that height selectivity not only occurs on plants but also on artificial supports such as wire fences (Castelo and Corley 2004).

Our model of oviposition height corresponds well with observed data for our study system. We have shown that high oviposition is a greater advantage for large egg clusters than for small ones. These findings are supported strongly by recent experimental data (Castelo and Corley 2004).

The model, however, includes some simplifications of the biology of the interaction of *M. ruficauda* and its hosts. By assuming that eggs are attached to the top segment of the plant, we ignore egg clutches that are attached to lower parts of plants. We justify this apparent lack of selection by the fact that in most cases where there is a low cluster, it is on a plant that also carries clusters at its top. Moreover, modifying this model assumption would require introducing density and frequency dependence and hence the use of ESS approaches instead of optimization models.

Furthermore, recall that the main assumptions of the model are that plants are sequentially assessed for height, that searching and handling are incompatible and that an optimal strategy is given by maximizing a long-term average rate of gain. Alternatively, decisions based on the maximization of immediate fitness, i.e. parasitism success of a given clutch, would lead to a different strategy, namely, “choose always the highest possible plant”. By contrast, the rate of gain includes immediate fitness gains but also losses in terms of missed opportunities (Stephens and Krebs 1986). The agreement between data and predictions could be further experimentally tested. For instance, the

increase in parasitism success with plant height might be assessed in experiments where height is controlled. It would be also interesting to evaluate this in other parasitic robber fly species and in habitats with different wind conditions.

It should be noted that height selectivity by dipteran parasitoids might relate to several other ecological features. For instance, oviposition by “sit and wait” visual hunters (Copello 1922) may occur on the tall vegetation where animals perch during prey vigilance and consuming bouts. Alternatively, egg clusters of some species may be found on tall plant species because females associate these with host abundance (Fournet et al. 2001). Note that host species may be root feeders that display preferences for certain plant species. Unfortunately, there is very little information on these other aspects that may influence oviposition site selection in parasitoids where there is no direct adult parasitoid–host encounter.

We suggest that plant height selection by ovipositing females may relate to dependence on wind-assisted larval dispersal. Our findings show a new interesting association between plants and parasitoids that differs from anything previously described (de Boer et al. 2005; Campan and Benrey 2004; Cortesero et al. 2000; Takabayashi et al. 1998). We show that just as plants that depend on wind to disperse pollen or seeds, larvae dispersal aimed at increased parasitism may follow simple and straightforward physical rules. This general framework may also be extended to the study of optimal strategies that aim to attain targets concealed in soil.

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Appendix A

The number of hosts parasitized by larvae issued from a single egg cluster is derived in two steps. First, the distribution of larvae on the ground after release from the plant is calculated, and then the number of host parasitized is evaluated.

A basic mechanistic model of seed dispersion by wind shows that the horizontal distance (x) a seed (here a larva) can travel by the wind is a linear function of the height of release (h), the mean horizontal wind speed during larvae

flight (u) and the terminal velocity (T) (Grenne and Johnson 1989, 1996; Nathan et al. 1996, 2001a,b).

$$x = \frac{uh}{T} \quad (2)$$

T is the falling velocity reached by the larvae shortly after release; this quantity depends on the characteristics of the larva (shape and weight).

Here, we further assume that the larvae are uniformly distributed within the shadow (the area that encompasses all the larvae after landing on the ground, see text). This shadow is a sector whose bisecting line length is given by Eq. 2 with $u=U$, the maximum wind speed the larvae experience during their drop.

Assuming random encounters between hosts and parasitoids, the probability that r larvae parasitize a given host is given by a Poisson distribution. The parameter of this distribution, the mean number of larvae per unit area, is given by

$$\lambda = \frac{Q}{a(h)}, \quad (3)$$

where Q is the number of larvae in the cluster and $a(h)$ is the non-isotropic shadow area (see text). The shadow being a sector of angle 2θ (θ takes values between 0 and p) and radius Uh/T , one gets

$$a(h) = \theta \left(\frac{Uh}{T} \right)^2. \quad (4)$$

Finally, the number of hosts parasitized by the Q larvae is the number of hosts present in the ground within the shadow (with density p), weighted by the probability that each host is found by at least one larva

