



# The potential of mass rearing of *Monoksa dorsiplana* (Pteromalidae) a native gregarious ectoparasitoid of *Pseudopachymeria spinipes* (Bruchidae) in South America

Danielle Rojas-Rousse, Karine Poitrineau, Cesar Basso

## ► To cite this version:

Danielle Rojas-Rousse, Karine Poitrineau, Cesar Basso. The potential of mass rearing of *Monoksa dorsiplana* (Pteromalidae) a native gregarious ectoparasitoid of *Pseudopachymeria spinipes* (Bruchidae) in South America. *Biological Control*, Elsevier, 2007, 41, pp.348-353. <hal-00146270>

**HAL Id: hal-00146270**

**<https://hal.archives-ouvertes.fr/hal-00146270>**

Submitted on 18 May 2007

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



1 The potential of mass rearing of *Monoska dorsiplana* (Pteromalidae) a native  
2 gregarious ectoparasitoid of *Pseudopachymeria spinipes* (Bruchidae) in South  
3 America.

4  
5 **Danielle Rojas-Rousse<sup>1</sup>, Karine Poitrineau and César Basso \***

6  
7 Institut de Recherche sur la Biologie des Insectes (IRBI), UMR du CNRS 6035

8 Faculté des Sciences et Techniques, Avenue Monge, 37200 – Tours – France

9 \* Facultad de Agronomía. Av. Garzón 780. 12900 Montevideo. Uruguay.  
10

11

12

13

14

15

16

17

18

19

20 1-Corresponding author : [rousse@univ-tours.fr](mailto:rousse@univ-tours.fr)

21 Phone number: 02 47 36 69 73

22 FAX number: 02 47 36 69 66

23

24

25

26 **Abstract**

27 In Chile and Uruguay, the gregarious Pteromalidae (*Monoska dorsiplana*) has been  
28 discovered emerging from seeds of the persistent pods of *Acacia caven* attacked by the  
29 univoltin bruchid *Pseudopachymeria spinipes*. We investigated the potential for mass rearing  
30 of this gregarious ectoparasitoid on an alternative bruchid host, *Callosobruchus maculatus*, to  
31 use it against the bruchidae of native and cultured species of Leguminosea seeds in South  
32 America.

33 The mass rearing of *M. dorsiplana* was carried out in a population cage where the density  
34 of egg-laying females per infested seed was increased from 1:1 on the first day to 5:1 on the  
35 last (fifth) day. Under these experimental conditions egg-clutch size per host increased, and at  
36 the same time the mortality of eggs laid also increased. The density of egg-laying females  
37 influenced the sex ratio which tended towards a balance of sons and daughters, in contrast to  
38 the sex ratio of a single egg-laying female per host (1 son to 7 daughters). The mean weight of  
39 adults emerging from a parasitized host was negatively correlated with the egg-clutch size, i.e.  
40 as egg-clutch size increased, adult weight decreased.

41 All these results show that mass rearing of the gregarious ectoparasitoid *M. dorsiplana* was  
42 possible under laboratory conditions on an alternative bruchid host *C. maculatus*. As *M.*  
43 *dorsiplana* is a natural enemy of larval and pupal stages of bruchidae, the next step was to  
44 investigate whether the biological control of bruchid *C. maculatus* was possible in an  
45 experimental structure of stored beans.

46

47 **Key words.** Gregarious parasitoid, egg-clutch size, theoretical offspring, observed  
48 offspring, sex ratio, bruchid host, *Callosobruchus maculatus*

