

# Female reproductive strategy in the longhorned beetle *Corymbia rubra* (Coleoptera, Cerambycidae)

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This study investigated the reproductive strategy of females of the xylem-feeding longhorned beetle *Corymbia rubra* (Coleoptera: Cerambycidae). It documents the number of eggs, average body mass of newly hatched larvae, clutch mass and coefficient of variation of body mass of larvae. Moreover, it reports the length of the laying eggs period as well as a day during the reproductive season when female started laying eggs. *C. rubra* females were found to lay many eggs, compared to other cerambycid beetles. The body size of newly hatched larvae depends on female size, while fecundity and clutch mass do not but, on the contrary, negatively correlate with time progress in season. The study shows that reproductive strategy of a cerambycid female could be explained in terms of the optimality models for multiseasonal species.

Key words: clutch mass, fecundity, offspring size, optimal resource allocation, reproductive strategy.

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## INTRODUCTION

The optimal resource allocation theory assumes that living organisms, constrained by limited resource acquisition or energy expenditures (Weiner 1992) and mortality (Kozłowski 1992), allocate differently the surplus resources into growth, reproduction and repair (Kozłowski 2000) in order to maximise fitness (Roff 1992, Kozłowski 2000). However, fitness depends not only on the total amount of resources allocated to reproduction but on number of offspring reaching reproductive age. Thus, offspring size and number, the components of the female reproductive effort, depend on the amount of energy allocated, and are generally a function of female size (Stearns 1992, Honek 1993; but see also Klingenberg & Spence 1997). The female reproductive strategy is to divide finite resources among the number of offspring of certain sizes in a way that maximises its fitness, while the individual offspring

survival increases with the investment in it (Smith & Fretwell 1974). Different physiological stages as well as environmental factors may influence the female strategy (Stearns 1992, Honek 1993, Fox & Czesak 2000). Many authors point out the considerable unexplained variance observed in the reproductive patterns in insects (Honek 1993, Klingenberg & Spence 1997, Javoš & Tammaru 2004), indicating that the mechanisms here are still far from being well understood.

In a present study, the adult longhorned beetles *Corymbia rubra* (*Leptura rubra*) L. (Coleoptera: Cerambycidae) were collected in a field in order to achieve a laboratory culture of newly hatched larvae for further breeding, and the experiment was not planned directly for reproductive performance description. However, interesting findings were collected on female reproductive strategy and these data were analysed. The cerambycid beetle group is still poorly understood

in terms of its biology and life history strategies and thus even limited data on this subject is of great value.

Investigated were the traits such as the number of eggs and body mass of newly hatched larvae, in relation to female size, the length of the egg laying period and the day within the season when a female started laying eggs.

## MATERIAL & METHODS

The female of *Corymbia rubra* (*Leptura rubra*) (Linnaeus), a longhorn beetle, lays up to 700 eggs into holes already existing in a stem (Dominik & Starzyk 2004). Larvae spend their whole life inside partly decayed trees, mostly pine (Starzyk & Starzyk 1981). They moult several times, and after 1-3 years, although predominantly between 2-3 years, the larvae pupate and leave a tree as adults. In Poland, the reproductive period of that species lasts from late June to September (Dominik & Starzyk 2004).

*C. rubra* adults were collected in August 2004 and June–August 2005 in the Niepołomice Forest near Krakow, Poland, from a nylon net traps stretched out above the pine stumps (sealed firmly, so that only insects emerging from inside the stump could be collected), the remnants of the trees cut down in 1999 and 2001, and from Umbelliferae flowers in the forest. The traps were checked every 1–3 days during one (2004) or three (early, middle and late season, 2005) periods of about two-three weeks and the traps were left open between periods of capture. Additionally, some adults were obtained after eclosion from the larvae kept in a laboratory for about three months. Thus, three types of females were included in the analyses, (i) virgin females captured in the traps (N = 8), (ii) virgin females from the laboratory (N = 3) and (iii) females captured in field outside the traps and assumed to have not started egg-laying according to their behaviour in the forest, relatively long lives after capture and the large number of eggs laid in a laboratory (N = 3). It should be mentioned that ‘old’ females captured in the field were easily distinguishable as they laid very few or no eggs

and died quickly.

