

ARTICLE

# Fitness consequences of feeding-by-remating interactions in female *Cerambyx welensii* (Coleoptera: Cerambycidae: Cerambycinae)

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## Abstract

The longhorn beetle, *Cerambyx welensii* (Küster) (Coleoptera: Cerambycidae), is considered a critical factor in oak decline in southwestern Iberia, but populations vary over space and time, depending on several ecological factors. Adults feed on ripe fruits and tree exudates, and evidence suggests that feeding could impact fitness in hot, dry summers, especially under climate change. In the present study, we assessed the impact of adult feeding (sugar-fed, water-fed, or unfed) and remating (monandrous *versus* polyandrous) on female reproductive output. Lifetime fecundity increased with female size in most feeding–remating combinations. Sugar-fed females achieved the highest longevity and fecundity, unfed females the lowest, and water-fed females had intermediate values. The daily fecundity pattern was strongly dependent on female feeding. Longevity and fecundity of once-mated and remated females were similar in both unfed and water-fed groups; however, in sugar-fed females, remating enhanced fecundity and shortened life span. Preoviposition, oviposition, and postoviposition periods were distinctly affected by both diet and remating. Results show that females require sugar to maximise reproductive output and that a water supply may partially mitigate the fitness decline of unfed females. We conclude that female feeding must be considered to explain *C. welensii* spatio-temporal occupancy–abundance patterns in oak woodlands.

## Introduction

Cerambycids, the so-called longhorn beetles, constitute a large and diverse group whose adults display a wide range of feeding habits (Duffy 1953; Haack 2017) and reproductive patterns (Hanks and Wang 2017). Adult diets show adaptations often linked to their phylogenetic background. Most Prioninae and other basal taxa do not feed as adults, as indicated by their atrophied digestive tract. Most Lamiinae require obligate maturation feeding to successfully reproduce, mainly feeding on the foliage and tender bark of the plant used as a larval host but also on other living plants, dead bark, and even fungal fruiting bodies. Maturation feeding may affect pheromone production (Xu *et al.* 2021) and female reproductive output, which depend on host tree species (Smith *et al.* 2002; Fujiwara-Tsujii *et al.* 2016). In the Cerambycinae, feeding habits and regimes appear to be more variable, including diets of mostly plant exudates, sapflows, mature fruits, and flowers (pollen and nectar), although some species feed on leaves or do not feed at all, and one genus, *Elytroleptus* Dugés (Coleoptera: Cerambycidae), has predatory habits (Duffy 1953; Linsley 1959; Švácha and Lawrence 2014; Haack 2017; Hanks and Wang 2017; Monné *et al.* 2017).

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*Cerambyx welensii* (Küster) (Coleoptera: Cerambycidae) and *Cerambyx cerdo* Linnaeus (Coleoptera: Cerambycidae) are two large sapro-xylophagous sympatric longhorn beetles in the Cerambycinae subfamily. Larvae bore into the living wood of healthy and decayed host trees (Bense 1995; Buse *et al.* 2007; Torres-Vila *et al.* 2017a). Both species have usually been reported as polyphagous (Picard 1929; Villiers 1978; Bense 1995; Vives 2000), but larval host trees other than oaks are currently considered unusual (Miroshnikov 2009; Torres-Vila *et al.* 2017a), a fact in line with the narrow host range characterising primary saproxylics (Speight 1989; Grove 2002). The impact of these longhorn species on oak woodlands has increased alarmingly in the last decades in Mediterranean areas and particularly in southwestern Iberia (Torres-Vila *et al.* 2022). Oak damage has typically been attributed only to *C. welensii*, but prior research shows that this attribution is not realistic (Torres-Vila 2017). As a consequence, both wood-borers are considered a critical factor in oak decline and a threat to the long-term conservation of oaks when the beetles' populations are excessive (González *et al.* 2010; Domínguez *et al.* 2022; Torres-Vila *et al.* 2022, 2023).

Longhorn beetle populations can fluctuate to a great extent in space and time, depending on multiple ecological factors (Torres-Vila *et al.* 2022, 2023). A trophic factor, often documented but unstudied in *C. welensii* and *C. cerdo*, involves adult feeding, which could critically impact longhorn beetle populations, especially in Mediterranean areas with hot and dry summers. Several reports and our own field observations show that *C. welensii* and *C. cerdo* adults often feed on the juice of ripe fruits, tree exudates, and sapflows, either from their hosts or other trees. Adults do not visit flowers as some congeneric species do and have never been reported feeding on leaves, shoots, or bark. The frequency and abundance of food and water sources available for longhorn beetles in oak forests during the summer may vary significantly between sites and years, depending on silvicultural practices and weather patterns. A major water source comes from occasional late-spring and early summer storms, with adult beetles drinking the rainwater deposited on the foliage and branches of trees. Rainwater may last for long periods of time when it collects in tree cavities, making it an important summer water source. Water in tree cavities may include nutrients from accumulated organic matter (typically leaf litter) and chemicals from stemflow water (Petermann and Gossner 2022). Dew may occasionally provide water during the summer in humid, cool, or elevated oak woodlands.

