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Benefits of extended maternal care in a mass-provisioning bee at the cusp of sociality

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Many invertebrates exhibit parental care, posited as a precursor to sociality. For example, solitary foundresses of the facultative social orchid bee *Euglossa viridissima* guard their brood for 6+ weeks before offspring emerge, when the nest may become social. Guarding comes at the fitness cost of foregoing the production of additional offspring. Yet it is unclear whether guarding (extended maternal care) can enhance offspring survival such that it outweighs those fitness costs, or if it is a consequence of the selective benefits of sociality, including extended female longevity. Experimental removal of solitary foundresses from nests of *E. viridissima* revealed an immediate fitness loss: decreased offspring survival. A mathematical model exploring the trade-off between extended maternal care versus non-guarding revealed that extended maternal care is immediately advantageous to a solitary mother if nest establishment takes longer than a threshold 1.7–12.5 days. Below this threshold, our model suggests that social fitness gains (acquiring helper daughters) need to be invoked to explain the evolution of extended maternal care. Enhanced survival of offspring through guarding and nest inheritance may nevertheless ease conditions for the evolution of sociality by favouring extended adult longevity and brood care in incipient social species like *E. viridissima*.

1. Introduction

Parental care is widespread in animals. In some species, it is crucial for offspring survival whereas in others it helps to increase offspring survival but is not necessary for their development [1]. Forms of parental care are various and include all behaviours that increase offspring fitness [2]. They may or may not involve direct offspring–parent contact [3] and can include behaviours such as choosing a suitable nest site, providing sufficient provisions for the developing offspring [1,4], building physical barriers between the brood and the outside environment [5] and brood guarding [6] that protects brood against enemies [7], pathogens and microbes [8,9] (e.g. through grooming or cleaning [10–14]).

The evolution of parental care hinges on the ability of a parent to increase offspring survival [15,16]. In annual species or those that reproduce once per reproductive season, it might pay for a parent to stay with the developing brood if this increases brood survival up to adulthood, when offspring are able to reproduce on their own [1]. However, iteroparous species face a trade-off between the costs and benefits of investing in current offspring, which have to be weighed against those of investing in future offspring [12,17–20]. Parental costs of brood care entail, among others, energetic costs, increased risk of predation and possible reduction in future reproductive attempts [21].

Parental care can involve both parents or just one. In bees and apoid wasps, females usually provide care by building or modifying a nest and provisioning brood cells therein, with some species additionally guarding their nests [22,23]. The majority of the more than 20 000 bee species are considered solitary and mass provision their brood cells [23], with no contact between adult and offspring [24]. In such solitary bee species, one foundress usually builds a nest and provides food for offspring development within brood cells in which she deposits eggs. She then closes the cell and ultimately deserts the nest or dies. The brood can then develop and emerge without the presence of an adult female. A question remains over why a solitary female should remain at the natal nest to provide extended care to developing offspring, as is seen in some mass provisioning species (e.g. [4]), as opposed to sealing the natal nest and establishing an additional nest to continue offspring production.

Predation pressure may favour the evolution of parental care [25]; the abundance of natural enemies might increase the amount of care that is invested in brood [26]. Females of solitary species may, for instance, invest in creating additional physical barriers, such as nest plugs, against brood parasitism or predation [27,28]. In the solitary bee species *Ceratina chalcites*, females choose between two strategies: guarding the brood or plugging the nest entrance and deserting, with guarding being more likely in nests with higher maternal investment (i.e. with a higher number of brood cells [29]). In a solitary population of the facultative social halictid bee *Halictus rubicundus*, fly predation was substantially higher in orphaned nests [30], providing further evidence for the importance of a female's presence in the nest for its protection against predation.

Extended maternal care (EMC) has been viewed as a precursor of sociality [31–33]. It is essential for progressive provisioning species, in which the offspring remain dependent upon an adult to feed them; for example, in progressive provisioning hover wasps, the assured fitness returns of adults at the nest in guaranteeing offspring survival is thought to have selected for social behaviour [34]. In mass-provisioning species, such as most bee species, extended maternal brood care may also immediately increase the fitness of the guarding mother through enhanced offspring survival [35] and the benefits of inheriting a suitable nest cavity in which to raise a second clutch of brood. Alternatively, EMC may be selected for as a delayed benefit to the mother of acquiring a daughter helper at the nest (e.g. [36]).

The socially polymorphic orchid bee species *Euglossa viridissima* Friese represents an interesting system to evaluate the relative strength of the selective forces shaping EMC. Despite being a mass provisioner, an *E. viridissima* solitary foundress guards its brood for 6+ weeks until offspring emergence, upon which the nest can be reactivated by the foundress alone (solitary) or with female offspring (social). We ask here whether EMC is a precursor to or a consequence of sociality; are enhanced brood survival and potential re-use of an already existing nest (nest inheritance) sufficient to account for the observed extended guarding period that females spend with their developing brood, instead of deserting that brood, establishing a new nest elsewhere and provisioning additional brood cells therein?

