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RESEARCH ARTICLE

Nest protection and foraging behaviour in solitary and social nests of the socially polymorphic orchid bee *Euglossa viridissima*

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Abstract

Natural enemies impose a selective pressure on solitary insects that may favour the evolution of sociality. In the socially polymorphic orchid bee *Euglossa viridissima*, females found nests solitarily and provision a first batch of brood. After brood maturity, a nest can remain solitary (all offspring disperse) or become social, when one or more subordinate daughters forage for nesting material and brood provisions for the dominant mother. Solitary females leave their nest unguarded when foraging whilst a female in a social nest can guard the nest while nestmates are foraging. By observing solitary and social nests, we found that subordinate foragers in social nests undertook longer provisioning trips than solitary females. The presence of a guarding female in a social nest protected the nest against intrusion, possibly favouring longer provisioning trips. Moreover, the frequency of successful attempts by intruders to enter nests was significantly lower in social nests. Our results provide strong support for the parasite defence hypothesis for the evolution of social behaviour.

Keywords Primitively eusocial · Foraging behaviour · Parasite · Kleptoparasite · Nest · Defence

Introduction

Parasites or natural enemies can exert a selective pressure on their hosts that may favour the evolution of sociality, particularly in Hymenoptera (e.g. Lin 1964; Lin and Michener 1972; Hogendoorn and Velthuis 1993; Evans 2009; Socias-Martínez and Kappeler 2019). One eusocial stingless bees species, *Tetragonisca angustula*, has even evolved a soldier caste, seemingly as a response to selection imposed by a natural enemy of the nest: the nest-raiding cleptobiotic stingless bee *Lestrimelitta* (Grüter et al. 2017). However, we know relatively little about the role of guarding in facilitating social evolution in incipiently social groups (e.g. Socias-Martínez et al. 2019), though they represent systems in which it may be feasible to measure the benefits of sociality in terms of improved defence against natural enemies.

Hymenopteran nests are commonly depredated by natural enemies (Starr 1985; Zammit et al. 2008; Wcislo and Fewell 2017), and several defence strategies are in place to reduce predation pressure, such as physical nest-entrance barriers or behavioural strategies, such as guarding (Wcislo 1996; Münster-Swendsen and Calabuig 2000). In solitary bee and wasp species, one female founds a nest on her own by taking up residence in a pre-existing cavity or by building or digging a suitable nest e.g. through excavating soil or other materials (Batra 1984; Danforth et al. 2019). The foundress female then forages to build and sequentially provision brood cells in which to lay eggs and produce offspring (Batra 1984). This is generally the case in mass provisioning species that provide their developing brood with all the resources necessary to complete development within the cell (Field 2005). Provisioning brood cells is a demanding and risky activity for a female (Donnell and Jeanne 1992). If the female is absent from the nest to collect brood cell provisions or even dies whilst foraging, its nest containing the brood may also be threatened (Korb and Heinze 2016) because the offspring are then left alone, and the nest is more vulnerable to predation (Kukuk et al. 1998; Ayasse and Paxton 2002; Mikát

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et al. 2016). As females of solitary species must leave their nest unguarded while foraging, defence mechanisms that depend on the physical presence of the female are less effective. Solitary females, therefore, face a trade-off between foraging for brood cell provisions and guarding (Hogendoorn 1991; Goodell 2003).

The foraging-guarding trade-off may not exist in social species. Adults in the nest can help reduce the impact of intruders at the nest by their presence and by active defence behaviours (Litte 1977; Starr 1985; Ayasse and Paxton 2002; Lucas and Field 2011; Wcislo and Fewell 2017, Lin and Michener 1972). With two or more individuals present in the nest, each nestmate can take over different tasks, specializing e.g. in foraging or guarding (Hogendoorn and Velthuis 1999, Lin and Michener 1972), ensuring that nests are better guarded against natural enemies compared to solitary nests, while at the same time being provisioned (Abrams & Eickwork 1981). Guarding can help to reduce intra-and interspecific resource robbing (Hogendoorn and Velthuis 1993; Dunn and Richards 2003; Boff et al. 2015) or cleptoparasitism (Abrams & Eickwork 1981). Thus, in social colonies, individuals can cooperate to maximize brood cell provisioning whilst the nest is still guarded. In addition, if one female dies, the nest and the offspring can be taken care of by the remaining individuals (Lin and Michener 1972), providing assured fitness returns (Smith et al. 2003).