49

50

## 51 **1. Introduction**

52

53 Bruchids constitute the largest single problem for native and cultured species of  
54 Leguminosea seeds in Latin America, attacking a number of economically important plant  
55 species. The common bean weevil *Acanthoscelides obtectus* (Say) and the Mexican bean  
56 weevil *Zabrotes subfasciatus* (Boh) are the main post-harvest pests of dry beans and currently  
57 constitute a major problem in the management of bean stocks in storage sites (Schmale *et al.*,  
58 2001; Alvarez *et al.*, 2005 ). In the last 30 years, these two bruchid species have also been  
59 recorded on new host plant species, such as *Cajanus indicus*, *Pisum sativum*, *Vicia faba*, and  
60 *Vigna unguiculata* (Jarry and Bonet, 1982; Johnson, 1983, 1990). This expansion of host  
61 range requires new integrated pest management strategies based on natural resources,  
62 including parasitoids. In South America, as in traditional storage systems in the African  
63 tropical belt, the parasitoid *Dinarmus basalis* (Ashm.) is currently the main candidate for the  
64 biological control of bruchids in stored beans (Schmale *et al.*, 2001; Sanon *et al.*, 1998; Dorn  
65 *et al.*, 2005).

66 The challenge now is to find one or more appropriate biological control agents which are  
67 native to Latin America. Two native Trichogrammatidae have recently been found as  
68 oophagous parasitoids of bruchid beetle eggs: *Uscana chiliensis* (Pintureau and Gering) on  
69 *Bruchus pisorum*, and *Uscana espiniae* (Pintureau and Gering) on *Pseudopachymeria spinipes*  
70 (Er.), (Pintureau *et al.*, 1999). In addition, one Pteromalidae (*Monoska dorsiplana*, Boucek)  
71 and two Eulophidae (*Horismenus spp.*) have been found emerging from seeds of the persistent  
72 pods of *Acacia caven* (Mol.) contaminated by the univoltin bruchid *P. spinipes* (Rojas-Rousse,  
73 2006). These persistent pods provide a natural reserve of parasitoids which are a potential  
74 resource for the biological control of Bruchidae. Previous investigations have shown that  
75 *Dinarmus vagabundus* and *Dinarmus basalis* (Pteromalidae), parasitoids of larval and pupal

76 stages of bruchids, can be mass-reared on a substitution bruchid host, *Callosobruchus*  
77 *maculatus* (Rojas-Rousse *et al.*, 1983; Rojas-Rousse *et al.*, 1988). Some life history traits of  
78 *M. dorsiplana* have been investigated under laboratory conditions using the substitution  
79 bruchid host *Callosobruchus maculatus*, and it was observed that with a low density of *M.*  
80 *dorsiplana* females per host, i.e. 1:1, the female laid one clutch of eggs during one oviposition,  
81 the parasitoid larvae developed gregariously, and the most common patriline was 1 male and  
82 7 females (Rojas-Rousse, 2006).

83 The aim of the present study was to test how egg-clutch size changed in a population  
84 cage when the density of females per host was increased from 1:1 to 5:1 over 5 consecutive  
85 days. Under these controlled conditions, mass production of *M. dorsiplana* on the alternative  
86 host *C. maculatus* could be investigated. The egg and offspring clutch sizes were compared  
87 and the trade-off between egg and offspring clutch sizes was studied through experimental  
88 manipulation of the egg-clutch size.

89

## 90 **2. Materials and Methods**

91

### 92 *2.1. Biological material.*

93

94 Host and parasitoid strains were mass-reared in a climatic chamber under conditions  
95 close to those of their zone of origin, with synchronous photo and thermo-periods: 30° / 20°C,  
96 12h / 12h L:D, and 70% RH.

97 The bruchid host *C. maculatus* was mass reared in the laboratory on *Vigna radiata* (L.)  
98 Wilszek seeds. After egg-laying, the bruchid females were removed and the seeds stored until  
99 the larvae inside the seed reached the final larval or pupal stage.