The main sugar sources for beetles are tree exudates and sap, particularly from oaks (Duffy 1953; Hellrigl 1974; Buse *et al.* 2007). These oak secretions usually come from poorly healed pruning or cork-harvest wounds and wet or bleeding cankers caused by bacteria; their prevalence may depend largely on the present and past silvicultural management of a forest stand. Furthermore, in some years, presumably because of bacterial alteration or physiological imbalances in oak trees, abundant exudates or guttations, the so-called honeydew, may be secreted in late spring and summer by immature acorns through cupule-nut insertion (Vázquez *et al.* 2000). Oak honeydew appears to be a phloem derivative because it includes sugars (sucrose, glucose, fructose), amino acids, proteins, and phenols (Kevan *et al.* 1983), making it a potential and previously unrecognised dietary source for longhorn beetles. Ripe and overripe fruits, mainly from natural and cultivated rosaceous shrubs and trees, are widely mentioned in historical and modern literature as a food source for *Cerambyx* adults (Mayet 1881; Picard 1929; Mendizábal 1944; Duffy 1953; Colas 1972; Hellrigl 1974; Villiers 1978; López-Pantoja *et al.* 2008), but they are scarce or unavailable in oak forests, particularly in the open oak woodlands of southwestern Spain.

In recent years, climate change impacts have been increasing in Spain, with more frequent and more intense heat waves that are often associated with episodes of extreme drought. For example, in the year 2022, several heat waves occurred in our study area (Extremadura, southwestern Spain), with maximum temperatures surpassing 40 °C over 12–14 days (as warm as 45 °C on some days) and only 2–5 mm of accumulated precipitation over four months (May–August). Under these extreme weather conditions, both direct rainwater and water-filled tree holes were absent, and oak sapflows became crystallised and inaccessible as food for adult beetles. Based on these

conditions, it follows that the availability of water and carbohydrates in oak woodlands is rather unpredictable in space and time in Mediterranean areas, especially under climate change as currently experienced and particularly during late spring–summer, when adult longhorn beetles are active.

Lack of food over long periods of time in insect species requiring a nutritional supply in the adult stage (the so-called income breeders) often constrains the insects' reproductive output and results in early death. A countermeasure that adult insects often employ when faced with starvation is to reduce reproductive investment in order to increase somatic maintenance and life expectancy (Zhang *et al.* 2019). Previous research has shown that remating (*i.e.*, multiple mating) does not affect fecundity in *C. welensii* and *C. cerdo* when females have access to a sugar source (Torres-Vila *et al.* 2016; Torres-Vila 2017). However, it has been proposed that remating may provide a fitness benefit to food-stressed females (Parker *et al.* 2013; Torres-Vila *et al.* 2016) if they can make up the feeding-derived shortfall through male-transferred seminal fluids acquired during mating as male donations or nuptial gifts (Vahed 1998; Arnqvist and Nilsson 2000; Fedorka and Mousseau 2002; Torres-Vila *et al.* 2004).

The objectives of the current study, which uses *C. welensii* as a model species, were twofold: (1) to evaluate the impact of food shortage on female reproductive output and (2) to explore whether male donations at the time of mating could counteract nutritional deficits in this polyandrous species.

## Material and methods

### Study species

*Cerambyx welensii* is univoltine in May–August, peaking in June, although the timing of emergence and peak flight fluctuates between years and sites, depending on weather. Adult diel activity is largely crepuscular and nocturnal. Adults are highly polyandrous (females mate multiple times) and polygynous (males mate multiple times; Torres-Vila *et al.* 2016). After mating, females lay eggs singly or in small groups into cracks, pruning cuts, and wounds in bark. Eggs hatch in about two weeks, and neonates bore through the bark and initiate feeding in the outer sapwood. As the larvae grow, they enter the heartwood, making increasingly wide and long galleries that extend through the host tree's trunk, main branches, and roots and cause significant physiological, mechanical, and structural damage to the host tree. Larvae develop for 2–4 years. Upon reaching maturity, they pupate in late summer or early autumn in a pupal cell excavated inside the host's wood. After about a month, the adult emerges but overwinters inside the pupal cell in a prereproductive stage. The following spring, the adult leaves the tree through an exit hole and reinitiates its life cycle. Adult longevity in the wild ranges from two to three weeks and up to two months, although longer lifespans (4–5 months) have been recorded in the laboratory (Torres-Vila *et al.* 2012, 2013, 2016, 2017b).