We hypothesize that the presence in the nest of an *E. viridissima* mother enhances brood survival and is selected for in mothers because of its immediate fitness payoff in terms of offspring survival and subsequent nest re-use (inheritance). To test this, we compared offspring emergence from solitary nests containing a resident mother to those in which the mother had been experimentally removed. We also compared the abundance and timing of nest intruders, which are a likely cause of low brood survival, and tested if brood care behaviours are correlated with the number and age of developing offspring. We then developed a mathematical model to define the lifetime fitness threshold at which guarding is favoured over deserting. Doing so allows us to evaluate whether enhanced brood survival and nest inheritance together provide a sufficient immediate fitness payoff to account for EMC, or whether guarding might have been selected because of delayed fitness benefits of social nesting with one or more offspring. Our model provides a theoretical framework to evaluate the role of offspring guarding as a precursor to versus a consequence of sociality.

2. Material and methods

In the socially plastic *E. viridissima*, nests are usually founded solitarily by a single, singly mated [37] foundress mother in a pre-existing cavity, in which the female sequentially mass provisions a batch of 1–13 brood cells [38–40]. She then seals the cavity from within and remains with the brood for 6+ weeks until offspring emergence. Thereupon, the nest is re-activated [39], which entails construction and provisioning of new brood cells. Re-activation may be performed by the original foundress alone (A.F. 2016–2018, personal observation) or the nest can become social, when one or more daughters remain at the natal nest. In the latter case, the original foundress usually takes a dominant reproductive position over her daughters, who repair old brood cells, build new ones and provision those cells with pollen and nectar (see figure 1) [37,38].

During brood development of the first batch of offspring, the nest entrance is generally closed with resin from within and the mother bee only occasionally opens the resin-sealed entrance and departs her nest for 5–50 min, presumably to feed [38]. Given that brood cells are mass provisioned and immediately sealed, with no direct physical contact with their mother, they are presumed not to be directly dependent on parental care [41].

Foundresses may remain in their natal nest and protect their clutch of brood because of the direct fitness benefits of (i) enhanced brood survival and (ii) the possibility to re-use their existing nest for a subsequent batch of brood cells, thereby avoiding the cost of having to find a new nest. These benefits accrue to females that remain solitary, which we term the collective 'solitary benefits' of EMC. Alternatively, or in addition, mothers may guard their brood because of the benefits that

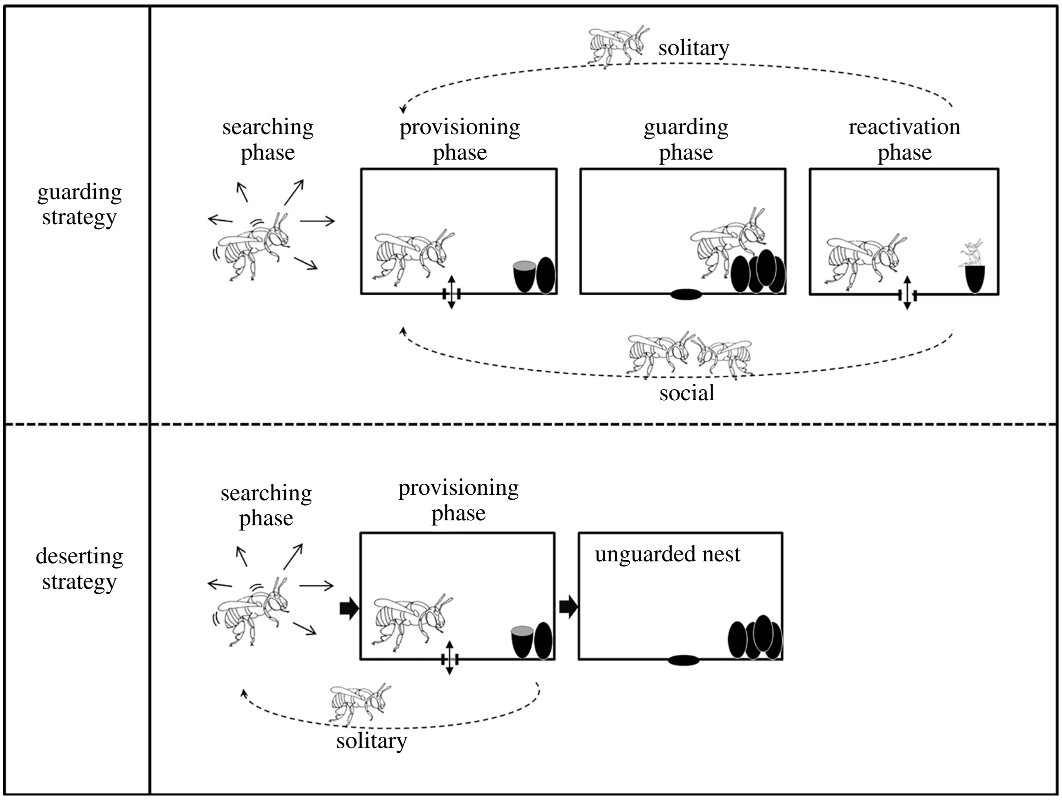

Figure 1. Scheme of *E. viridissima* nesting phases. A solitary foundress female searches for a pre-existing cavity to establish a new nest (searching phase), then sequentially builds and provisions a clutch of brood cells within the nest (provisioning phase). In this time, the female frequently leaves her nest unguarded to forage for brood cell provisions and cell building material. After the female has finished brood production, she seals the entrance from within and guards the nest until offspring emerge (guarding phase); during this time, she rarely leaves the nest unattended. After offspring emerge, the foundress female can reactivate her nest (reactivation phase) either alone (solitary) or the nest can be reactivated together with female offspring (social) or even by several female offspring in the absence of the mother. Reactivation happens within the same nest. Thus, a female can circumvent the search for a nesting cavity and can begin directly with another round of brood cell provisioning (guarding strategy). Alternatively, a foundress female could abandon its nest after having finished brood production (unguarded nest) and search for a new nesting cavity (searching phase) by herself (solitary) followed by another round of provisioning and producing brood cells, which will again be abandoned (deserting strategy).

accrue to them through the acquisition of potential worker offspring at their emergence, which may assist the foundress in subsequent brood production. In this case, maternal guarding is selected for because of the benefits of acquiring workers, which we term the ‘social benefits’ of guarding.