100 Host size, determined by its developmental stage, is one of the main factors contributing  
101 to variations in egg-clutch size, and therefore only the largest *C. maculatus* hosts were

102 presented to the egg-laying *M. dorsiplana* females (Terrasse *et al.*, 1996; Pexton and Mayhew,  
103 2002; Pexton and Mayhew, 2005). For this, the seeds were examined under a microscope lens  
104 and only seeds with 1 to 3 hosts, i.e. the fourth-instar larvae, prepupae and pupae, were  
105 offered to the parasitoid females. Because *C.maculatus* larvae were not directly accessible to  
106 parasitoids, the female parasitoid generally introduced her ovipositor through the hole drilled  
107 by the neonatal host larvae (van Alebeek *et al.*, 1993). The parasitoid females located these  
108 holes from the egg shells remaining on the seed tegument (personal observations).

109

## 110 2.2. Parasitization of the substitution bruchid host *C. maculatus* in a population cage.

111

112 The experiments were conducted in a special ‘altuglass’ population-rearing cage  
113 (40x30x25 cm) simulating a ventilated storage structure. In this cage, 120 *V. radiata* seeds  
114 with one, two or three hosts were introduced every day with 120 newly mated *M. dorsiplana*  
115 females (mating occurred immediately after emergence of females). The bruchid-infested  
116 seeds were exposed for 24h to the parasitoids and renewed daily on 5 consecutive days, unlike  
117 parasitoid females which were not removed. In this way, theoretically the density of females  
118 per seed increased from 1:1 on the first day (120 females for 120 infested seeds) to 5:1 on the  
119 last (fifth) day (120x5 females for 120 infested seeds). The seeds removed every day were  
120 divided into two sets, one with 40 and the other with 80 seeds. All the seeds in the first set  
121 were opened to investigate the parasitism of each host, and the second set was used as a  
122 control.

123

## 124 2.3. Analysis of egg-clutch size, theoretical offspring, and relative mortality

125

126 The data recorded for each opened seed included the number and developmental stage  
127 of hosts, whether the host was parasitized or not, and if so, the egg-clutch size. Each  
128 parasitized host was incubated individually in a small plastic tube (30° / 20°C, 12h / 12h L:D,  
129 and 70% RH) to identify the developmental stage of the parasitoids, the weight of each  
130 parasitoid pupa before the moult, and the number and sex of the emerging adults.

131

#### 132 *2.4. Observed offspring*

133

134 All the seeds of the control set were incubated individually in a small plastic tube (30° /  
135 20°C, 12h / 12h L:D, and 70% RH). This control set was used to determine the number and  
136 sex of parasitoid adults emerging from each parasitized seed without experimental  
137 manipulation.

138

#### 139 *2.5. Data analysis*

140

141 For each set of seeds, the various parameters were analysed for the 5 days of activity of  
142 the parasitoid females. Seeds with one or two parasitoid hosts were analysed separately.  
143 These two sets were compared with regard to the distribution of egg-clutch sizes, the  
144 offspring observed per parasitized host, the development time of each sex and the dry weights  
145 of emerging male and female parasitoids. An ANOVA was performed (XLStats 6 for  
146 Windows) to assess the intra- and inter-variability of the sets. If the variances were  
147 statistically different, the Student-t test was performed. The Chi-square test was used to  
148 evaluate the of distribution of egg-clutch sizes between the hosts in the seeds. The influence  
149 of egg-clutch size on the parasitoid adult weight was tested by a simple linear regression  
150 (XLStats 6 for Windows).



151

### 152 **3. Results**

153

#### 154 *3.1 Parasitized hosts*

155

156 In the 200 opened seeds (40 seeds per day for 5 days), there were 323 hosts. Of these  
157 seeds, 45.5% (91/200) contained one host, 47.5% (95/200) two hosts, and 7% (14/200) three  
158 hosts. Only 67% of the hosts (216/323) were actually parasitized, i.e. contained egg clutches  
159 (Table 1). The seeds with a single parasitological host per seed were 100% attacked (Table 1).  
160 Those with two hosts were attacked less, with 59.47% of hosts parasitized (113/190), and  
161 when there were three hosts, only 28.57% of the hosts (12/42) were parasitized (Table 1).