### General procedures

The *C. welensii* adults used in the study were collected from oak woodlands in the Extremadura region (southwestern Spain) during October–April, when they were overwintering inside their pupal cells in the wood of host trees, which ensured adults were virgins. Collections were made as part of a prior investigation dealing with the larval distribution and assemblage of large saproxylic cerambycids in oak trees (Torres-Vila *et al.* 2017a), mainly holm (*Quercus ilex* Linnaeus), cork (*Q. suber* Linnaeus), and Pyrenean oak (*Q. pyrenaica* Willdenow) (Fagaceae). We mostly sampled main branches that had recently fallen as a result of wind. These were cut with a chainsaw, and the resulting bolts dissected with metal wedges and a sledgehammer and examined for *C. welensii* adults. Field-collected adults were taken to the laboratory, arranged separately in plastic containers, and kept in the dark in a refrigerator (6–10 °C) until they completed overwintering.

In mid-May, adults were removed from the refrigerator and held singly in rolls of laboratory blotting paper (15–20 mm diameter, 21 cm long) that simulated a pupal cell. The paper roll diameter was adjusted so that adults were held neither too loosely nor too tightly. Paper rolls with overwintering adults inside were sealed on both ends with staples, arranged horizontally in cardboard racks (head facing out), placed in emergence cages by sex to avoid unnoticed matings at emergence, and held in a controlled environmental chamber to complete sexual maturation. Emergence cages were lightly sprayed with water to avoid excessive adult dehydration and checked every 2–3 days or daily after the first emergence occurred. Upon reaching sexual maturity, the adults pierced the paper tube at the head-facing end and emerged as they would in a tree pupal cell in the wild. The day of emergence was considered “day 0” for female age estimates. Emerged adults were measured to the nearest millimetre and individually marked by sex with correlative numbers.

We used 16-L cardboard cages with transparent covers as mating and oviposition chambers. The same cage was assigned to each tested female throughout her lifetime to prevent handling errors. Males were kept singly in well-aerated 240-mL clear plastic containers when they did not share cages with females during mating. Unlike females, all males were fed *ad libitum* with a saturated sucrose–water paste. Cork oak wood disks (70–80 mm diameter, 20 mm thick) were provided as egg-laying substrates within the cages. The cork layer was detached from the cambium with a penknife, replaced in the same position, and held in place with a rubber band, which facilitated daily inspections and egg removal. Ovipositing females seem to find the small space between the cambium and cork layer extremely attractive, with most eggs found in the space (Torres-Vila *et al.* 2016). All tests were performed in a controlled environmental chamber at  $25 \pm 1$  °C,  $60 \pm 10\%$  relative humidity, and a 15 + 1-hour:8-hour light:dark photoperiod. The first 15 photophase hours were maintained at 1000 lux luminosity, and the light levels were lowered to 25 lux for the last hour to simulate dusk. Laboratory tests were conducted in the summer, coinciding with the presence of active adults in the field. For more information on general procedures, see Torres-Vila *et al.* (2016).

### Female experimental groups

To study the effects of feeding, remating, and their interaction on *C. welensii* female reproductive output, we formed six random experimental groups resulting from the combination of both treatments. Adults obtained from different host tree species were randomly assigned to each experimental group. We used three feeding regimes – unfed (starved), water-fed, and sugar-fed females – and two (re)mating protocols – once-mated (monandrous) and remated (polyandrous) females. Feeding regimes were maintained throughout a female’s lifetime as follows: unfed females were maintained in strict fasting; water-fed females were allowed to drink water *ad libitum*; and sugar-fed females were allowed to feed *ad libitum* on a saturated sucrose–water paste. Water and sugar paste were provided within the cages in Petri dishes (9 cm diameter), which were replaced every 2–3 days.

For the mating protocol, we proceeded as described in Torres-Vila *et al.* (2016). All females were allowed to mate 1–3 days after emergence, with two males being caged with each female 15 minutes before the onset of artificial dusk. When mating occurred, the unmated male was removed immediately from the cage to prevent male fights, leaving the pair-bonded adults in the cage. The mated male was removed the next morning when mating was completed, leaving the female isolated in its cage. When mating was unsuccessful, the protocol was repeated the next day.

Females allocated to the monandrous groups were kept isolated in their cages for life, whereas, in the polyandrous groups, new males were regularly added and removed, as explained above, every 3–4 days throughout the female’s lifetime. As the number of males needed to complete the mating routine in the polyandrous groups was large, males were typically reused. However, in order to maintain their vigour, they were given at least 4–5 days of rest, as well as food, between matings. Additional field-captured males were also used. Matings were always observed at dusk

**Table 1.** Sample sizes and mean lifetime number of matings per female *Cerambyx welensii* in each experimental group, according to feeding regime and remating

Feeding regime	Monandrous		Polyandrous	
	Female number	Mating number mean $\pm$ SE [range]	Female number	Mating number mean $\pm$ SE [range]
Unfed	17	1.0 $\pm$ 0.0 [1–1]	15	3.9 $\pm$ 0.3 [3–6]
Water-fed	20	1.0 $\pm$ 0.0 [1–1]	15	8.4 $\pm$ 0.6 [6–13]
Sugar-fed	24	1.0 $\pm$ 0.0 [1–1]	20	18.2 $\pm$ 1.1 [9–26]
Total	61		50	

SE, standard error of the mean.

and, if necessary, also in the scotophase using a small red LED flashlight. The experiment ended when all the females being tested died. Table 1 notes sample sizes and the mean lifetime number of matings per female in each tested group. Voucher specimens of *C. welensii* from the Extremaduran populations used in the present study (codes SSV\_WP) are deposited in the entomological collection of the Plant Health Service at Mérida, Junta de Extremadura, Spain.