(a) Study site

A semi-field experiment was set up at the Department of Apiculture of the Campus de Ciencias Biológicas y Agropecuarias of the Universidad Autónoma de Yucatán in Xmatkuil, Yucatán Peninsula, Mexico. We lined wooden observation boxes (approx. 7 × 3 × 3 cm) with a mix of stingless bee resin and honey bee wax to attract female orchid bees to nest in them (e.g. [39]). The boxes had a 10 mm diameter entrance hole in a side wall, and a glass roof with a removable wooden cover to facilitate observation. Nests in which a female had already constructed two brood cells and was in the process of constructing a third one were brought into the laboratory and opened carefully. The resident female in each nest was uniquely marked on the thorax with a diamond tipped pen and returned to her nest. Nests were then returned to their original location until brood production was complete. A female was considered to have ended brood production when she did not build or provision a new brood cell and stayed inside her nest with the entrance closed for five consecutive days. As nests were established in new observation boxes, we assumed nests to be the first breeding attempt of females.

(b) Removal experiment

Nests with females that had finished brood production were randomly assigned to one of two categories: treatment (T) or control (C) in a paired design (see below), with $n = 11$ pairs of nests. Females in control nests remained with their brood while females in treatment nests were removed. All treatment and control nests were established between 16 October 2017 and 9 September 2018 (see electronic supplementary material, figures S1 and S2). Ten of the removed females were Sanger sequenced at the olfactory receptor gene *or41* following Séguret *et al.* [42], which can differentiate between *E. viridissima* and the cryptic sister species *E. dilemma* [43]. Nine of ten females were identified as *E. viridissima*; see electronic supplementary material, S3.

During the period of extended maternal presence in a nest post-brood cell provisioning, which we term ‘guarding’, females generally closed the nest entrance from within (figure 1). Nest entrances were always naturally closed at the time of experimental female removal, which created similar starting conditions for control (C) and treatment (T) nests. A pair of nests (one C, one T) was initiated at approximately the same time (±7 days) to account for seasonal variation in environmental conditions. Nests were then monitored for adult brood emergence and the presence of intruders three times a day until all brood had emerged or until the last brood cell was considered to have failed. Brood cell failure was assumed if adult emergence was not observed within 100 days after sealing of the brood cell. We chose a threshold of 100 days because the longest observed egg-to-adult development time in this study was 96 days. After all brood cells in a nest had produced a new adult or failed, we carefully opened failed brood cells and inspected their contents. We did not find living brood of *E. viridissima* in any of the failed brood cells. Instead, the content of these brood cells was either covered in mould or comprised a decomposed *E. viridissima* brood that had not fully developed.

Euglossini face a range of enemies that can harm their nests and developing brood [44]. Some common natural enemies of orchid bees at our field site and some aspects of their parasitic behaviour that we observed towards *E. viridissima* are described in electronic supplementary material, info S1, with a brief review of reported natural enemies and their potential impact on their hosts in electronic supplementary material, table S1.

(c) Intranidal behaviour

We used 12 solitary nests (5 control nests from the removal experiment plus 7 additional nests that were not included in the removal experiment) to observe the intranidal behaviour of the mother during guarding. For these observations, we brought nests into a darkroom inside a laboratory at ambient temperature. Females were observed under a red light through the glass roof of their nest, with the nest entrance always closed naturally from within. Observations commenced on the day after a female had finished brood cell provisioning, and each nest was observed on 2.75 ± 0.35 (mean ± s.e.) days (range 1–4 days). Once a new adult eclosed from the first brood cell, observations ceased.

We carried out observations on these 12 nests across the day (09:00–17:00) to avoid diurnal bias. Observations were performed at different stages of brood development. After bringing a nest into the lab, females were allowed to acclimatize to the new environment for 5 min. We then observed female behaviour for two 15-min periods, with a 5-min break between periods. Then a nest was returned to its original location in the field. All behaviours that occurred during observations were scored (electronic supplementary material, table S2) and their duration and number of occurrences noted. Behaviours were then grouped into five categories: brood care (b) such as brood cell grooming and physical contact with brood cells, nest defence (d), including passive behaviours such as sitting at the nest entrance and active behaviours directed towards intruders, nest maintenance (m), self-grooming (g), and other (o) (see electronic supplementary material, table S2 for an ethogram).

(d) Modelling the costs and benefits of guarding versus deserting strategies

To evaluate whether the immediate solitary benefits of guarding are sufficient to account for its expression, we modelled the solitary pay-offs of two alternative strategies: guarding the brood by staying in the nest during the period of brood development (guarding strategy, i.e. EMC), and deserting to found additional nests in which to produce more brood (deserting strategy) (see figure 1). Table 1 presents the parameters and values of the model. For further details of the model, see electronic supplementary material, info S2.