162 Because 3 hosts per seed were rarely observed, our analysis was restricted to a  
163 comparison of seeds enclosing one and two hosts. The percentage of parasitized hosts was  
164 significantly greater among seeds enclosing only one host (t-test for percentage comparison  $t$   
165 = 6.95; at the level of significance  $\alpha = 0.05$   $t_{[.05]}_{\infty} = 1.96$ ).

166

#### 167 *3.2. Distribution of egg-clutch size with one parasitized host per seed*

168

169 The distribution of egg-clutch size observed per parasitized host varied from 1 to 29  
170 eggs with the modal class from 9 to 10 eggs (Figure 1). With one host enclosed per seed, the  
171 average clutch size was  $9.37 \pm 1.12$  eggs, and with two hosts per seed it was  $8.48 \pm 0.97$   
172 (mean  $\pm$  standard error of the mean). The distribution of egg-clutch sizes showed no  
173 significant difference from the normal distribution and the difference between the two means  
174 was not significantly different [Kolmogorov-Smirnov test: 1 host per seed,  $N(6.07; 37.35)$ ,

175  $D=0.176 < D_{0.05} = 0.338$ ; 2 hosts per seed  $N(5.13; 32.83)$ ,  $D=0.241 < D_{0.05} = 0.338$ ,  
176 (Student test:  $t=1.07$  at the level of significance  $\alpha = 0.05$   $t_{[.05]}_{\infty} = 1.96$ ).

177

### 178 *3.3 Distribution of egg-clutch size with two hosts per seed*

179

180 With two hosts per seed, the females could parasitize only one of the two hosts (Figure  
181 1). When both hosts were parasitized, the modal class (1-2 eggs per parasitized host)  
182 corresponded to the smallest egg clutch size (Figure 1). The modal class was larger (9-10 eggs  
183 per clutch) when one of the two hosts was parasitized (Figure 1). There was a significant  
184 difference in the mean clutch size when both hosts were parasitized,  $4.17 \pm 1.06$  (mean  $\pm$   
185 standard error of the mean), and when one of the two hosts was parasitized:  $9.37 \pm 1.12$  eggs  
186 (Student-t test:  $t=5.3$  at the level of significance  $\alpha = 0.05$   $t_{[.05]}_{\infty} = 1.96$ ). This difference  
187 was confirmed by an irregular distribution of the observed frequencies, ranging from 1-2 to  
188 13-14 eggs per host (Chi-square test using Yates correction:  $\chi^2_{\text{calculated}} = 27.25$ :  $\alpha =$   
189  $0.05$ ,  $\chi^2_{\text{ddl } 6} = 12.59$ ).

190

### 191 *3.4 Theoretical offspring and sex-ratio of observed offspring with one parasitized host per* 192 *seed*

193

194 As each parasitized host was incubated individually up to the adult stage, it was  
195 possible to calculate the relative mortality:  $\text{number of eggs} - \text{number of emerged adults} /$   
196  $\text{number of eggs}$ . The correlation between egg-clutch size and relative mortality was strong:

197 R=0.99, P <0.0001, with mortality rising as egg-clutch size increased, i.e. not all the eggs of  
198 one clutch would reach adulthood.

199 On average,  $4.12 \pm 0.39$  males and  $3.84 \pm 0.28$  females emerged from one parasitized  
200 host (mean  $\pm$  standard error of the mean). As the variances of emerged males and females  
201 were equal, the difference observed between their means was not statistically different  
202 [ANOVA:  $F_{(0.05), 1, 427}$  calculated = 1.245 with P= 0.265:  $F_{\text{critical value}} = 3.86$ ].