The socially polymorphic, mass provisioning orchid bee species *Euglossa viridissima* represents an interesting model to test hypotheses about factors that may favour the evolution of social behaviour because solitary and social phenotypes occur simultaneously in the same population, making it possible to compare alternative social phenotypes in a common environment. More specifically, *E. viridissima* is an excellent species to evaluate the benefits of sociality through improved nest protection and enhanced foraging activity. A solitary foundress usually guards its brood for six or more weeks until offspring emergence, upon which the nest can be reactivated, i.e. brood production recommences. Reactivation can be by the old foundress alone (the nest remains solitary) or together with one or more female offspring, when the nest becomes social, which happens in 15–38% of reactivated nests in our study site (Cocom Pech et al. 2008; May-Itzá et al. 2014; see Fig. 1).

In the context of the hypothesized benefits of sociality in terms of defence against natural enemies, we compared solitary and social nests of *E. viridissima* in order to assess how sociality impacts nest protection and female foraging behaviour. Specifically, we tested (i) whether social nests are more intensively guarded compared to solitary nests; (ii) whether foraging females in social nests undertake longer foraging trips compared to solitary females, and (iii) whether the number of nest intruders is greater in solitary versus social nests.

Materials and methods

Study species

The nests of the socially polymorphic *E. viridissima* are usually founded by one singly mated (Zimmermann et al. 2009) foundress in a pre-existing cavity in which the female alone sequentially mass provisions a batch of 1–13 brood cells (Cocom Pech et al. 2008; May-Itzá et al. 2014; Boff et al. 2015). She then seals the cavity from within and remains within it until offspring emergence. Thereupon, the nest can be re-activated (May-Itzá et al. 2014), which entails construction and provisioning of new brood cells. The re-activation may be performed by the original foundress alone, by one of her daughters alone (A Friedel personal observation) or the nest can become social (15–38% of reactivated nests; see Fig. 1), with usually one or more daughters that remain at the natal nest with their mother. In the latter case, the original foundress usually takes the reproductive dominant position over her daughters, who take on the tasks of repairing, building and provisioning brood cells with pollen and nectar (see Fig. 1; Cocom Pech et al. 2008; Zimmermann et al. 2009). The dominant female typically lays most or all of the eggs, as in the sister species *Euglossa dilemma* (Saleh et al. 2024), though reproductive skew does seem to be complete in *E. viridissima* as subordinates may also contribute to reproduction (e.g. Cocom Pech et al. 2008, Zimmermann et al. 2009, Friedel et al. 2019). Social nests are usually made up of mother–daughter associations; however, other types of nest association have been reported for this species (Zimmermann et al. 2009). The social dynamics between dominant and subordinate female include oophagy by both partners, and threatening behaviour of the dominant towards the subordinate female but not the other way around (Cocom Pech et al. 2008).

Study set-up

In a semi-field set up at the Department of Tropical Apiculture of the Campus de Ciencias Biológicas y Agropecuarias of the Universidad Autónoma de Yucatán in Mérida-Xmatkuil (UADY), Yucatán, México, we lined wooden observation boxes (ca. 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. May-Itzá et al. 2014). 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 of the nest and its inhabitants (Fig. 2). The nests in which a female had already constructed two brood cells and was in the process of constructing a third were