(e) Statistical analyses

We performed all statistical analyses in R version 3.5.0 [45].

We first tested if the number of brood cells differed between treatments (mother removed or not) using a generalized linear mixed model (GLMM) with Poisson error distribution and with nest pair as a random factor. Statistical significance of the predictor was assessed with likelihood ratio tests (LRTs) on models with and without the predictor (package spaMM [46]). We also used a GLMM with a binomial error distribution to test for the effect of treatment on the proportion of failed brood cells, using the cbind() function in R to combine successfully emerged and failed brood cells as a combined response variable, again with nest pair as a random factor. This allowed us to take variation in brood cell number between nests into account.

We monitored the intensity of intruders in C and T nests three times daily as the number of days in which intruders were found within the nest divided by the number of observation days per nest. We used a GLMM with Poisson error distribution to test the effect of treatment (female removal) on the number of days in which intruders were found in the nest, which was used rather than the number of intruders per day to avoid counting the same intruder multiple times on the same day. We note, however, that this does not exclude the possibility that the same intruder was recounted if, e.g. it had stayed in a nest for a prolonged period of time. The number of observation days was used as an offset variable in this model as the number of days on which observations were carried out (from the day after a female had finished closing the last brood cell till the day an adult offspring emerged from the last brood cell or was considered to have failed) differed between nests. Nest pair was again included as random factor.

Finally, we used a GLMM to test if the duration of intranidal behaviours of the 12 solitary nests could be explained by the number of brood cells and the age of the developing brood (number of days after a female had sealed the last brood cell), with nest as a random factor and assuming a negative binomial error distribution. We checked for correlations between behavioural categories by calculating Pearson's correlation coefficient r using the cor() function of the basic R package 'stats' and p-values corresponding to the significance levels were calculated using the rcorr() function of the 'Hmisc' package [47].

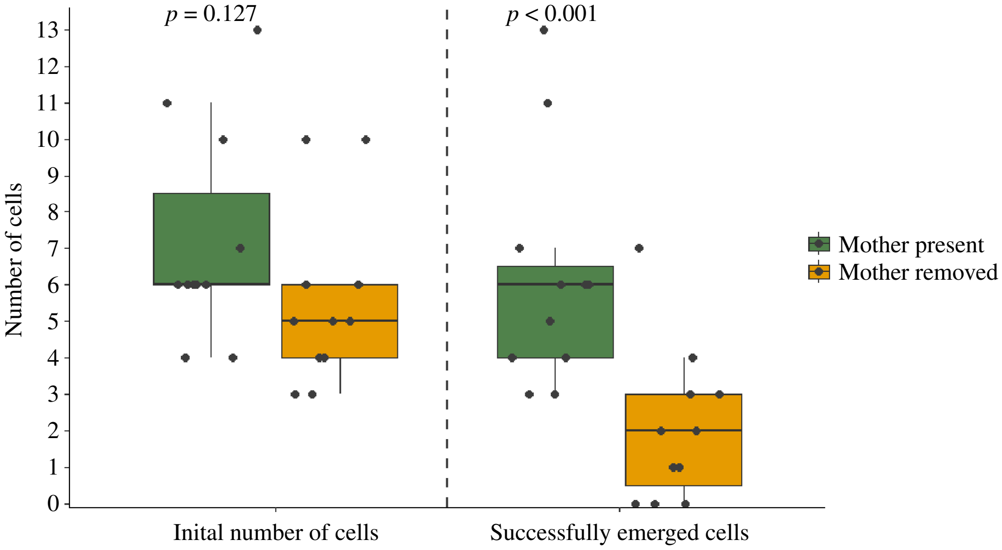

Figure 2. Number of initially produced and successfully emerged brood cells in nests in which the mother was present (green, $n = 11$) or experimentally removed (orange, $n = 11$); the initially produced number of brood cells at the start of the experiment did not differ significantly between treatments (GLMM $\chi^2 = 2.3207$, df = 1, $p = 0.127$); removal of the mother significantly reduced brood success (GLMM $\chi^2 = 40.01$, df = 1, $p < 0.001$). Boxplots show median, 25%–75% quartiles, whiskers calculated as Q1/Q3 ±1.5 * IQR, and jittered raw data points.

Table 1. Parameters and values used in the modelling of nesting strategy. *F* denotes the time for a female to find a new nest; *a* denotes the nest reactivation rate for guarding females and *s* denotes the daily probability of female survival during nest establishment and provisioning, which is identical for both female strategies (guarding and deserting). Values for the deserting strategy are derived from observations and are averaged across nests from which mothers had been experimentally removed; corresponding values for the guarding strategy are derived from unmanipulated nests, which are also averaged.

parameter / value	guarding female	deserting female
time to find a new nest	$(1 - a)F$	F
duration of brood production	17 days	17 days
time guarding a completed nest	62 days	0
one round of nesting	$(1- a)F + (17+62)$ days	$F + 17$ days
number of brood cells per nest	6	6
hatching rate of brood cells	0.85	0.39
daily probability of survival during nest establishment and provisioning	s	s

We checked assumptions of all models through diagnostic tests and plots implemented in the package ‘DHARMa’ [48]. GLMMs were performed with the package ‘lme4’ [49]. Unless otherwise stated, we present means ± s.e.