203

### 204 *3.5 Development time*

205

206 Observations indicated that in each clutch the male(s) emerged first while the  
207 emergence of females was spread over time. The shortest time (19 days) was for males with an  
208 average of  $20.88 \pm 0.15$  days, and the longest (30 days) for females with an average of  $21.06$   
209  $\pm 0.19$  days (mean  $\pm$  standard error of the mean). Analysis of the total development time from  
210 egg to adulthood (male or female), showed that the difference observed between the means  
211 did not significantly differ [ANOVA:  $F_{(0.05), 1, 378}$  calculated = 1.912 with P= 0.168:  $F_{\text{critical}}$   
212  $\text{value} = 3.86$ ].

213

### 214 *3.6. Dry weights of males and females in each clutch*

215

216 Dry weight distribution indicated that the lowest values (from 0.1mg to 0.9 mg) were for  
217 males and the highest (up to 1.6 mg) for females. The mean dry weight of females ( $0.717 \pm$   
218  $0.05$ ) was double that of males  $0.391 \pm 0.02$  (mean  $\pm$  standard error of the mean). The  
219 variances of these dry weights being statistically different, the difference between the mean  
220 weights of emerged females and males was statistically different [ANOVA:  $F_{(0.05), 1, 378}$

221 calculated =151.58 with  $P = 0.0001$ :  $F_{\text{critical value}} = 3.02$ , Student-t test:  $t = 11.7$  at the level  
222 of significance  $\alpha = 0.05$   $t_{[.05] \infty} = 1.96$  ]. For each sex and clutch, mean adult weight and  
223 egg-clutch size were negatively correlated (Figure 2A, B). This negative correlation indicated  
224 that the mean adult weight decreased as the egg-clutch size increased.

225

#### 226 4. Discussion

227

228 In this study, *M. dorsiplana* was successfully mass-reared in a population cage. With both  
229 one and two parasitological hosts per seed but only a single host actually parasitized, the most  
230 frequent egg-clutch size was 9 to 10 eggs and the largest was 29 eggs. With a density of one  
231 to five females and one parasitological host per seed, a modal class of egg-clutch size close to  
232 that observed with one egg-laying female per host was produced (Rojas-Rousse, 2006). The  
233 smallest egg-clutch size (1 or 2 eggs) was observed when two parasitological hosts per seed  
234 were parasitized. In this situation, egg-laying was disturbed by numerous contacts between  
235 the females (personal observations).

236 In theory, the number of eggs laid on a host's body corresponds to the number of  
237 offspring. However, this theoretical offspring clutch size differed significantly from the actual  
238 offspring numbers emerging from parasitized hosts in the control group, indicating that not all  
239 the eggs reached the adult stage. The correlation between egg-clutch size and relative  
240 mortality was high ( $R=0.99$ ,  $P < 0.0001$ ), with mortality rising as the egg-clutch size increased.  
241 This could be the outcome of a scramble competition between gregarious larvae to share  
242 resources (Godfray, 1994). The possibility of aggressive behaviour by the first-instar larvae of  
243 a gregarious species could explain why egg clutches were larger than the number of offspring  
244 in mass rearing of *M. dorsiplana*. In fact, when the parasitized hosts are superparasitized,  
245 aggressive encounters between the pteromalid first-instar larvae of *M. dorsiplana* are likely

246 due to their great mobility and well-developed mandibles. In the following phase, although  
247 the larvae are immobile and unarmed (personal observations), it is also possible that some  
248 brood reduction could occur in hosts containing a large number of gregarious larvae due to  
249 over-crowding (Pexton and Mayhew, 2001, Pexton et al., 2003).