Females were paired with males found in the traps or in the forest and pairs were held outdoor in 1.8L plastic containers covered with nylon net, in shade. Adults were provided with fresh Umbelliferae flowers and water. Dead males were replaced with live ones, so some females could potentially mate with two males (N = 4). Firm pieces of pinewood cut from partly decayed stumps with the crevices removed with a penknife were used as oviposition sites. They were removed from the containers after the females’ death; all eggs were counted and transferred to Petri dishes containing moist gypsum to maintain humidity. The Petri dishes were maintained at a constant temperature of about 21°C (2004) and 24°C (2005) in a laboratory and checked daily for hatching. Larvae were weighed individually on the Sartorius supermicro balance (d = 0.0001 mg) no later than the second day after hatching. The body mass of newly hatched larvae was assumed to be equivalent to the egg mass (in the sample of N = 7 larvae, the egg shell constituted about 3% (CV = 0.13) of the egg mass). The length of a forewing (elytron) of a dead female was measured with millimeter paper and was considered a female body size measure. Moreover, dead females were dissected and all not laid eggs were counted.

The mean temperature in Krakow for the years 2004 and 2005, calculated from monthly means in the June-September period are  $17.1 \pm 2.4$  SD and  $17.4 \pm 2.1$  SD centigrades, respectively. The monthly mean temperatures are shown in Table 1.

The female reproductive parameters analysed included the number of eggs laid, sum of eggs (laid and not laid), average body mass of newly hatched larvae, coefficient of variation (CV) of larvae body mass and clutch mass, calculated as follows:  $\text{sum of eggs} \times \text{sum of body mass of weighed larvae} / \text{number of weighed larvae}$ .

The following covariates were included in the analyses: (i) approximate egg laying period (LEP), calculated as a period from the day when a

**Table 1.** The monthly mean temperatures (°C) for Krakow during the reproductive season of *C. rubra* in 2004 and 2005.

	2004			2005		
	Tmean	Tmax	Tmin	Tmean	Tmax	Tmin
June	17.2	22.6	12.6	17.3	22.8	12.2
July	18.6	24.3	14.1	20.0	26.1	14.9
August	18.9	25.3	14.2	17.5	22.9	13.3
September	13.6	20.3	9.2	14.9	22.1	10.0

female was paired with a male until the day before the female's death was observed, (ii) the day in season when a female was paired with a male (starting from 29th June when the earliest female was captured) and (iii) female size.

Data from the years 2004 and 2005 were analysed together. In total, 1617 larvae were weighed and the average of 34 (2–166) not laid eggs per female was found in 14 females. The data were analysed with the Statistica 6.1 package. Five multiple regression models were applied to determine the covariates' influence on the number of eggs, sum of eggs, average body mass of newly hatched larvae, clutch mass and CV of the larvae body mass.

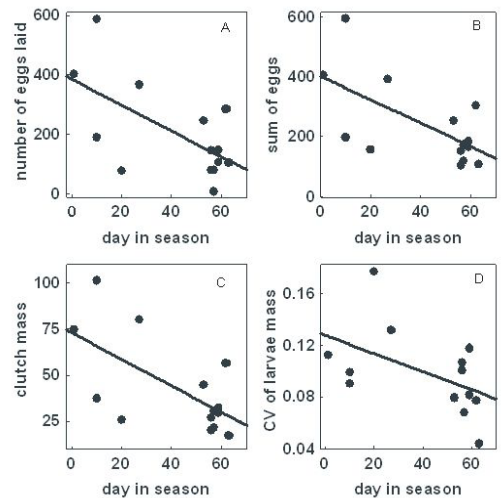
## RESULTS

*C. rubra* females laid on average 203 (CV = 0.79) eggs within a period of about 10 (CV = 0.44) days (LEP). However, the average number of eggs produced including the number of not laid eggs, was 236 (CV = 0.60). In one case a female laid only 8 eggs (two larvae hatched) and died after 9 days while 166 not laid eggs were found after its dissection. In other females the number of unlaidd eggs varied from 2 to 78 (mean = 23; CV = 1). The body mass of newly hatched larvae calculated from the means for females was 0.18 mg (CV = 0.07). Part of the eggs were destroyed during transfer to the Petri dishes but, as this was a random factor, it should not have affected the mean body mass of larvae. It was observed that almost 100% of the larvae from the eggs not destroyed hatched.

