

# Age-related fecundity and sex ratio variation in *Apanteles galleriae* (Hym., Braconidae) and host effect on fecundity and sex ratio of its hyperparasitoid *Dibrachys boarmiae* (Hym., Pteromalidae)

F. Uçkan<sup>1</sup> and A. Gülel<sup>2</sup>

<sup>1</sup>Department of Biology, Faculty of Science-Art, Balıkesir University, Balıkesir, Turkey; <sup>2</sup>Department of Biology, Faculty of Science-Art, 19 Mayıs University, Samsun, Turkey

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**Abstract:** Age-related progeny production and sex ratio of *Apanteles galleriae* Wilkinson, a koinobiont, solitary, larval endoparasitoid of two lepidopteran species, *Galleria mellonella* (L.) and *Achoria grisella* Fabr., were studied at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity, and a photoperiod of 12 : 12 h (L : D). The effect of host type on fecundity and sex ratio of the hyperparasitoid *Dibrachys boarmiae* (Walker), an idiobiont, gregarious pre-pupae or pupae ectoparasitoid on *A. galleriae* was also investigated. Total progeny produced by *A. galleriae* showed very little host-dependent variation. The mean total number of offspring produced by a female was 232.6 and 239.7 on *G. mellonella* and *A. grisella*, respectively. Progeny production and proportion of females per host by *A. galleriae* decreased directly with parental age. Fecundity of *D. boarmiae* on *A. galleriae* pupae reared on *G. mellonella* and *A. grisella* was 3.3 and 2.9 respectively. Host type had no significant influence on progeny production and sex ratio of *D. boarmiae*.

## 1 Introduction

Parasitoid wasps have been of primary importance at least as much as *Apis mellifera* and *Bombyx mori* for their contribution to protecting ecosystems and the resulting benefits for humanity. Thus, they might be regarded as hidden ecological life vests. Parasitoid species are also among the foremost candidates in reconstruction of ecological balance and biological control applications. Because they are closely attuned to their hosts, they tend to be host-specific and pose lower environmental risks (HOKKANEN and LYNCH, 1995; ANDOW et al., 1997).

Prior research on different parasitoid species has demonstrated that fecundity, progeny sex ratio and parasitization ability of females vary depending on parasitoid age (MELTON and BROWNING, 1986; DROST and CARDE, 1992; MORALES-RAMOS and CATE, 1993; MEDEIROS et al., 2000), host species (ANDOW et al., 1997), host instar (ŞENONCA and PETERS, 1993), whether or not the host is already parasitized (VAN ALPHEN and VISSER, 1990), number of eggs laid by the female (PETITT and WIETLISBACH, 1993), time passed till finding hosts (ORR et al., 1986), host abundance (HIRASHIMA et al., 1990) and presence of hyperparasitoid species (GODFRAY, 1994). In addition, it has been shown that fecundity and sex ratio are affected by quantitative and qualitative nutritional factors provided by either host species or environment during larval development (HAGLEY and BARBER, 1992).

In classical biological control programmes, the success rate is closely related to behavioural and physiological interactions between parasitoid and host (ANDOW et al., 1997). This rate can be improved through greater knowledge about the physical, chemical and mechanical variables involved in these interactions, and the biological characteristics including fecundity, sex ratio and ecology of host and parasitoid species. Therefore, recent growth in contributions on these subjects will contribute to the success in biological control applications and mass production of parasitoids. The objectives of this study were to assess age-dependent changes in fecundity and sex ratio of *Apanteles galleriae* and host-dependent fecundity and sex ratio of its hyperparasitoid *Dibrachys boarmiae*.

## 2 Material and methods

Laboratory colonies of *A. galleriae* and *D. boarmiae* were reared on early instar larvae of greater wax moth, *Galleria mellonella* and lesser wax moth, *Achoria grisella*. Pupae of *A. galleriae* reared on either host species were used as hosts for *D. boarmiae* to determine its host-related fecundity and sex ratio. Laboratory cultures of host, parasitoid and hyperparasitoid were established and maintained using the methods described in previous studies (GÜLEL, 1982; UÇKAN and GÜLEL, 2000). All host exposures, rearing and experiments were conducted in a rearing room at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity (RH), and a photoperiod of 12 : 12 h (L : D).

Studies on the relationship between parasitoid age and fecundity or female sex ratio were conducted by assigning a male and female pair (2–4-day-old) of *G. mellonella* or *A. grisella* in each of five 1-l jars. Either host pairs were held for 1 week in each jar and then removed. Total number of early instar larvae produced by a mated female host in 1 week was called one female equivalent host (FEH). Taking egg to larval developmental time into account, individual pairs (1 ♂, 1 ♀) of *A. galleriae* adults (= 1-day-old) were transferred to jars which contained one FEH on the eighth and tenth day of host placement for *A. grisella* and *G. mellonella*, respectively. Parasitoid pairs were kept together with one FEH for 1 week. After 1 week, parasitoid adults were transferred to a new jar containing one FEH. This process was repeated weekly until parasitoid females died. The number of males and females that emerged from each jar was recorded and converted to percentage of females. The weekly and total number of progeny of a single mated female and female sex ratio per week was determined. Results obtained from two host species were compared. In order to assess host-related variation in fecundity, pupae of *A. galleriae* developing on either host were placed individually in each of five glass tubes containing 50% honey solution for hyperparasitoid feeding. One male and one female *D. boarmiae* adult (1–3-day-old) was placed in each tube containing *A. galleriae* pupa and removed from tubes after 24 h. The number and sex ratio (% females) of *D. boarmiae* developing to the adult stage in these tubes were determined. All experiments using five jars and five glass tubes were repeated three times with specimens taken from different populations at different times.