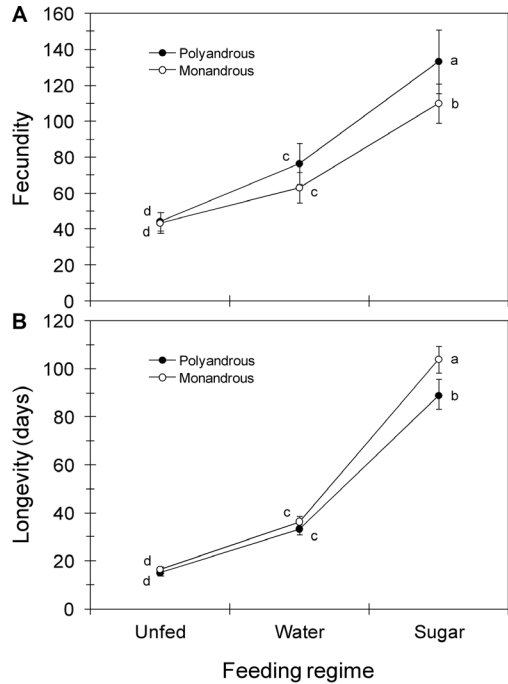
The wood disks were inspected daily, and any eggs laid on or in the disks were carefully detached, counted, stored by date in well-aerated 30-mL plastic vials, and incubated at 25 °C. A number of variables were noted in order to describe the reproductive output of females in each feeding/remating combination: lifetime fecundity (total eggs), daily fecundity, fertility (% hatched eggs), preoviposition period (elapsed time between mating and first oviposition), oviposition period (time between first and last oviposition), postoviposition period (time between last oviposition and female death), and longevity.

### Statistical analyses

The variables involved in female reproductive output (mostly semiquantitative) that were studied were usually not normally distributed after a preliminary Shapiro–Wilk test. Because of that, generalised linear models were used to assess the effects of feeding and remating as explanatory variables. Generalised linear models using Poisson distribution with log-link were computed in all instances except with fertility, for which a generalised linear model using binomial distribution with logit-link was selected. Poisson and binomial family errors were tested for over- and under-dispersion, and residual plots were checked to verify the assumptions of the fitted models. Analysis of deviance (Type II Wilks' likelihood-ratio test [LR Chi<sup>2</sup>]) was used to assess the effects of feeding, remating, and their interaction on the reproductive variables studied. *Post hoc* Tukey contrasts ( $|z|$  values,  $P < 0.05$ ) were completed when necessary to establish homogeneous groups among the six feeding/remating combinations. Female size (body length) was included in the model analysing fecundity to control for a potential hidden effect of female size. This precaution was taken even if a preliminary analysis showed no significant differences in mean female size among groups (feeding: LR Chi<sup>2</sup> = 1.93,  $df = 2$ ,  $P = 0.38$ ; remating: LR Chi<sup>2</sup> = 0.16,  $df = 1$ ,  $P = 0.69$ ; feeding  $\times$  remating: LR Chi<sup>2</sup> = 1.53,  $df = 2$ ,  $P = 0.47$ ). Lastly, linear regression analysis was used to compare the correlations between lifetime fecundity and female size in the six feeding/remating combinations. All statistics were computed with R (R Core Team 2021).

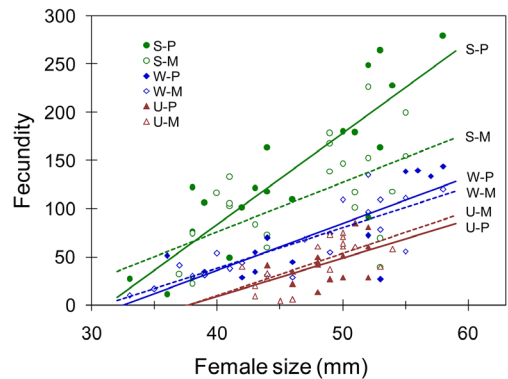
### Results

Lifetime fecundity was significantly affected by feeding (LR Chi<sup>2</sup> = 1758.75,  $df = 2$ ,  $P < 0.001$ ) and remating (LR Chi<sup>2</sup> = 53.95,  $df = 1$ ,  $P < 0.001$ ) when controlling for female size



**Figure 1.** Effect of feeding regime and remating (monandrous vs. polyandrous) on either **A**, lifetime fecundity or **B**, longevity (mean ± standard error) in female *Cerambyx welensii*. Different lowercase letters in each graph show significant differences among the six feeding/remating combinations after a *post hoc* Tukey contrast. See text for a full statistical analysis.