3. Results

(a) Removal experiment

The mean number of brood cells per nest across the entire observation period was 6.36 ± 0.58 (see electronic supplementary material, figure S1 for data by date of nest initiation). In control nests, where the mother was not removed, the total number of brood cells at the start of the experiment (7.18 ± 0.87, median = 8) did not differ significantly from treatment nests, where the mother was removed (figure 2; 5.54 ± 0.73; median = 5; GLMM: LRT $\chi^2 = 2.32$, df = 1, $p = 0.12$).

The presence of the adult female significantly enhanced brood survival (figure 2; GLMM: LRT $\chi^2 = 40.01$, df = 1, $p < 0.001$). In nests where the mother was present, 85% (68 out of 79) of brood cells produced a new adult while an average of 1.00 ± 0.40 brood cells failed per nest. In contrast, in nests where the mother was removed, only 39% (23 out 61) of brood cells produced a new adult and on average 3.45 ± 0.76 of the initially produced brood cells failed per nest.

(b) Presence of intruders

A variety of intruders from a range of taxonomic groups was found in our experimental nests including a chalcid wasp (*Melittobia* sp.) that was identified through barcoding and was not yet known to parasitize *E. viridissima*. Details of the intruders that we recorded in our experimental nests are described in the electronic supplementary material, info S1 and table S2.

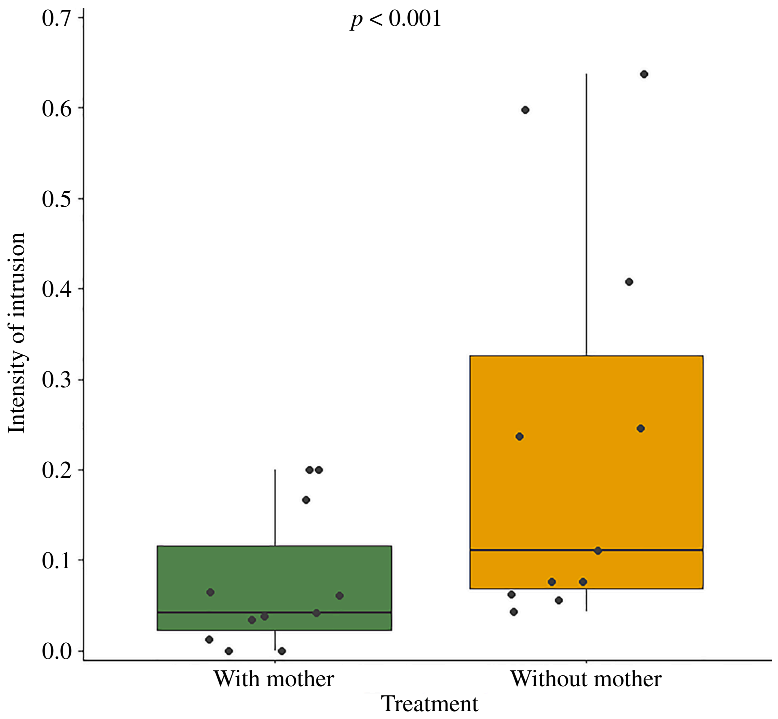

Figure 3. Intensity of nest intrusion (number of days on which intruders were detected, divided by the number of observation days) in nests where the mother was present (green, $n = 11$) or experimentally removed (orange, $n = 11$); removal of the mother significantly increased the intensity of intrusion (GLMM $\chi^2 = 75.54$, df = 1, $p < 0.001$). Boxplots show the median, 25%–75%, whiskers calculated as Q1/Q3 ±1.5 * IQR, and jittered raw data points.

In control nests with a resident mother, intruders were found on average on 5.0 ± 2.14 days, while in treatment nests without a mother they were found on 16.18 ± 6.46 days. In control nests in which the mother was present, the intensity of intrusion, taking into account the total observation time per nest, was significantly lower (0.07 days ± 0.02) than in treatment nests from which the mother had been experimentally removed (0.23 ± 0.06) (figure 3; GLMM: LRT: $\chi^2 = 75.54$, df = 1, $p < 0.001$). For an overview of the intensity of intrusion per intruder type, see electronic supplementary material, figure S3.

(c) Intranidal behaviour

We observed a total of 1065 min of intranidal behaviour in 12 solitary nests with varying numbers of brood cells (range: 1–13 brood cells per nest). The most prevalent intranidal behaviour during 88.75 ± 12.58 min of behavioural observations per nest was brood care (35.82 ± 1.28 min), followed by nest defence (29.75 ± 3.55 min) and nest maintenance (13.28 ± 1.71 min). Other behaviours and self-grooming were the least expressed behavioural categories, at 10.52 ± 2.74 and 1.85 ± 1.44 min, respectively. For a detailed record of all scored behaviours and their respective grouping into behavioural categories, see the ethogram (electronic supplementary material, table S2). Because our behavioural data were compositional, summing to the total observation time, behavioural categories were non-independent and inversely correlated (electronic supplementary material, table S3).