250 In a rearing population cage of *M. dorsiplana* with a density of 1 to 5 females per seed,  
251 when one host was parasitized per seed, the sex ratio tended towards a balance of sons ( $4.12 \pm$   
252  $0.39$ ) and daughters ( $3.84 \pm 0.28$ ), in contrast to the ratio observed with a density of one egg-  
253 laying female per host (1 son and 7 daughters) (Rojas-Rousse, 2006). This increase of sons  
254 has also been observed in previous experiments with two or three egg-laying *M. dorsiplana*  
255 females per host, where the distribution of the associations of 1, 2, 3 or X sons with 1, 2, 3 or  
256 X daughters indicates that the common patriline is 2 sons and 8 daughters (Rojas-Rousse,  
257 2006; Stevoux, 1997). The same pattern has been observed among the gregarious pteromalid  
258 *Dinarmus vagabundus*, a parasitoid of *C. maculatus*: increasing the density of egg-laying  
259 females from one to three per host leads to a greater increase of sons than daughters, the sex  
260 ratio ( $\frac{\text{♂}}{\text{♀}}$ ) increasing from 0.33 to 1 (Rojas-Rousse et al., 1983). Different models have  
261 shown the influence of parasitoid density on host-parasitoid population dynamics through  
262 local mating competition (LMC) (Hamilton, 1967), the number of female offspring per host  
263 being influenced by the density of ovipositing females (Hardy and Ode, 2006). The  
264 constraints of mass rearing *M. dorsiplana* in a population cage might prevent the precise  
265 application of Hamilton's LMC theory. Some of these constraints need to be tested to  
266 understand better the observed fluctuations of the sex ratio of *M. dorsiplana*. For example,  
267 asymmetrical mate competition between the broods of different females could occur in a  
268 mass-rearing population cage, and females might visit and lay eggs sequentially on different  
269 hosts, producing different sex ratios in a patch (Shuker and West, 2004; Shuker et al., 2005).  
270 The dispersion of *M. dorsiplana* males from their natal patch before mating has frequently

271 been observed due to the gregarious nature of the hosts in a patch (Jervis and Copland, 1996;  
272 Gu and Dorn, 2003), which raises the likelihood of a partial local mating competition in this  
273 species.

274 Studies of the nutritional balance during the development of the gregarious  
275 ectoparasitoid *D. vagabundus* have shown that the mean weight of both sexes decreases  
276 significantly at higher larval densities (Rojas-Rousse et al., 1988). In a population rearing  
277 cage with a high level of ovipositing *M. dorsiplana* females per host, the mean weights of  
278 adults emerging from a parasitized host were negatively correlated with egg-clutch size, the  
279 larger the egg clutch, the lower the weight. As in other parasitoid species, the different egg-  
280 clutch sizes laid by *M. dorsiplana* females might have a considerable impact on offspring  
281 fitness (Bezemer et al., 2005; Elzinga et al., 2005; Milonas, 2005; Traynor and Mayhew,  
282 2005 a and b).

283 Overall, this biological information about the newly discovered pteromalid *Monoska*  
284 *dorsiplana* in Latin America indicates that this native gregarious parasitoid could be a  
285 promising resource for the biological control of bruchid beetles. When climatic conditions  
286 become favourable, the *C. maculatus* bruchid population in storage structures increases  
287 rapidly over successive generations (Ouedraogo et al., 1996). To determine whether  
288 *M.dorsiplana* could be used as a natural enemy to control this increase in storage systems, its  
289 action during regular intervals of introduction need to be analysed after ascertaining that it can  
290 move around inside experimental storage systems and locate its hosts, even when these are  
291 scarce.

292  
293 **Acknowledgments**

294  
295  
296 This article has been read and corrected by Inter-Connect, translation and proof-reading  
297 services.

298 **References**

299

300 Alvarez, N., Mckey, D., Hossaert-Mckey, M., Born, C., Mercier, L., and Benrey, B., 2005.

301 Ancient and recent evolutionary history of the bruchid beetle, *Acanthoscelides obtectus* Say, a  
302 cosmopolitan pest of beans. *Molecular Ecology*. 14, 1015-1024.

303 Bezemer, T. M., Harvey, J.A., and Mills, N.J., 2005. Influence of adult nutrition on the  
304 relationship between body size and reproductive parameters in a parasitoid wasp. *Ecol.*  
305 *Entomol.* 30, 571-580.