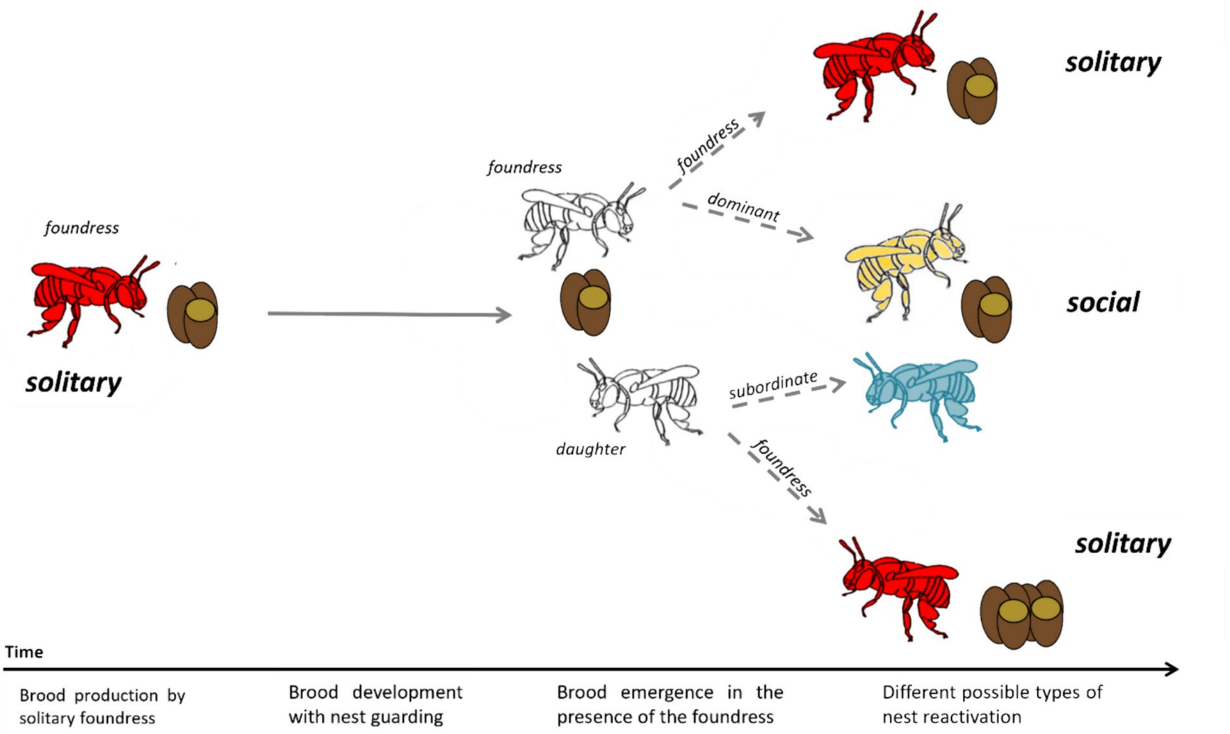

Fig. 1 *Euglossa viridissima* nesting cycle. A solitary foundress usually starts a nest alone in a pre-existing cavity. She sequentially builds, provisions and oviposits a first batch of brood cells. Thereafter, she closes the nest entrance from within and waits inside the nest until offspring emerge. Upon offspring emergence, the nest can be reactivated either by the old foundress alone, who then produces a next batch of brood cells by herself, or, if one or more of her daughters stay in the nest, the nest can become social, with usually the old solitary foundress assuming the dominant role with the main task of guarding and oviposition while the daughter(s) assumes a subordinate position(s), with the main tasks of foraging and brood cell building. Daughters can, however, also disperse from the natal nest and become solitary foundresses themselves. Figure 1 depicts solitary nest phenotypes with one foundress, the brood emergence phase and, after brood has emerged, different possible types of nest reactivation, either solitary or social. The social nest phenotypes have at least a dominant and a subordinate female. Here we show a social nest with the original foundress as the dominant female and a daughter as subordinate female. Bees pointing to the right indicate the same original foundress in her potential roles, bees pointing to the left indicate the daughter in her potential roles; brown ovals indicate brood cells. Solid arrow means a chronological sequence of events; dashed arrows indicate a potential choice