One-way ANOVA with the least significant difference (LSD) *post hoc* test was used to test the effect of parasitoid age on male, female, and total number of progeny and sex ratio (% females) of *A. galleriae* reared on either host species (SAS INSTITUTE, 1987). Sequential *t*-tests were conducted to compare

age-related fecundity and female sex ratio between host species. We used the same analysis to test host-dependent male, female, and total number of progeny and sex ratio (% females) of *D. boarmiae* (SAS INSTITUTE, 1987). Data were transformed before analysis by taking the arcsine square root of the female sex ratio in each experimental group.

### 3 Results

The age-related variation in fecundity and sex ratio of *A. galleriae* on *G. mellonella* is shown in table 1. Mean numbers of total progeny per female significantly varied ( $F = 153.8$ ; d.f. = 4, 70;  $P < 0.0001$ ) in relation to parasitoid age (weeks) except for the first 2 weeks. Fecundity was relatively higher in the first 2 weeks with no significant difference ( $P > 0.05$ ). Similarly, female sex ratio was inversely related to age ( $F = 32.7$ ; d.f. = 4, 70;  $P < 0.0001$ ). Total number of progeny produced by a single mated female was 232.6 (100.5 ♀♀ and 131.3 ♂♂).

Table 2 gives age-related fecundity and sex ratio changes of *A. galleriae* on *A. grisella*. Fecundity was considerably high in the first 2 weeks. A significant decline was then recorded ( $F = 206.8$ ; d.f. = 5, 84;  $P < 0.0001$ ). Sex ratio became female unbiased as a function of age ( $F = 117.2$ ; d.f. = 5, 84;  $P < 0.0001$ ). The mean fecundity of a single mated female was 239.7 (106.8 ♀♀ and 132.6 ♂♂).

Total number of progeny produced by a single mated female did not differ significantly between host species ( $t = 0.31$ ; d.f. = 9;  $P = 0.38$ ). The highest fecundity was obtained in the second week on either

**Table 1.** Age-related fecundity and sex ratio of *Apanteles galleriae* reared on *Galleria mellonella*

Age (weeks)	Fecundity and sex ratio					
	Females		Males		Total progeny (mean ± SE)	Female sex ratio (%)
	Range	Mean ± SE	Range	Mean ± SE		
1	29–47	37.7 ± 1.2 a	30–52	37.1 ± 1.6 a	74.9 ± 2.1 a	50.4 a
2	30–42	35.7 ± 1 a	26–54	42.3 ± 2 b	78 ± 2.4 a	45.7 a
3	9–28	19.1 ± 1.1 b	21–38	30.3 ± 1.2 c	50.1 ± 2.3 b	38.6 a
4	0–19	6.4 ± 1.6 c	0–29	15.2 ± 2 d	21.6 ± 3.4 c	29.6 b
5	0–7	1.6 ± 0.6 d	0–18	6.4 ± 1.5 e	8 ± 2.1 d	20c

Numbers in columns followed by the same letter are not significantly different at  $P = 0.05$  (LSD test).

**Table 2.** Age-related fecundity and sex ratio of *Apanteles galleriae* reared on *Achoria grisellae*

Age (weeks)	Fecundity and sex ratio					
	Females		Males		Total progeny (mean ± SE)	Female sex ratio (%)
	Range	Mean ± SE	Range	Mean ± SE		
1	28–49	39.7 ± 1.7 a	25–57	35.8 ± 2.9 a	75.5 ± 3.3 a	52.7 a
2	30–73	43.4 ± 3 a	30–54	43.6 ± 1.8 b	87.7 ± 4.2 b	49.9 a
3	11–27	18.9 ± 1.2 b	19–49	35.3 ± 2 a	54.1 ± 2.5 c	34.8 b
4	0–18	4.5 ± 1.2 c	7–32	14.9 ± 1.6 c	18.8 ± 2.3 d	23.3 c
5	0–2	0.3 ± 0.2 d	0–7	3.2 ± 0.7 d	3.5 ± 0.8 e	9.3 d
6	–	–	0–1	0.1 ± 0.1 d	0.1 ± 0.1 e	–

Numbers in columns followed by the same letter are not significantly different at  $P = 0.05$  (LSD test).