Females with a greater number of brood cells spent significantly more time on brood care behaviours (electronic supplementary material, figure S4a; GLMM LRT: $\chi^2 = 6.50$, df = 1, $p = 0.01$). In addition, females spent more time on brood care when brood was young than when brood was at a more advanced age and stage of development (electronic supplementary material, figure S4b; GLMM; LRT: $\chi^2 = 5.98$, df = 1, $p = 0.01$). There was an inverse correlation between time spent on brood care and nest defence (electronic supplementary material, table S3; Pearson's $r = -0.65$, $p < 0.001$), with nest defence decreasing with the number of brood cells and increasing with brood age, likely because of the inverse relationship of time spent on nest defence versus brood care (electronic supplementary material, table S3).

(d) Modelling alternative strategies—are solitary benefits sufficient to account for guarding?

To understand whether the guarding strategy is favoured over the deserting strategy because of the benefits accruing to a solitary female (through increased brood survival and nest re-use for the production of a subsequent clutch of brood), we developed a mathematical model to compare the fitness gains of purely solitary female bees that pursued either the guarding or the deserting strategy (electronic supplementary material, info S2). According to our model, the deserting strategy is favoured when

$$0.39\frac{1-s^{F+17}e^{\lambda(s^{F+17}-1)}}{1-s^{F+17}} > \frac{0.85}{s^{\alpha \cdot F}} \tag{3.1}$$

where

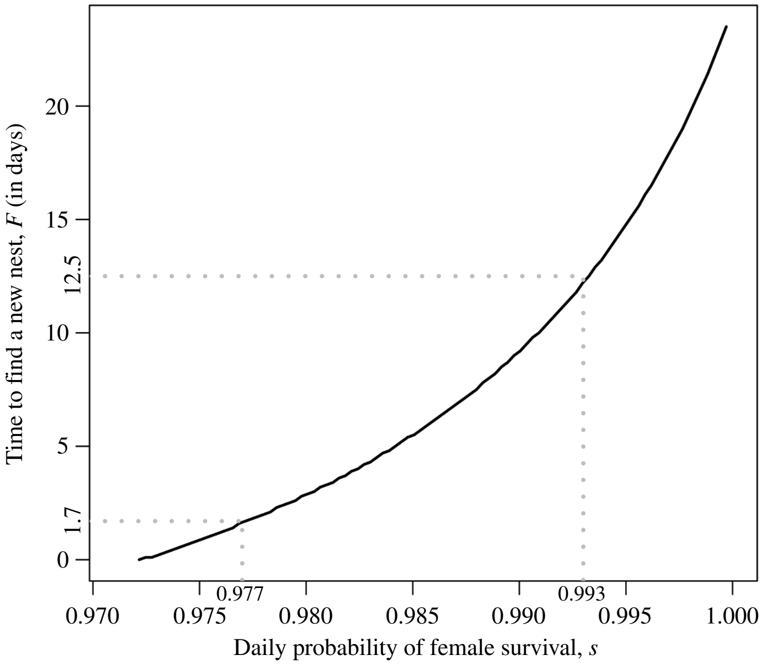

Figure 4. Curve indicating the evolutionary dynamics of guarding versus deserting strategies as driven by two parameters: the mean time (in days) required to find a new nest (*F*) by an orchid bee female, and the daily probability of female survival (s) outside the nest, when finding and establishing a nest or collecting provisions for brood cells. Guarding is favoured in the parameter space above the curve. Deserting is favoured in the parameter space below the curve. Dashed lines represent the threshold number of days above which the guarding strategy is favoured (12.5 days, upper dashed line) and below which the deserting strategy is favoured (1.7 days, lower dashed line) for a range (95% credible intervals) of plausible rates of daily survival. Where the guarding strategy is favoured, the solitary benefits of guarding (enhanced brood survival, inheritance of nest) are sufficient to explain why EMC is favoured. When the deserting strategy is favoured, additional social benefits of guarding (acquisition of a daughter worker) in addition to the solitary benefits need to be invoked to explain why EMC is nevertheless exhibited.

$$\lambda = \left(\frac{(1-\alpha)F + 79}{F + 17}\right) - 1.$$

In inequality (3.1), F is the time taken by a deserting bee to find and establish a new nest, α is the nest reactivation rate by a guarding bee and s is the daily probability of survival (during nest founding and provisioning) for female *E. viridissima* regardless of the strategy they pursue. For the details of the model's derivation, see electronic supplementary material, info S2.

Figure 3 shows the graphic representation of this inequality assuming $\alpha = 0.52$, which is estimated based on our monitored bees (see electronic supplementary material, info S2, for details). As the risk of death of a female in search of a new nest increases (i.e. as the probability of survival per day, s, while searching for a new nest, decreases), the threshold number of days under which the deserting strategy is favoured decreases almost exponentially. For example, a 2% increase in the risk of death (a drop in the probability of adult female survival from 100% to 98% per day) decreases the threshold of F from 27 to 3 days. This means that, with a probability of adult survival of 98% per day, the deserting strategy is favoured if a female can find and establish a new nest within a maximum of three days; if it takes longer than three days to find and establish a nest, the solitary benefits that a foundress would reap by EMC are sufficient to explain guarding.

To update our modelling of the female strategy by using a realistic value of the daily probability of survival for female orchid bees, we used a Bayesian model to estimate survival based on 61 nest reactivations of the marked and monitored *E. viridissima* females at the study site (electronic supplementary material, table S4). We estimated adult survival to be 0.986 per day (95% credible interval: 0.977–0.993). See electronic supplementary material, figure S5, for details of this estimation.