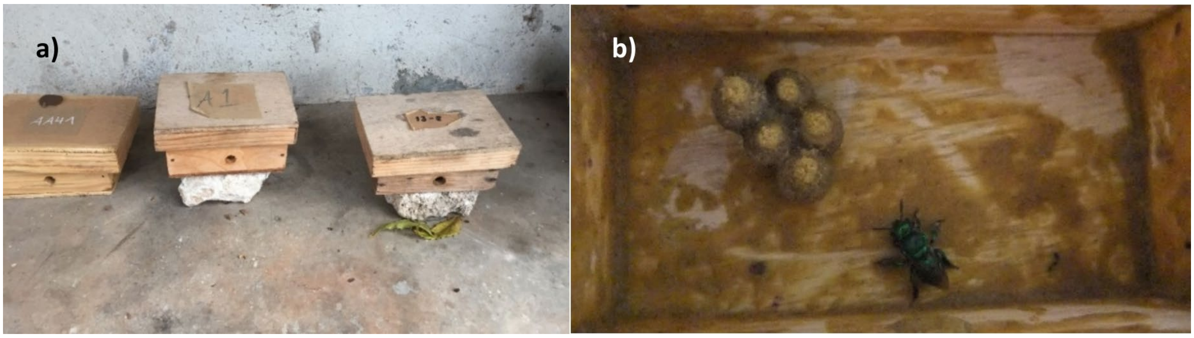

Fig. 2 **a** Examples of observation boxes designed for *Euglossa* bee nesting (Cocom-Pech et al. 2008) in the Meliponario of UADY in Mérida-Xmatkuil, Mexico; **b** the inside of an observation box showing a solitary nest with a *Euglossa viridissima* female and her brood cells (aerial view from above, taken through the glass sheet after removing the wooden lid)

brought into the laboratory and opened carefully. The resident female in each nest was given a unique symbol etched into the thorax with a diamond tipped pen and returned to her nest (Séguret et al. 2021). The nests were then returned to their original location.

A total of 13 solitary and ten social nests was observed. Social nests always consisted of two females, classified behaviourally as a dominant female and a subordinate female, with social status assigned through observation of female behaviour prior to our collection of quantitative foraging data. The female of the nest that was observed foraging, bringing pollen in its corbiculae into the nest and provisioning brood cells was assigned subordinate female status whereas the female that remained predominantly in the nest, spent most time over brood cells and laid eggs was considered the dominant female. As there is no morphological (e.g., size) difference between dominant and subordinate females in *E. viridissima*, these behavioural differences have been frequently used to define social status in the species, which has been confirmed by observations of physical dominance and oophagy by the dominant of the subordinate and its eggs (e.g. Cocom Pech et al 2008, Boff et al. 2015, Séguret et al 2021). A caveat of our study is that we did not assess social roles using, for example, genetic analysis of brood to assign maternity or cuticular hydrocarbon (CHC) analysis of adults, which, in the sister species *E. dilemma*, differentiates behavioural castes (Saleh et al. 2021). Notwithstanding this caveat, we have been able to define the principal forager (subordinate) and the principal non-forager (dominant) in our social nests prior to the collection of observational data to explore the impact of sociality on foraging.

Observations were performed between 31 January 2018 and 22 February 2019, with a total of 217 h of observation, either by video recording the nest entrance or by direct observation of nest entrances. Cameras for video recording were placed approximately 1–1.5 m away from the nest on a tripod to avoid the disturbance of in-and-outgoing bees. Video angles were chosen so that the unique thoracic symbols of bees could be identified. Flight behaviour was observed during the brood production phase of nests, i.e. when brood cells were being built. Before starting an observation session, the inside of the nest box was briefly checked by lifting the nest lid and the presence and identity of bees was noted. From subsequent video observations of the same nest, it was then possible to deduce the presence and likely absence of each bee. On days when bees did not open their nest entrance in the morning, e.g. during unfavourable weather conditions, flight behaviour was not observed. The recordings were performed once per nest or over multiple observation sessions on different days. The average observation duration per nest was 3.73 h (minimum: 0.51 h; maximum: 6.85 h). During each session, continuous footage of nest entrances was captured. When bees closed their nest entrance during an observation session, the session was stopped.