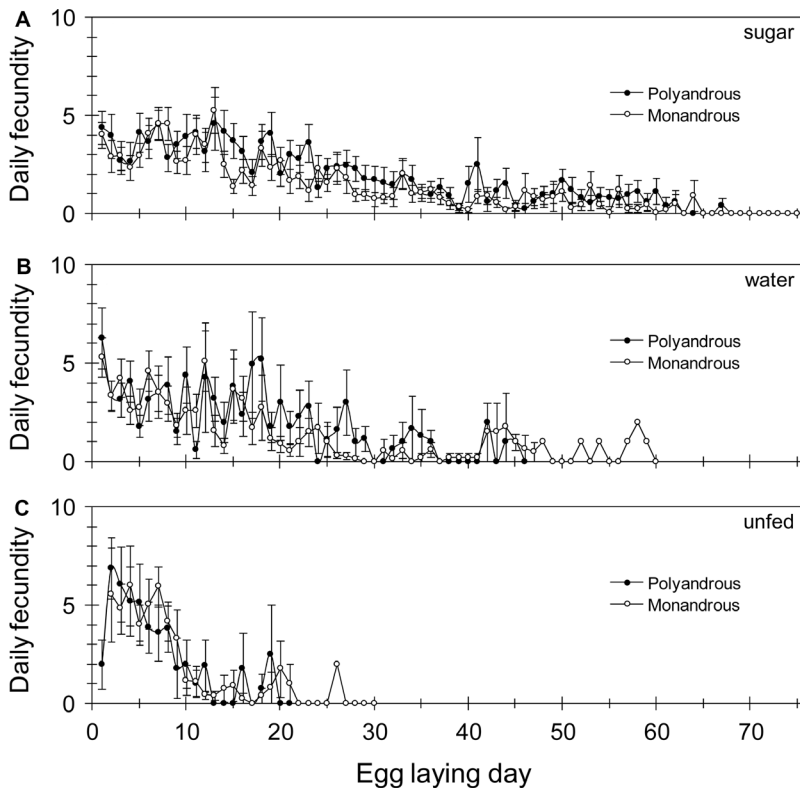
**Figure 2.** Correlations between female size (body length, mm) [*x*] and lifetime fecundity [*y*] in female *Cerambyx welensii* depending on each combination between feeding regime and remating. Feeding regimes: unfed (U), water-fed (W), and sugar-fed (S); remating: monandrous (M) and polyandrous (P). Regression lines and statistics for each feeding/remating combination were:  
 S-P:  $y = 9.44x - 294.02$ ,  $R^2 = 0.73$ ,  $F_{1,18} = 49.29$ ,  $P < 0.001$ ;  
 S-M:  $y = 5.13x - 128.94$ ,  $R^2 = 0.33$ ,  $F_{1,22} = 10.97$ ,  $P < 0.01$ ;  
 W-P:  $y = 4.87x - 158.91$ ,  $R^2 = 0.61$ ,  $F_{1,13} = 20.27$ ,  $P < 0.001$ ;  
 W-M:  $y = 4.20x - 129.84$ ,  $R^2 = 0.69$ ,  $F_{1,18} = 40.16$ ,  $P < 0.001$ ;  
 U-P:  $y = 3.96x - 149.12$ ,  $R^2 = 0.22$ ,  $F_{1,13} = 3.71$ ,  $P = 0.08$  ns;  
 and U-M:  $y = 4.38x - 165.61$ ,  $R^2 = 0.44$ ,  $F_{1,15} = 11.87$ ,  $P < 0.01$ .



(LR  $\chi^2 = 1487.34$ ,  $df = 1$ ,  $P < 0.001$ ), but a feeding  $\times$  remating interaction was also observed (LR  $\chi^2 = 33.21$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 1A). A *post hoc* test among the six feeding/remating combinations showed that, in both monandrous and polyandrous groups, sugar-fed females achieved the highest fecundity, unfed females achieved the lowest, and water-fed females displayed intermediate values (Fig. 1A). The fecundity of monandrous and polyandrous groups was similar in unfed and water-fed females, but among sugar-fed females, fecundity was higher in polyandrous females (Fig. 1A). Figure 2 illustrates how the correlations between female size and lifetime fecundity change depending on the feeding regime and remating experienced by *C. welensii* females. Fertility ( $70 \pm 2\%$  hatched eggs) was unaffected by either feeding (LR  $\chi^2 = 0.45$ ,  $df = 2$ ,  $P = 0.80$ ), remating (LR  $\chi^2 = 0.48$ ,  $df = 1$ ,  $P = 0.49$ ), or their interaction (LR  $\chi^2 = 0.64$ ,  $df = 2$ ,  $P = 0.73$ ).