By using a daily estimate of probability of survival ranging between 97.7% and 99.3% in the parameter space for the evolutionary dynamics of guarding versus deserting strategies (inequality (3.1); see figure 4), the threshold number of days lies between 1.7 and 12.5 days, which means that the guarding strategy is favoured purely through solitary benefits when the time needed to found and establish a new nest is above a maximum threshold of 1.7–12.5 days. Given that *E. viridissima* females always perform EMC of brood, if founding and establishing a new nest takes considerable time (>12.5 days), the solitary benefits of guarding are sufficient to account for its expression. In contrast, if nest founding is rapid (<1.7 days), the social benefits of guarding need to be additionally invoked for guarding to be of selective advantage. If founding a new nest takes between 1.7 and 12.5 days, precisely which selective factors favour guarding (just solitary benefits, or solitary and social benefits) depend on prevailing rates of adult female mortality when establishing a nest or provisioning brood cells therein (figure 4).

Including brood size as a parameter in an extension of the model, we found that, with up to eight brood cells, which is slightly above the observed mean number of brood cells of 6.36, the guarding strategy might be favoured if the time needed to found a new nest takes between 0 and 7 days. (electronic supplementary material, figure S7). On the other hand, the guarding strategy should always be favoured with a brood size >20. See electronic supplementary material, S2-B for further details.

4. Discussion

In this study, we addressed the question of whether solitary benefits (enhanced brood survival, re-use of an existing nest) can account for why females engage in EMC (i.e. whether nest guarding can be viewed as a precursor to sociality) instead of deserting a fully provisioned nest to establish a new nest in which to provision additional brood cells. Our removal experiment with *E. viridissima* showed that the presence of the mother can have a substantial positive effect on brood survival. Furthermore, *E. viridissima* females performed considerable brood care and nest defence behaviours, the duration of which were correlated with the number of brood cells and brood development. With our model, we could define the parameter space—in terms of speed of nest founding and adult survival—under which solitary fitness benefits could explain EMC and select for extended female lifespan, i.e. EMC as a precursor to sociality. For much of parameter space, especially when brood size is large, the solitary benefits of guarding may be sufficient to account for guarding i.e. EMC and selection for extended lifespan may be precursors to sociality. However, the evolution of extended longevity may have been additionally facilitated through the benefits of being social; indeed, the extended longevity favoured by sociality might change the benefits of guarding in the solitary phase of the colony cycle.

(a) Implications of extended maternal care for the brood

Guarding the nest throughout brood development seems to be a strategy of mothers to avoid parasites and predators or to reduce their impact on brood. Plugging and repairing the nest entrance are commonly observed in solitary sphecid wasps [50] and by the halictid bee *Megalopta genalis* [51]. We could show that the presence of the mother in nests significantly improved offspring emergence compared with nests in which the mother was absent. Indeed, Saleh & Ramírez [52] hypothesized that parasitism might have played an important role in the evolution of extended maternal presence in the nest in the closely related species *Euglossa dilemma*. Furthermore, Sakagami & Maeta [53] have suggested that the guarding and brood care behaviour of *Ceratina* spp. females lowers brood mortality through parasite infestation or fungal infection. Similar observations have been made in a range of other bee species [30,32,54].

We attribute the significantly higher rate of offspring survival in the control group (mother not removed) not only to extended maternal presence but also to the behavioural repertoire of mothers inside the nest. During the period in which females stayed inside their nests, they spent a substantial amount of time on brood care and nest defence. Brood care behaviour included antennation of brood cells, manipulating resin on the brood cell surface and brood cell grooming. These could be mechanisms to avoid the spread of fungi and pathogens, as is seen in leaf-cutting ants that tend their fungus garden [55,56] or in other ants that remove fungal spores from pupae [13]. Egg grooming has also been shown to be an effective mechanism for earwig mothers to remove fungal spores from their brood [9,57]; in earwig nests from which the mother had been removed, developing brood was often infested by fungi and did not reach adulthood. It is hypothesized that fungal infections and other pathogens might have selected for extended parental care, particularly in the tropics [5,25].

We found that the expression of brood care behaviours decreased with advancing age of the developing brood. The concomitant increase in nest defence behaviours with advancing age might simply be due to the compositional nature of our data, with an increase in one behavioural repertoire leading to a decrease in another, possibly because brood are less susceptible to microbial infection as they age and therefore they require less care by the mother, allowing more time for the mother to sit at the nest entrance (i.e. guarding). A variety of other insects exhibit decreasing brood care with advancing age of the brood, indicating a recurrent behavioural pattern of putative adaptive significance [58–62].

We also found that *E. viridissima* females spent more time on brood care behaviour with increasing brood size. Gross [19] claims that the number of offspring should be a good predictor for how much a parent will invest in the brood because, with increasing number, the brood becomes more valuable. Moreover, parental investment theory suggests that greater nest defence, in general terms, should be made in nests with a greater number of offspring [63,64]. Though defence behaviour appears to decrease with the number of brood cells, this is more likely a statistical consequence of more brood cells equating with more brood care behaviour and, as a consequence of the compositional nature of our data, less defence behaviour.

