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Biological Control 37 (2006) 206–213
Biological Control
www.elsevier.com/locate/ybcon

The influence of host deprivation and egg expenditure on the rate of dispersal of a parasitoid following field release

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Received 11 July 2005; accepted 10 September 2005
Available online 21 October 2005

Abstract

With a view of improving the establishment of *Mastrus ridibundus*, a potential candidate for the biological control of the codling moth in California, a series of studies were undertaken to investigate the effect of a pre-release treatment with or without hosts on different performance characteristics. The post-release dispersal of *M. ridibundus* females was investigated in this study, using mark-release-recapture experiments with immunological markers. The results suggest that, in general, *M. ridibundus* is high dispersive. In the absence of any host stimuli for at least 4 days before release, females showed a strong dispersal response with an average dispersal rate of 81.50 m^2/h. In contrast, females continuously provided with hosts before release or deprived of hosts for only a short period of time (1–2 days), showed a lower rate of dispersal averaging 2.07 m^2/h. These results suggest that to enhance local establishment in a fragmented environment parasitoids should be given access to hosts prior to release. In contrast, for regional establishment in a less fragmented environment, host deprivation could be used to encourage broader dispersal if large numbers can be released at each release site to counteract the dilution effect of dispersal.

Keywords: Codling moth; *Cydia pomonella*; Hymenoptera; Ichneumonidae; *Mastrus ridibundus*; Classical biological control; Parasitoid establishment; Post-release dispersal

1. Introduction

Classical biological control involves the introduction of an exotic control agent from the region of origin of an exotic pest into a new area invaded by the pest. The first and crucial phase, before any significant impact or reduction of pest abundance, is the establishment, or the colonization of the new environment by the introduced control agent (Mills, 2000). Factors influencing the probability of establishment of a natural enemy in biological control programs have been discussed mostly in term of numbers of individuals released and/or, number of releases (Grevstad, 1999; Hopper and Roush, 1993; Shea and Possingham, 2000) and very little attention has been paid to the potential to improve the field performance of the individuals released. However, there is strong evidence that the condition of the individuals released will contribute to the success of their establishment (Mills, 1994, 2000).

In the context of introductions, parasitoid performance is strongly dependent on adult female size and reproductive capacity (Godfray, 1994; Papaj, 2000). The release of large individuals that retain a high reproductive potential may be extremely important in generating a sufficient growth rate to carry founder populations over the initial hurdle of establishment. During rearing, parasitoid size could be increased by manipulating the quality (primarily the size) of the hosts provided. Similarly, following adult emergence, reproductive capacity, mainly shaped by egg load, i.e., the number of mature eggs stored in the reproductive system, could be controlled by manipulating access to hosts during the pre-release period.

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doi:10.1016/j.biocontrol.2005.09.001

Dispersal from the release point is also a factor of importance in successful establishment. Distances moved by the released parasitoids should be great enough to discover the potential hosts available at the targeted release sites, but limited enough to avoid having the parasitoids disperse out of the area. This concern has been addressed previously in the context of augmentative biological control, i.e., when the aim is the immediate impact of mass released natural enemies rather than their establishment, as a high propensity to disperse could result in poor effectiveness in controlling the pest (Bellamy et al., 2004; Corbett and Rosenheim, 1996; Keller et al., 1985).

Mastrus ridibundus (Gravenhorst) (Hymenoptera: Ichneumonidae) has been selected as a potentially effective parasitoid for the biological control of the codling moth *Cydia pomonella* L. (Lepidoptera: Tortricidae) in California (Mills, 2005). It has been imported from Central Asia and released in California since 1995. Successful establishment has been reported in some orchards in some years, but on many other occasions parasitoids have failed to establish in an orchard despite favorable conditions. *M. ridibundus* is a gregarious synovigenic cocoon parasitoid with low fecundity and no egg resorption (Bezemer and Mills, 2003; Bezemer et al., 2005). Earlier studies were undertaken to understand how to manipulate female access to hosts prior to their release to increase their potential for establishment. The results showed that a pre-release treatment of host deprivation seemed preferable to access to excess hosts for two main reasons: first, because of the short peak of high reproduction that can be induced once hosts become available (Hougardy et al., 2005), and second, because host-deprived females do not suffer a reduction in host finding ability as compared to females provided with hosts continuously after emergence (Hougardy and Mills, 2005). In this paper, we investigated the effect of egg expenditure and host deprivation on *M. ridibundus* dispersal after release using mark-release-recapture experiments. Despite a recognized need to better understand parasitoid movement in the field, studies of dispersal are still rare because of methodological difficulties in measuring this parameter for insects of small size.

2. Materials and methods

2.1. Mark-release-recapture

The mark-release-recapture experiments were undertaken in a 1 ha block (14 rows of 32 trees) of walnuts (variety Chandler) in an orchard located in Brentwood, CA. This orchard was selected because of the very low level of naturally occurring codling moths and thus the absence of *M. ridibundus*. For each experiment, three groups of *M. ridibundus* females representing three levels of a pre-release treatment (either egg expenditure or host deprivation) were released simultaneously at the center of the orchard block. Following Hougardy et al. (2005) and Hougardy and Mills (2005), the egg expenditure treatment consisted of three groups of parasitoids given continuous access to excess codling moth hosts for either 1–2, 4–5 or 7–8 days. The host deprivation treatment consisted of three groups of parasitoids deprived of hosts for the same intervals of time following initial exposure to hosts for the first 6 h after emergence. The three levels of egg expenditure and host deprivation were necessarily correlated with female age. The *M. ridibundus* used in the experiments were reared in the Insectary and Quarantine Facility at the University of California, Berkeley according to Bezemer and Mills (2003). One replicate of each pre-release treatment was conducted in 2002 and a second in 2003 (see Table 1 for dates and weather conditions, and Table 2 for numbers of parasitoids released). As it was necessary to keep the parasitoids in the laboratory for different lengths of time according to the levels of pre-release treatments, the number released per treatment level varied from 930 to 1800. This did not affect the data analysis, however, as dispersal was analyzed separately for each treatment level (see below). The experiments were carried out in September and October as this is the time of the year when *M. ridibundus* is most active (Mills, 2005), with at least a two week interval between experiments to ensure that parasitoids from the first mark-release-recapture would no longer be alive at the start of the second.

As body size is known to influence dispersal ability (Bezemer and Mills, 2003), only intermediate sized parasitoids

Table 1
Data and weather conditions during the mark-release-recapture experiments (data from CIMIS, 2005)

Pre-release treatment	Date of release	Day of recapture	Temperature (°C)			Wind (m/s)		Relative humidity (%)	
			Min	Max	Average	Direction	Speed	Min	Max
Egg expenditure	Oct. 8 2002	1	11.7	32.2	22.0	NW	2	24.6	73.0
		2	14.4	29.4	21.9	NW	0	28.6	79.7
	Sept. 17 2003	1	15.0	28.3	21.7	W	4	18.8	69.3
		2	11.7	31.7	21.7	SW	3	15.3	48.9
Host deprivation	Oct. 22 2002	1	6.7	22.2	14.5	W	2	47.8	95.8
		2	5.0	17.8	11.4	W	2	61.0	100
	Oct. 7 2003	1	11.7	29.4	20.6	S	2	29.2	81.9
		2	11.1	30.6	20.9	S	3	19.7	94.2