Nest protection

We calculated the time that a nest remained unguarded as the time that females were absent from their nest box. For solitary nests, this time equated with the time during which the (solitary) female was outside the nest, collecting resources for brood cells (pollen, nectar, resin). In social nests, both females had to be outside the nest in order for it to be considered unguarded. A nest was considered to be guarded when the solitary foundress was present (solitary nests) or if one or both females were present in a social nest. Our definition of guarding includes actively blocking the nest entrance from within the nest, and the mere presence of a bee inside the nest box. This definition is justified, because when inspecting a nest's interior at the start of observations, we observed bees inside a nest to regularly patrol the nest interior and to groom the brood cells therein. We could not record their within-nest behaviours by filming them through the nest entrance with our video cameras focused at the nest entrance.

Frequency and duration of foraging trips

Incoming and outgoing bees were recorded and identified by their unique thoracic mark. A foraging trip was defined as the time interval between a female leaving its nest and returning to it, regardless of whether she visibly brought back pollen, nesting material, or no material on her hind legs. As we did not always observe a female leaving her nest, e.g. at the beginning of a video observation, or we missed the return of a female at the end of her foraging trip (because she arrived when video observations had already stopped), we measured the frequency of foraging trips as the number of times a female returned to her nest per hour and not directly from the duration of foraging trips. The foraging trips that were not recorded as complete were not incorporated into the analyses of foraging trip duration.

Occurrence of intruders

During the observation of foraging flights, we also recorded the number of any organism that entered solitary and social nests and whether intrusion occurred while the nest was guarded (bee present) or unguarded (no bee present). From the information in the videos, we could not identify intruders to a higher taxonomic level, but we could differentiate between ants, wasps, flies, other bees, non-nestmate *Euglossa* individuals and a group of unidentified intruders, which we call 'others'. As most intruders were ants, and not many other intruders were observed entering the nests (Table S1), we treated all intruders equally in the analyses. The number of intruders that inspected a nest entrance but ultimately did not enter the nest was recorded (Table S1). Table S2 lists all intruders, which we consider to be potential natural enemies of *E. viridissima*.

Statistical analyses

We performed all statistical analyses in R version 3.5.0 (R Core Team 2017). We tested if the time that a nest was unguarded differed between solitary and social nests with a generalized linear mixed model (GLMM) with a negative binomial distribution, and nest identity and observation day as random factors. We used the log of the observation time as an offset variable to account for variation in the duration of recording between observation sessions in this and following analyses. To test if the duration of foraging trips differed between solitary and social nests, we used a GLMM with gamma distribution and log link function, with observation day and nest identity as random factors. For the analysis of the duration of foraging trips, we excluded observation events in which a female did not perform any foraging activity, i.e. when a female did not leave her nest throughout the whole observation period, which was the case for some dominant females, or in which we did not record a complete foraging trip. We fitted a GLMM with Poisson distribution to test for differences in the frequency of foraging trips between social and solitary nests, measured as the number of returns to the nest, with observation day and nest identity as random factors. The log of the observation time was again used as an offset variable. To test if the number of intruders differed between solitary and social nests, we also performed a GLMM with Poisson error distribution, observation day and nest identity as random factors and the log of the observation duration as an offset variable. To test whether protection status (guarded vs unguarded) had an effect on the number of intruders, we performed a GLMM with an interaction between protection status and sociality, with a negative binomial error distribution, nest identity and observation day as random factors, and the log of the observation time as offset variable. Furthermore, to test whether protection status (guarded vs unguarded) had an effect on the number of intruders that went to the nest entrance but did not enter the nest, we performed a GLMM with an interaction between protection status and sociality, with a Poisson error distribution, nest identity and observation day as random factors, and the log of the observation time as offset variable.