The LEP parameter could not be treated as the

exact female lifespan because traps were not checked each day and the exact moment of eclosion could vary from 1 to 3 days before capture. Also as to females obtained from the laboratory, their exact moment of eclosion was not known. In one case, a female laid eggs for only 2 days, which indicates that it would probably have been found in a laboratory several days after eclosion. Thus, LEP is only an approximation of a female imago lifespan.

The multivariate analyses show that (i) the number of eggs laid as well as egg production (sum of eggs) decreases significantly as the season progressed (Table 2, Figure 1A, B); (ii) clutch mass



**Figure 1.** The relationships between day in season (where day 1 = 29 June) and different reproduction parameters for *C. rubra*: number of eggs laid (A); sum of eggs (B); clutch mass (C) and coefficient of variation of larvae body mass (D).

**Table 2.** Results of the multivariate regression analyses of reproductive parameters in *C. rubra* beetle.

reproductive parameter	adjusted R <sup>2</sup>	P for covariates		
		female size	LEP	day in season
number of eggs laid	0.44	0.26	0.20	<b>0.02</b>
sum of eggs	0.47	0.16	0.27	<b>0.01</b>
body mass of larvae	0.20	<b>0.04</b>	0.58	0.42
clutch mass	0.51	0.09	0.33	<b>0.01</b>
CV of larvae mass	0.27	0.34	0.13	0.06

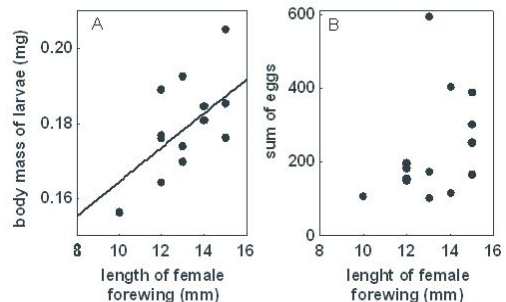
decreases with time progress in season (Table 2, Figure 1C), (iii) the CV of larvae body mass tends to decrease with time progress in season (Table 2, Figure 1D) and (iiii) the average body mass of newly hatched larvae increases with female size (Table 2, Figure 2A), while the egg production does not (Table 2, Figure 2B). Neither the female size nor LEP changed as the season progressed ( $p = 0.998$  and  $p = 0.697$ , respectively). LEP did not depend on female size ( $p = 0.462$ ).

**DISCUSSION**

The *C. rubra* females laid many eggs compared to other cerambycid species. In the other laboratory surveys, *Semanotus japonicus* laid 7–181 eggs (Kato et al. 2000), *Monochamus carolinensis* had, on average 220±99 SD, 138±90 SD and 116±77 SD eggs, depending on the quality of wood where the larvae had developed (Akbulut & Linit 1999) while *Anoplophora glabripennis* laid in China on average 25 eggs and in the USA 50–75 eggs (up to 170) (Keena 2002, Table 3). The trait distinguishing the three above mentioned species from *C. rubra* is the woody tissue that comprises a food source for newly hatched larvae. The recruits of *S. japonicus*, *M. carolinensis* and *A. glabripennis* all feed in the subcortical zone consuming mostly phloem and cambium, which are the most nutritious parts of a tree stem (Haack & Slansky 1987). The newly hatched larvae of *C. rubra* feed on xylem, the least nutritious and the most demanding tissue with regard to its digestion (Haack & Slansky 1987). The mixed strategy is represented by, e.g., *Cryocephalus rusticus*, the larvae of which start feeding under the bark and go deeper into the wood in the later stages (Dominik

1958). The potential number of eggs produced in *C. rusticus* females is up to 200 (Dominik 1958) and is closer to the number of the three cambium-feeding species. Another recognizable trait associated with the nutritional value of larval food is the development time of larvae which increases as food quality decreases (Table 3). Despite the lack of complete data on reproductive parameters of other cerambycid beetles, the interspecific trade-off between offspring mass and number could be observed when comparing *C. rubra* and *S. japonicus* (Table 3). A possible explanation for this could be that *S. japonicus* invests relatively more in each offspring because there is a stronger competition for the nutritious-rich phloem than for the nutritious-poor xylem.