$$f(h) = pa(h)(1 - e^{-\lambda}). \quad (5)$$

Similarly, the number of hosts superparasitized is given by the probability that each host is found by at least two larvae,

$$pa(h)(1 - e^{-\lambda} - \lambda e^{-\lambda}) \quad (6)$$

To take into account the possible heterogeneity in host distribution, we substitute the Poisson distribution, by the negative binomial distribution (see discussion on aggregation in host distribution in the main text). The probability of a given host being found by at least one larva becomes

$$f(h) = pa(h) \left(1 - \left(1 + \frac{\lambda}{k} \right)^{-k} \right), \quad (7)$$

where k is the shape parameters of the negative binomial distribution. As k departs from 0 and becomes larger, the

host distribution becomes less aggregated, and at the limit $k \rightarrow +\infty$ one recovers the Poisson distribution. The second parameter of the negative binomial distribution is its mean, here equal to l (see Eq. 3).

Appendix B

Numerical simulation model

Larvae dispersal was simulated by means of a spatially explicit model, using a grid of 200×200 cells, each cell representing an area of 400 cm^2 . The grid represents the soil surface where the larvae drop, and contains only one egg cluster at variable height, placed in the centre of the grid (oviposition site). Hosts are distributed in patches of variable size of constant density (1,600 hosts per grid on average).

Larvae are dislodged from the oviposition site and can fall in any cell, depending on the dispersal direction and the distance travelled (x). Dispersal direction is fixed and it is assumed constant during the larvae falling. Travel distance, the horizontal distance covered by a larva while dropping, is given by Eq. 2 with $u=U'$, where U' is the mean horizontal wind velocity during the falling of the larvae and T is the terminal velocity of one larva that falls without wind. Terminal velocity depends of both the size and weight of the particle and the fluid in which it displaces (Okubo 1980). Host distribution inside patches is modelled through a cell occupation probability. Density in each patch is assigned by means of an occupation probability, which by default is set at 50% on average. The wind spreads the larvae in the grid at random with given angle spans and degrees of variation in intensity, leading to a cone-shaped dispersion pattern (Nathan et al. 2001a; Wagner et al. 2004).

The definition and numerical values of the physical and biological parameters of the model related to the movement of larvae are given in Table 1 (see main text).

With this model, for each height of egg laying, we simulated different host distributions changing parameter values (a “grid”). A total of 90 grids were considered for each height, and 100 larvae falling cycles (100 egg clusters) were simulated for each grid. We thus obtained a total 9,000 cycles per oviposition height. We considered 16 height values, from 0 to 4 m, in intervals of 0.10 m.

We assumed the following: the larval drop is uniform due to its terminal velocity; the larva reaches quickly the terminal velocity after its release from the egg cluster, so that travelled vertical distance is negligible; there are no interactions or turbulence during the drop process; each cell may be only occupied by a single host and all larvae falling on an occupied cell will parasitize or superparasitize; and dispersal direction is randomly defined.

Appendix C

The oviposition strategy is defined by the probabilities p_i of choosing each type- i plant upon encounter. This strategy is obtained by maximizing the rate of fitness gain (fitness over time), which comes from calculating the following (Stephens and Krebs 1986):

$$\frac{\partial}{\partial p_j} \left(\frac{\sum_{i=1}^n r_j f_i p_i}{1 + \tau \sum_{i=1}^n r_j p_i} \right) \quad (8)$$

One can show that p_j is either 0 or 1, the latter occurring if

$$\frac{f_j}{\tau} > \frac{\sum_{i \neq j} r_j f_i}{1 + \tau \sum_{i \neq j} r_i} \quad (9)$$

This leads to the guess that higher plants are better since the fitness they allow is larger. This can be proven by recurrence, and one can derive a procedure for choosing the optimal plants (Stephens and Krebs 1986). Finally, the optimal oviposition strategy consists of accepting taller plants, those whose type j is larger or equal to i^* . The threshold i^* is the smallest j such that inequality (Eq. 1) in text, derived from Eq. 9, is verified.

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