The daily fecundity pattern clearly tended to decrease with female age in all experimental groups, but the declining pattern depended on the feeding regime, which was consistent with the

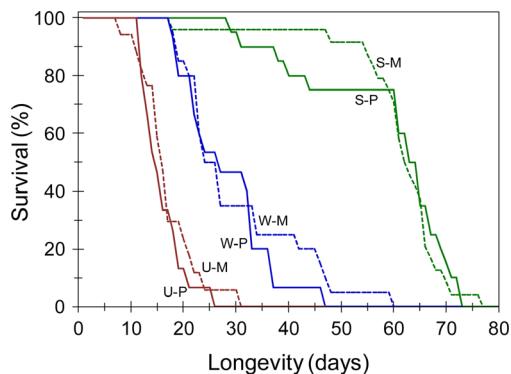




**Figure 3.** Effect of feeding regime (**A**: sugar-fed, **B**: water-fed, **C**: unfed) and remating (monandrous versus polyandrous) in female *Cerambyx welensii* on daily fecundity (mean  $\pm$  standard error) depending on egg-laying day. See text for a full statistical analysis.

lifetime fecundity values shown above. The egg-laying decline was much more pronounced in unfed females than in sugar-fed females, with water-fed females showing an intermediate pattern (Fig. 3). These data were analysed by pooling weekly the daily fecundity values over the first four weeks, the period in which data were available in all three feeding groups. A preliminary generalised linear model of the effects of feeding, remating, and week on daily fecundity showed no feeding  $\times$  remating interaction, so remating data were pooled. Analyses showed that daily fecundity depended on feeding (LR  $\text{Chi}^2 = 437.61$ ,  $df = 2$ ,  $P < 0.001$ ) and week (LR  $\text{Chi}^2 = 1550.97$ ,  $df = 3$ ,  $P < 0.001$ ) but also on a feeding  $\times$  week interaction (LR  $\text{Chi}^2 = 1191.47$ ,  $df = 6$ ,  $P < 0.001$ ), supporting the hypothesis that egg-laying decline was strongly dependent on feeding regime (Fig. 3). Additional analyses comparing within-week feeding regimes showed that in the first week, daily fecundity was similar between sugar-fed and water-fed females (Tukey test,  $|z| = 0.96$ ,  $P = 0.60$ ), but unfed females displayed significantly higher daily fecundity than either water-fed ( $|z| = 4.65$ ,  $P < 0.001$ ) or sugar-fed females ( $|z| = 5.86$ ,  $P < 0.001$ ), which was an unexpected result. Over the next three weeks, the daily fecundity of unfed females was always significantly lower than that of either water- or sugar-fed females (all cases  $|z| > 6.08$ ,  $P < 0.001$ ; Fig. 3).

Longevity was significantly affected by feeding (LR  $\text{Chi}^2 = 2695.50$ ,  $df = 2$ ,  $P < 0.001$ ) and remating (LR  $\text{Chi}^2 = 27.18$ ,  $df = 1$ ,  $P < 0.001$ ), with no feeding  $\times$  remating interaction observed (LR  $\text{Chi}^2 = 1.58$ ,  $df = 2$ ,  $P = 0.46$ ; Fig. 1B). A *post hoc* test showed that, in both monandrous and polyandrous groups, sugar-fed females lived longer than unfed females, and water-fed females reached intermediate longevity. The longevity of monandrous and polyandrous groups was



**Figure 4.** Survival rate (%) versus longevity (Kaplan-Meier curves) in female *Cerambyx welensii* depending on each combination between feeding regime and remating. Feeding regimes: unfed (U), water-fed (W), and sugar-fed (S); remating: monandrous (M) and polyandrous (P).

similar in unfed and water-fed females, but within sugar-fed females, monandrous females lived longer than polyandrous ones (Figs. 1B and 4).

Preoviposition period depended on feeding regime (LR  $\chi^2 = 30.05$ ,  $df = 2$ ,  $P < 0.001$ ) but not on remating (LR  $\chi^2 = 0.48$ ,  $df = 1$ ,  $P = 0.49$ ), with no feeding  $\times$  remating interaction observed (LR  $\chi^2 = 0.66$ ,  $df = 2$ ,  $P = 0.72$ ). The six feeding/remating combinations were subjected to a *post hoc* test, which produced the homogenous groups given in Figure 5A. Interestingly, the preoviposition period was significantly shorter in unfed females than in sugar-fed females, whereas water-fed females displayed transitional values (Fig. 5A).