The other feature of the reproductive strategy of *C. rubra* females is that the body mass of newly hatched offspring depends on female size, yet the progeny number does not but is, in contrast, negatively correlated with seasonal time progression. This was true for both



**Figure 2.** Body mass of larva (A) and sum of eggs (B) with relation to female size.

**Table 3.** Reproductive parameters for cerambycid species of phloem (inner bark)-feeders, cambium-feeders and xylem (wood)-feeders.

Species	Food source of larvae	Female body mass (mg)	Female lifespan (days)	Development (larvae)	Avg. no. of eggs	Mass of newly hatched larvae (mg)	References
<i>Monochamus carolinensis</i>	phloem and cambium	268	47	95 days	158	?	Akbulut & Linit 1999
<i>Semanotus japonicus</i>	phloem	189	?	1 year	94	0.4-1.4	Kato et al. 2000
<i>Anoplophora glabripennis</i>	cambium and xylem	1232.5	80	1-2 years	67	?	Keena 2002
<i>Corymbia rubra</i>	xylem	256	10.5	2-3 years	203	0.18	present study

fecundity measures: the number of eggs laid and the overall egg production (Table 2, Figure 1, 2). This finding was contrary to Honek (1993), who points out that, generally, there is a strong positive interspecific relationship between fecundity and female size in insects, which is a consequence of the limited available space inside the female body. He also writes that the slopes of egg size/female size regressions are lower than that of fecundity/female size. However, he observed that the differences in these patterns could be at least partly caused by differences in sources of energy allocated to reproduction: whether it is fixed in the larval stage or further determined in the adult stage. *C. rubra* seems to be a capital breeder (using stored energy for reproduction; Stearns 1992) as it lives relatively shortly as imago and females start laying eggs just after capture and copulation with a male (personal observations). On the contrary, long-lived subcortical cerambycid species (Table 3) could represent income breeders (organisms using energy acquired during reproductive period for reproduction; Stearns 1992), what could be supported by the fact that the females of *A. glabripennis* were found not to start ovipositing until the second week after hatching (Keena 2002). In *S. japonicus*, the fecundity/female size relationship is stronger than that of the

offspring size/female size (Kato et al. 2000) and, if this species was also an income breeder, the differences in the reproductive patterns between *S. japonicus* and *C. rubra* would corroborate Honek's hypothesis.

The fact that, despite similar sizes and LEPs, late females laid significantly fewer eggs than early ones, could be explained by the optimality models for organisms living in a seasonal environment (Kozłowski & Wiegert 1987, Kozłowski et al. 2004). These models predict that females that did not eclose early in the season face the 'dilemma' of eclosing late in the season, with impaired reproductive output or waiting with maturation to the next season, so running the risk of mortality during a hostile winter season. As a result, both decrease of reproductive allocation with season progress and variability of life cycle length should appear as is the case in *C. rubra*, which, as was mentioned before, fulfills its development within 2 or 3 years.

The season effect in the present study cannot be statistically separated from the year effect, but, as the whole development of the investigated species lasts up to three years, the year effect is unlikely. Additionally, the meteorological data for Krakow suggest that these two years were



similar with respect to temperature during the reproductive season (Table 1).

To conclude, the reproductive strategy of *C. rubra* females is being described in the present study. The females of this xylem-feeding species lay more eggs on average than those of cambium-feeding species. Moreover, female size was found to be a better predictor of body mass of newly hatched larvae than of fecundity. Finally, it is suggested that the female reproductive output changes as the season progresses, as females that eclosed late laid fewer eggs than those eclosing at the beginning of the season, which could be explained in terms of the optimality models for multiseasonal species.

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