**Table 3.** The fecundity and sex ratio of *Dibrachys boarmiae* reared on *Apanteles galleriae* pupae developed on either *Galleria mellonella* or *Achoria grisella*

Host type	Female (mean ± SE)	Male (mean ± SE)	Total progeny (mean ± SE)	Female sex ratio (%)
<i>G. mellonella</i>	2.2 ± 0.2 a	1.1 ± 0.2 b	3.3 ± 0.2 c	67.3 d
<i>A. grisella</i>	1.9 ± 0.1 a	1 ± 0.2 b	2.9 ± 0.2 c	65.1 d

Numbers in columns followed by the same letter are not significantly different ( $P > 0.05$ ).

host species. *Apanteles galleriae* did not produce a significantly different proportion of female progeny when reared on two different hosts ( $t = 0.62$ ; d.f. = 9;  $P = 0.30$ ).

The fecundity and sex ratio of *D. boarmiae* obtained from *A. galleriae* pupae reared on either *G. mellonella* or *A. grisella* are given in table 3. The fecundity of *D. boarmiae* was slightly higher when *A. galleriae* pupae were reared on *G. mellonella*. However, differences between mean female ( $t = 1.52$ ; d.f. = 28;  $P = 0.19$ ), male ( $t = 0.27$ ; d.f. = 28;  $P = 0.59$ ) and total progeny ( $t = 1.28$ ; d.f. = 28;  $P = 0.87$ ) were not significant. Female sex ratio did not differ significantly, either ( $t = 0.17$ ; d.f. = 28;  $P = 0.94$ ).

#### 4 Discussion

Our results demonstrating that total progeny production and sex ratio might vary depending on host species and female parasitoid age were also evidenced by studies conducted on other parasitoid species (MENDEL et al., 1987; ORR and BOETHEL, 1990; WONG et al., 1990; NEVASERO and ELZEN, 1992; MEDEIROS et al., 2000). Regardless of the type of host species, the mean fecundity of *A. galleriae* was inversely related to age. The effects of continuous host exposure to parasitoid, host suitability, host movement and parasitization success of the parasitoid could suggest an explanation for this result. On the other hand, other studies on this parasitoid demonstrated that fecundity and sex ratio varied, depending on the number of host, parasitoid and host-parasitoid (UÇKAN and GÜLEL, 1998, 1999). Total production of progeny for *A. galleriae* reached the highest level at the second week and rapidly decreased afterwards (tables 1 and 2). Similar results were reported for *D. boarmiae* (GÜLEL, 1982), *Allorhogas pyralophagus* (MELTON and BROWNING, 1986), *Anastatus semiflavus* (MENDEL et al., 1987), *Telenomus cristatus* (ORR and BOETHEL, 1990) and *T. calvus* (ORR et al., 1986). The decrease in parasitoid fecundity as a function of age may be due to the decreasing physiological activity related to ageing, number of eggs laid and parasitization capability of females. The declining fecundity period also varies with the type of species (MELTON and BROWNING, 1986; ORR and BOETHEL, 1990).

Parasitoid population density depends on host-parasitoid interactions. Sex ratio regulation depending on the presence and characteristics of host species is important in determining subsequent population density of parasitoids (VAN ALPHEN and VISSER, 1990). Generally, it has been determined that progeny sex

ratio is female biased during most of the fecundity plateau period, but becomes male biased during the declining fecundity period (ORR et al., 1986; MENDEL et al., 1987). The results obtained with *A. galleriae* were in conformity with this situation. The decrease in progeny sex ratio as the adult ages may stem from unfertilization of eggs due to depletion or degeneration of spermatozooids. The host-dependent change in the progeny sex ratio of *A. galleriae* was not significant (tables 1 and 2), and can be explained by a similar host suitability or preference of the females for either host species. The significant impact of maternal age on levels of offspring production and sex ratio along with the greatest fecundity occurring in the first 2 weeks regardless of host species might be of importance for mass rearing of this biological control agent.

The slight difference in the fecundity and female sex ratio of *D. boarmiae* may be related to the host size (table 3). This relation was also found in studies on other host species (GÜLEL, 1982). Fecundity of *D. boarmiae* reared on *A. galleriae* was low compared with that on *G. mellonella* and *A. grisella* pupae (GÜLEL, 1982). The slight difference in fecundity obtained when *A. galleriae* reared on the pupae of *G. mellonella* with respect to that of *A. grisella* can be explained by the rapid larval development and forming greater pupae of the former host species. The insignificant difference between female sex ratio on either host may result from similarity of hyperparasitoid age. Having a hyperparasitoid species exhibiting a high rate of age-dependent fecundity and a great reproductive potential (GÜLEL, 1982) like *D. boarmiae* may decrease the potential of *A. galleriae* for use in biological control programmes.

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**Authors' addresses:** Dr FEVZİ UÇKAN (corresponding author), Department of Biology, Faculty of Science-Art, Balıkesir University, Balıkesir, Turkey. E-mail: uckanf@balikesir.edu.tr; Prof. Dr ADEM GÜLEL, Department of Biology, Faculty of Science-Art, 19 Mayıs University, Samsun, Turkey.