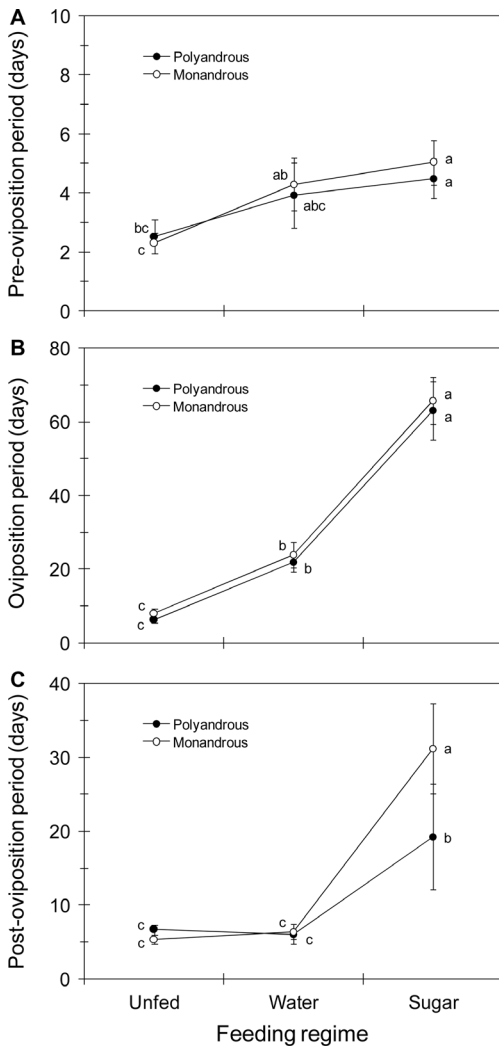
Oviposition period depended on feeding (LR  $\chi^2 = 2092.98$ ,  $df = 2$ ,  $P < 0.001$ ) and marginally on remating (LR  $\chi^2 = 4.05$ ,  $df = 1$ ,  $P < 0.05$ ), with no feeding  $\times$  remating interaction observed (LR  $\chi^2 = 2.89$ ,  $df = 2$ ,  $P = 0.24$ ). A *post hoc* test showed that the oviposition period in sugar-fed females was significantly longer than in water-fed females, and that this in turn was significantly longer than in unfed females (Fig. 5B).

Postoviposition period depended on feeding (LR  $\chi^2 = 727.75$ ,  $df = 2$ ,  $P < 0.001$ ), remating (LR  $\chi^2 = 40.05$ ,  $df = 1$ ,  $P < 0.001$ ) and feeding  $\times$  remating interaction (LR  $\chi^2 = 24.38$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 5C). A *post hoc* test showed that, in both monandrous and polyandrous groups, sugar-fed females displayed longer postoviposition periods than unfed and water-fed females did. However, within sugar-fed females, the postoviposition period was significantly longer in monandrous than in polyandrous females (Fig. 5C). Lastly, the postoviposition period was not significantly different between unfed and water-fed females, irrespective of remating (Fig. 5C).

## Discussion

Our results show that *C. welensii* female reproductive output is extremely sensitive to food shortages and starvation. Even so, unfed females were able to mate and reproduce successfully, although their reproductive fitness was dramatically affected. In relation to unfed females, water-fed females increased lifetime fecundity (1.5–1.7 times), longevity (2.2–2.3 times), and oviposition period (3.0–3.6 times), whereas sugar-fed females further increased lifetime fecundity (2.6–3.0 times), longevity (6.0–6.5 times), and oviposition period (8.3–10.5 times). Unlike fecundity, percent fertility was unaffected by either feeding regime or remating. Note that because experiments were conducted at a relative humidity of about 60%, dehydration stress was not severe. Under more desiccating conditions, reproductive output in unfed females would be even lower due to water loss through respiration and evaporation not compensated by drinking (Simmons *et al.* 2023). Fecundity and longevity are also improved with adult feeding in other cerambycine beetles such as *Phoracantha semipunctata* (Fabricius) (Coleoptera: Cerambycidae), *Phoracantha recurva* Newman (Coleoptera: Cerambycidae) (Millar *et al.* 2003), and *Aromia bungii* (Faldermann) (Coleoptera: Cerambycidae) (Russo *et al.* 2020). As expected, fecundity





**Figure 5.** Effect of feeding regime and remating (monandrous vs. polyandrous) on **A**, preoviposition, **B**, oviposition, or **C**, postoviposition period (mean  $\pm$  standard error) in female *Cerambyx welensii*. Different lowercase letters in each graph show significant differences among the six feeding/remating combinations after a *post hoc* Tukey contrast. See text for a full statistical analysis.

showed a close positive correlation with female size (Torres-Vila *et al.* 2016), although regression lines depended on feeding regime and remating. A positive correlation between fecundity and female size is widespread in insects (Honěk 1993), specifically in longhorn beetles, including both lamiines (Lawrence 1990; Togashi 1997, 2007; Keena 2002; Togashi *et al.* 2009) and cerambycines (Iwabuchi 1988; Matsumoto and Irianto 1998; Wang *et al.* 1998, 2002; Kato *et al.* 2000; Torres-Vila *et al.* 2016; Torres-Vila 2017; Russo *et al.* 2020).