306 Dorn, S., Schmale, I., Wäckers, F.L., and Cardona, C., 2005. How host larval age, and nutrition  
307 and density of the parasitoid *Dinarmus basalis* (Hymenoptera: Pteromalidae) influence  
308 control of *Acanthoscelides obtectus* (Coleoptera: Bruchidae). *Bull. Entomol. Res.* 95, 145-150.

309 Elzinga, J.A., Harvey J. A., and Biere A., 2005. Age-dependent clutch size in a koinobiont  
310 parasitoid. *Ecol. Entomol.* 30, 17-27.

311 Godfray, H.C.J., 1994. "Parasitoids. Behavioral and Evolutionary Ecology". Princetown Univ.  
312 Press, Princetown, NJ.

313 Gu, H., and Dorn, S., 2003. Mating system and sex allocation in the gregarious parasitoid  
314 *Cotesia glomerata*. *Animal Behav.* 66, 259-264.

315 Hamilton, W. D., 1967. Extraordinary sex-ratios. *Science* 156, 477-488.

316 Hardy, I., and Ode, P. 2006. Parasitoid sex ratios and biological control. *International*  
317 *Conference on Behavioural Ecology of Insect Parasitoids*

318 Jarry, M., and Bonet, A., 1982. La bruche du haricot, *Acanthoscelides obtectus* Say,  
319 (Coleoptera : bruchidae), est-elle un danger pour le cowpea, *Vigna unguiculata* (L.) Walp ?  
320 *Agronomie* 2, 963-968.

321 Jervis, M.A., and Copland, M.J.W., 1996. The life cycle, in "Insects Natural Enemies: Practical  
322 Approaches to their study and Evaluation". Chapman & Hall, London, 63-160.

323 Johnson, C.D., 1983. Ecosystematics of *Acanthoscelides* (Coleoptera : bruchidae) of southern  
324 Mexico and Central America. *Miscellaneous Publications of the Entomological Society of*  
325 *America* 56, 1-370.

326 Johnson, C.D., 1990. Systematics of the seed beetle genus *Acanthoscelides* (Bruchidae) of  
327 northern South America. *Transactions of the American Entomological Society* 116, 297-618.

328 Milonas, P.G., 2005. Influence of initial egg density and host size on the development of the  
329 gregarious parasitoid *Bracon hebetor* on three different host species. *Biol. Control* 50, 415-  
330 428.

331 Pexton, J.J., and Mayhew, P.J., 2001. Immobility: the key to family harmony ? *Trends in*  
332 *Ecology & Evolution* 16, 7-9.

333 Ouedraogo, A. P., Sou, S., Sanon, A., Monge, J.P., Huignard, J., Tran B., and Credland, P.F.,  
334 1996. Influence of temperature and humidity on populations of *Callosobruchus maculatus*  
335 (Coleoptera: Bruchidae) and its parasitoid *Dinarmus basalis* (Pteromalidae) in two climatic  
336 zones of Burkina Faso. *Bull. Ent. Research* 86, 695-702.

337 Pexton, J.J., and Mayhew, P.J., 2002. Siblicide and life-history evolution in parasitoids.  
338 *Behavioral Ecol.* 13, 690-695.

339 Pexton, J.J., Rankin, D.J., Dytham, C., and Mayhew, P.J., 2003. Asymmetric larval mobility  
340 and the evolutionary transition from siblicide to nonsiblicidal behaviour in parasitoid wasps.  
341 *Behavioral Ecol.* 14, 182-193.

342 Pexton, J.J., and Mayhew, P.J., 2005. Clutch size adjustment, information use and the evolution  
343 of gregarious development in parasitoid wasps. *Behav. Ecol. Sociobiol.* 58, 99-110.

344 Pintureau, B., Gerding, M., and Cisternas,, E.1999. Description of three new species of  
345 Trichogrammatidae (Hymenoptera) from Chile. *Canad. Entomol.* 131, 53-63.