For all pairwise comparisons, we used the 'tukey' function implemented in the package "emmeans" (Lenth 2024). We checked for overdispersion of variables and residuals, and ensured that all models met GLMM assumptions with the DHARMA package (Hartig 2022). GLMMs were performed using the R package "glmmTMB" (Brooks et al. 2017). Unless otherwise stated, we present means ± SD in the text. The median values with the respective observed minimum and maximum values are given in figures. Full model outputs and diagnostic plots can be found in the supplementary material S1.

Results

Nest protection

As expected, solitary nests were left unguarded for significantly longer than social nests (GLMM: $z = 8.29$, $p < 0.001$). The mean proportion of time during which nests were unguarded, calculated as the duration that a nest was unguarded [minutes] divided by the total observation time of that observation session [minutes], was 0.32 ± 0.21 for solitary nests ($n = 26$ observation sessions),

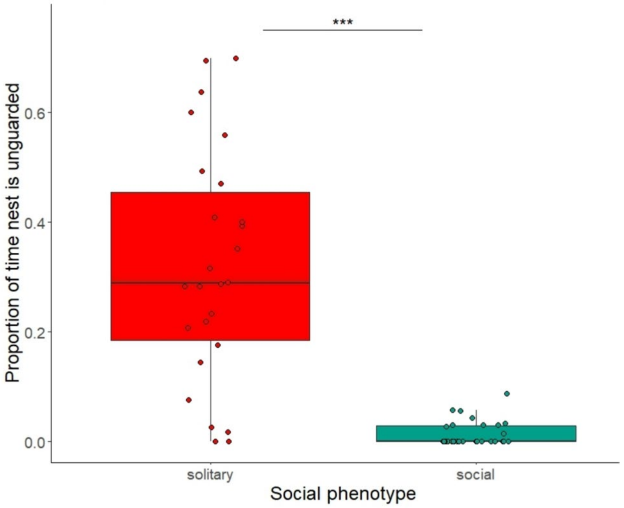

Fig. 3 Proportion of time that solitary nests (red, left) and social nests (green, right) are unguarded (no bee present in nest). Solitary nests are unguarded for significantly longer compared to social nests (GLMM: $p < 0.001$). Proportion is calculated as the time that a nest was unguarded divided by the total observation time. Boxplots show median, the 25th and 75th quartile and 1.5 * Inter Quartile Range (IQR), dots represent independent observation events. The figure shows the proportion of the total observation time during which nests were observed to be unguarded (statistical modelling used total observation time as an offset variable). The median proportion of time during which nests were unguarded was 0.29 min (minimum: 0.00, maximum: 0.69) for solitary nests ($n = 26$ observation sessions), and 0.00 min (median; minimum: 0.00, maximum: 0.09) for social nests ($n = 31$ observation sessions)

and 0.01 ± 0.02 for social nests ($n = 31$ observation sessions; Fig. 3).

Frequency of foraging trips

As social dominant females did not show substantial foraging activity (low frequency and short duration; see Fig. 5 for foraging duration of social dominant females), we consider here only solitary females versus social subordinate females in comparison of the frequency of foraging trips. The frequency of foraging trips, measured as the number of returns per hour for solitary females (0.77 ± 0.45, $n = 26$ observation sessions) and social subordinate females (0.87 ± 0.63, $n = 31$ observation sessions) did not differ significantly (GLMM: $z = -0.29$, $p = 0.77$; Fig. 4). For full model output, see supplementary material S1.