For the evolution and expression of extended maternal care, nest architecture might play a pivotal role. Cavity nesting, as in *E. viridissima*, may be a prerequisite for foundresses to be able to defend successfully their brood cells. The effect of nest architecture on the expression of extended parental care has been a controversially discussed topic [61,65–67]. Plateaux-Quénu [61] argues that, whatever the true effect, it is certain that cavity nesting facilitates brood care behaviours because all cells are built in close proximity to each other. Moreover, resources that are of value and potentially scarce, such as nest cavities, can be strong selective agents for the evolution of parental care [68] and can favour individuals staying in the nest for an extended period of time, across generations, thus potentially creating the opportunity for an overlap of generations, given the extended longevity of females [69].

(b) Implications of extended maternal care for social evolution

Our modelling shows how the probability of adult mother's survival and the time to establish a new nest are two critical parameters that determine the potential fitness payoff of the guarding versus deserting strategy. The lower the survival during nest founding/provisioning and the longer to establish a new nest, the greater are the benefits of EMC.

There are no data on rates of mortality of females when establishing a new nest, or on their speed of nest founding. We suggested that the daily probability of survival during nest searching and establishment are likely similar to the probability of survival while foraging for brood cell provisions, namely 98.6%. For this daily rate of survival, the deserting strategy is favoured when the time needed to find a new nest is less than an interval of 1.7–12.5 days. If searching for a new nest site is associated with higher risk of death than when foraging, then parameter space favouring the deserting strategy is even more restrictive. We do not know the time females require to find and establish a new nest, but our quantitative model shows the conditions under which the guarding versus the deserting strategy is favoured through its solitary benefits to the mother. That we did not observe solitary *E. viridissima* foundress females to pursue the deserting strategy suggests that higher brood survival or the rapid re-use of a nest (nest inheritance) for a subsequent clutch of brood cells might be important selective solitary benefits of guarding. Emerging offspring in turn might benefit from staying in the natal nest because of the potential inheritance of the nest, in addition to any inclusive fitness benefits they may reap from helping raise more kin [36,70]. Guarding of a pre-existing nest for future reuse could therefore be considered another pre-social behaviour potentially facilitating the formation of social groups [71].

We estimated the probability of adult survival based on data that we collected from females during the provisioning phase. We are aware that foraging might entail different mortality factors than when searching for a new nest site. In both phases, bees are exposed to predation. However, scouting for a suitable nest site could be risker than flying within the home range of an already established nest. Furthermore, overnight mortality might be higher in females searching for, yet still lacking, a nest. Thus, our estimated probability of survival during nest founding might be overestimated. With a decreasing probability of survival, the threshold time for founding a new nest under which deserting is favoured would drop (<1.7 days), reducing further the need to invoke social benefits to explain guarding.

Michener [23] noted that solitary bee species with extended lifespans are closely related to eusocial taxa, which is also the case for orchid bees. Orchid bees are basal to the eusocial corbiculate bees and are likely ancestrally solitary or weakly social [72,73]. EMC (guarding) and the associated increased lifespan have been considered precursors of sociality [53,58,74–76]. The origins of eusociality via sub-sociality, with overlapping generations [23,77], is considered the most likely route to the evolution of eusociality in bees [78,79]. Generational overlap, when it arose, may have reinforced selection on longevity (in queens) and in brood care (by workers). Although we cannot disentangle whether longevity in female *E. viridissma* has been selected for through the benefits or guarding (when solitary) of through the benefits of being social, we can define the extent to which guarding pays a female following the guarding strategy during the solitary phase when stripped of any additional benefits accruing through becoming social. The evolution of extended longevity may also have been facilitated by both the benefits of guarding (when solitary) and through the benefits of being social; indeed, the extended longevity selected by sociality might change the benefits of guarding in the solitary phase of the colony cycle.

If it pays a foundress to stay with her developing brood, then adult female offspring may subsequently reap fitness benefits by remaining at the natal nest and enhancing the survival of juvenile sibs, the offspring of their mother. Benefits would also accrue if the original foundress dies and a daughter can take over the tasks of nest defence and sibling care. Such so-called assured fitness returns are usually considered to apply to progressive provisioning species of wasps and bees [34,80,81], though they may also apply to mass provisioning species with appropriate life histories encompassing high juvenile mortality [32,35].

Our study highlights the importance of an underexplored research question: the role of guarding as a precursor to sociality. We offer a model that can be used to test which conditions (guarding versus deserting) are favoured. Studies of additional solitary and social species within the Arthropoda, including other bees, aphids, thrips and spiders that display similar guarding behaviour, could provide additional insights into whether EMC and its corollaries: guarding and extended longevity, are traits leading to or following on from the evolution of sociality.

Ethics. Sampling permit: SPARN/DGVS/01546/23

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Data accessibility. Datasets and R code are available in Dryad [82].

Supplementary material is available online [83].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, supervision, validation, visualization, writing—original draft, writing—review and editing; A.S.: conceptualization, methodology, software, supervision, validation, writing—original draft, writing—review and editing; H.S.: formal analysis, methodology, validation, visualization, writing—original draft, writing—review and editing; S.T.: formal analysis, methodology, software, validation, visualization, writing—review and editing; S.B.: methodology, validation, writing—review and editing; V.R.E.B.J.: data curation, investigation, writing—review and editing; J.J.G.Q.-E.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, validation, writing—review and editing; R.J.P.: conceptualization, funding acquisition, methodology, resources, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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