346 Rojas-Rousse, D., Eslami, J., and Lagrange, P., 1983. Conséquence de la variation des effectifs  
347 des femelles de *Dinarmus vagabundus*, sur le parasitisme de l'un de leurs hôtes  
348 *Callosobruchus maculatus*. *Ent. Exp. & Appl.* 34, 317-325.

349 Rojas-Rousse, D., Eslami, J., and Periquet, G., 1988. Reproductive strategy of *Dinarmus*  
350 *vagabundus* Timb. (Hym., Pteromalidae): real sex-ratio, sequence of emitting diploid and  
351 haploid eggs and effects of inbreeding on progeny. *J. Appl. Ent.* 106, 276-285.

352 Rojas-Rousse, D., 2006. Persistent pods of the tree *Acacia caven*: a natural refuge for diverse  
353 insects including Bruchid beetles and the parasitoids Trichogrammatidae, Pteromalidae and  
354 Eulophidae. *J. Insect Sci.* 6, 08.

355 Sanon, A., Ouedraogo, A. P., Tricault, Y., Credland, P.F., and Huignard, J., 1998. Biological  
356 control of bruchids in cowpea stores by release of *Dinarmus basalis* (Hymenoptera:  
357 Pteromalidae) adults. *Biol. Control* 27, 717-725.

358 Schmale, I., Wäckers, F. L., Cardona, C., and Dorn, S., 2001. Control potential of three  
359 hymenopteran parasitoid species against the bean weevil in stored beans: the effect of adult  
360 parasitoid nutrition on longevity and progeny production. *Biol. Control* 21, 134-139.

361 Shuker, D.M., and West, S.A., 2004. Information constraints and the precision of adaptation:  
362 sex-ratio manipulation in wasps. *PNAS* 101, 10363-10367.

363 Shuker, D.M., Pen, I., Duncan A.B., Reece, S.E., and West, S.A., 2005. Sex ratios under  
364 asymmetrical local mate competition: theory and a test with parasitoid wasps. *The American*  
365 *Naturalist* 166, 301-316.

366 Stevoux, V., 1997. Sex ratio de la descendance de *Monoxsa dorsiplana* en fonction de la densité  
367 de femelles pondéuses. *Master's internship report*, Université de Tours, France, 1-20.

368 Terrasse, C., Nowbahari, B., and Rojas-Rousse, D., 1996. Sex ratio regulation in the wasp  
369 *Eupelmus vuilleti* Craw an ectoparasitoid on the bean weevil larvae. *J. Insect Behav.* 9, 91-99.

370 Traynor, R.E., and Mayhew, P.J., 2005 a. A comparative study of body size and clutch size  
371 across the parasitoid Hymenoptera. *Oikos* 109, 305-316.

372 Traynor, R.E., and Mayhew, P.J., 2005 b. Host range in solitary versus gregarious parasitoids:  
373 a laboratory experiment. *Ent. Exp. & Appl.* 117, 41-49.

374 Van Alebeek, F.A.N., Rojas-Rousse, D., and Lévèque, L.,1993. Interspecific competition  
375 between *Eupelmus vuilleti* and *Dinarmus basalis*, two solitary ectoparasitoids of bruchidae  
376 larvae and pupae. *Ent. Exp. & Appl.* 69, 21-31.

377

378

*Table 1.* Distribution of parasitized and non-parasitized hosts in a global set of 200 seeds (40 seeds per day for 5 days). Each seed was opened to observe whether the host was parasitized or not.

	<b>Total seeds</b>	<b>Presented hosts</b>	<b>Parasitized hosts</b>	<b>Non-parasitized hosts</b>
<b>1 host per seed</b>	91	91	N=91 91/91= <b>1</b>	0
<b>2 hosts per seed</b>	95	190	N=113 113/190= <b>0.59</b>	77
<b>3 hosts per seed</b>	14	42	N=12 12/42 = <b>0.28</b>	30
<b>Total</b>	<b>200</b>	<b>323</b>	<b>216</b>	<b>107</b>

Observed Frequencies