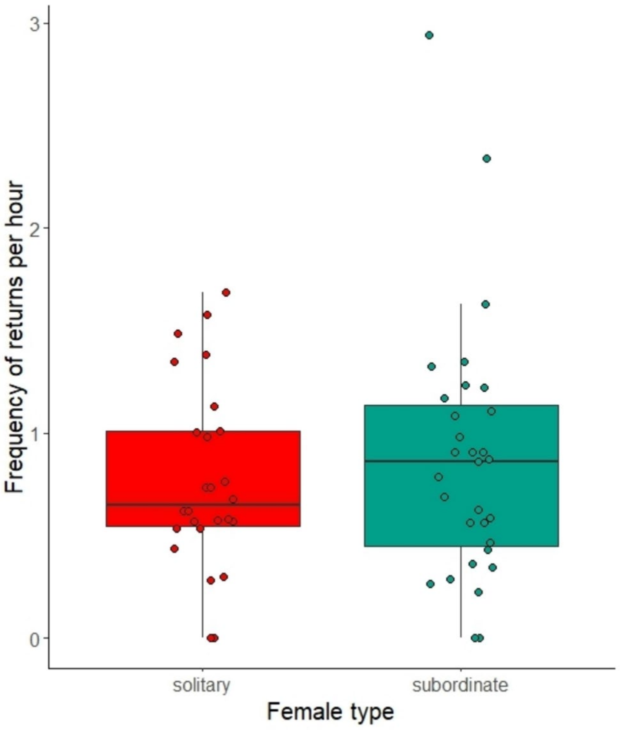

Fig. 4 The frequency of foraging trips of solitary females (red, left) and social subordinate females (green, right) did not differ significantly (GLMM: $p = 0.33$). The frequency of foraging trips is measured as the number of returns (to the nest) per observation time [hour]. Boxplots show the median, the 25th and 75th quartiles and 1.5 * IQR, dots represent independent observation events. The median frequency of foraging trips for solitary females was 0.64 (minimum: 0.00, maximum: 1.68, $n = 26$ observation sessions) and 0.85 for social subordinate females (minimum: 0.00, maximum: 2.93, $n = 31$ observation sessions)

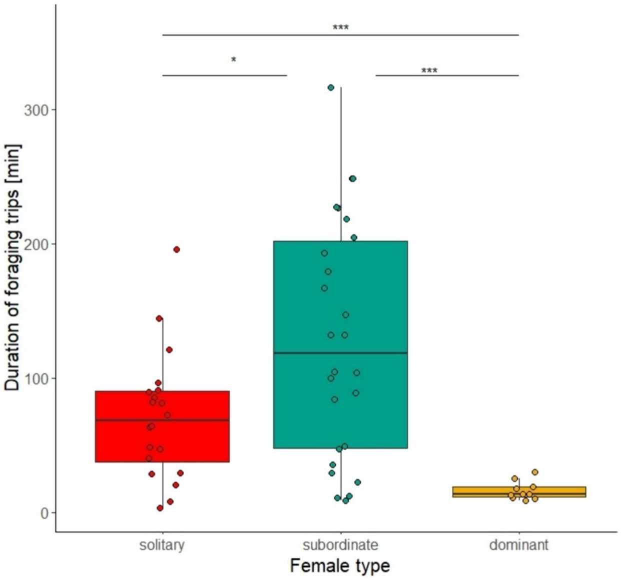

Fig. 5 Mean duration of foraging trips of solitary females (red, left), social-subordinate females (green, middle) and social-dominant females (yellow, right). Boxplots show the median, the 25th and 75th quartiles and 1.5 * IQR, dots represent independent observation events. The median foraging trip duration for solitary females was 68.21 min (minimum: 3.66, maximum: 195.65, $n = 20$ observation events). For social subordinate females the median trip duration was of 118.21 min (minimum: 8.65, maximum: 316.00, $n = 26$ observation events) and social dominant females were observed to have the shortest flight duration (median: 13.88 min, minimum: 8.91, maximum: 30.11, $n = 10$ observation events). ***, $p < 0.001$; *, $p < 0.05$