Daily fecundity decreased with female age, in line with previous research (Torres-Vila *et al.* 2016). However, daily fecundity decline was exacerbated by a food limitation, which resulted in shorter oviposition periods. Remarkably, following mating, unfed females displayed both shorter preoviposition periods and higher daily fecundity than did water- and sugar-fed females. These physiological responses suggest that, when *C. welensii* females face a food shortage, they respond by accelerating egg production, possibly anticipating a short life expectancy. The postoviposition period was quite short in both unfed and water-fed females (about 5 days), lengthening substantially in sugar-fed females and less in polyandrous (4 $\times$ ) than in monandrous females (6 $\times$ ). Hence, unfed and water-fed females oviposited practically for all their lifespan, whereas sugar-fed females showed a more or less long period late in life in which egg laying was

fully arrested. These results suggest a mismatch between somatic and reproductive reserves in laboratory female beetles when food is plentiful, because natural selection in the wild is expected to maximise fitness by balancing oviposition period and female lifespan (Rosenheim *et al.* 2008).

Carbohydrates are a major source of fuel for insects and play a central role in the metabolism and energy budget (Zhang *et al.* 2019). Results show that *C. welensii* females are able to use carbohydrates as an energetic resource, pointing out the presence of the digestive enzyme  $\alpha$ -glucosidase, involved in the catabolism of a number of saccharides (Cavallini *et al.* 2023). A source of carbohydrates is essential for *C. welensii* females to reach their potential fitness, although water is capable of partially mitigating a lack of sugar. As a result, water-fed females usually reached intermediate reproductive values between unfed and sugar-fed females. In contrast, in lamiine longhorns, which usually require maturation feeding (Lu *et al.* 2013), and in a buprestid beetle (López and Hoddle 2014), both unfed females and water-only-fed females typically laid no eggs.

Regarding the effect of *C. welensii* female remating and its interaction with the feeding regime, our results show that sugar-fed females were less fecund and lived longer when mated once than when remated. These results are not consistent with a previous study in which remating had no significant effect on the lifetime fecundity and longevity of sugar-fed females (Torres-Vila *et al.* 2016). The contradictory results could derive from the fact that, in the present study, we compared two groups of sugar-fed females that greatly differed in mating number (once-mated *versus* 18-times mated on average; range 9–26 times). Fecundity and longevity differences were detected only in sugar-fed females and not in unfed or water-fed females, which was contrary to our expectations that, if male ejaculates had a nutritional effect, it would be more evident in food-stressed females. That hypothesis is fulfilled in the moth, *Yponomeuta cagnagella* (Hübner) (Lepidoptera: Yponomeutidae), in which honey-fed females always produce more eggs than unfed females, but fecundity differences between unfed and fed females are much greater if females only mate once (Parker *et al.* 2013).

There were no fecundity differences between once-mated and remated females (either unfed or water-fed), and a lower fecundity (about 18%) in once-mated females than in remated ones (sugar-fed). These results could derive from the higher acquisition of material benefits by sugar-fed remated females *via* male donations, as a result of these females having more mating opportunities as they lived longer. However, factors other than nuptial gifts may account for increased fecundity, including no sperm limitation, male-transferred accessory substances, mechanical stimulation, or even cryptic female choice (Arnqvist and Nilsson 2000; Torres-Vila *et al.* 2004; Gwynne 2008; Torres-Vila 2013). The impact of remating on fecundity in cerambycids is still imprecise, with few studies available. For instance, in *Tetraopes tetraophthalmus* (Forster) (Coleoptera: Cerambycidae) (Lawrence 1990) and *Oemona hirta* (Fabricius) (Coleoptera: Cerambycidae) (Wang *et al.* 1998), a positive correlation has been reported between polyandry and fecundity, but such a relationship is lacking in *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae) (Iwabuchi 1988), *P. semipunctata* (Bybee *et al.* 2005), *Glenea cantor* (Fabricius) (Coleoptera: Cerambycidae) (Lu *et al.* 2013), and *C. cerdo* (Torres-Vila 2017), whereas in *C. welensii*, we found apparently contradictory results between a previous study (Torres-Vila *et al.* 2016) and this study. A large array of biological, behavioural, and environmental traits may drive differences in remating-mediated reproductive output and fitness among species (or populations) within a group as diverse as the longhorn beetles.

In summary, our results indicate that *C. welensii* females require a sugar supply to maximise their reproductive output, although a water supply may partially mitigate the strong decline in reproductive output of unfed females. Therefore, the availability of a feeding or drinking source (interacting with female remating) must be considered as a main factor to explain the spatio-temporal occupancy–abundance patterns of these longhorn beetles in the wild, particularly in highly unpredictable Mediterranean habitats.

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