Duration of foraging trips

The trip duration differed significantly between solitary nests and social nests, with social nests including trips of the subordinate female treated separately from those of the dominant female (GLMM: LRT $\chi^2 = 56.27$, df = 2, $p < 0.001$; Fig. 5). Social subordinate females had the longest foraging trip duration, with a mean duration of 128.36 ± 88.41 min ($n = 26$ observation events). The mean foraging trip duration for solitary females was 70.61 ± 46.97 min ($n = 20$ observation events). The social dominant females were observed to have the shortest mean flight duration with 16.24 ± 6.85 min ($n = 10$ observation events). There was a significant difference in trip duration between solitary females and social subordinates (Tukey: $t = -2.71$, df = 50 $p = 0.02$, Fig. 5) and between solitary females and social dominant females (Tukey: Estimate: $t = -5.12$, df = 50, $p < 0.001$). The social subordinates also performed significantly longer trips than social dominants (Tukey: $t = -7.501$, df = 50, $p < 0.001$; Fig. 5). For full model output, see supplementary material S1.

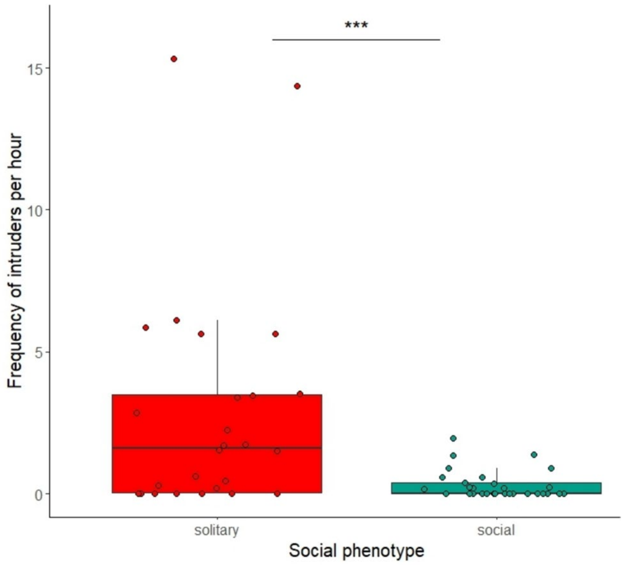

Fig. 6 Number of intruders that entered solitary nests (red, left) and social nests (green, right) per hour. Boxplots show the median, the 25th and 75th quartiles and 1.5 * IQR, dots represent independent observation events. The figure shows the proportion of intruders with respect to the observation time (statistical modelling used observation time as an offset variable). For solitary nests the median number of intruders that entered was 1.60 (minimum: 0.00, maximum: 15.33, $n = 26$ observation sessions) for social nests the median number of intruders that entered was: 0.00 (minimum: 0.00, maximum: 1.96, $n = 31$ observation sessions). ***, $p < 0.001$

Occurrence of intruders

The number of intruders differed significantly between solitary and social nests (GLMM $z = 3.58$, $p < 0.001$; Fig. 6). More intruders entered solitary nests (2.94 ± 4.06, $n = 26$ observation sessions) than social nests (0.30 ± 0.50, $n = 31$ observation sessions). For full model output, see supplementary material S1.

We found that slightly more intruders entered guarded versus unguarded solitary nests, though the difference was not significant (Fig. 7a). In solitary nests, 1.70 ± 2.48 ($n = 26$ observation sessions) intruders entered per hour while the nest was guarded, i.e. when the female bee was inside the nest, and 1.24 ± 2.15 ($n = 26$ observation sessions) intruders entered per hour when the nest was unguarded, i.e. when the female bee was not inside (Fig. 7a), a difference that was not statistically significant (GLMM: $t = 0.932$, df = 107, $p = 0.78$). In social nests, we also found that slightly more intruders entered guarded versus unguarded nests; for social nests, the difference was marginally statistically significant (Fig. 7b). The mean number of intruders that entered while the nest was guarded was 0.27 ± 0.45 ($n = 31$ observation sessions) versus 0.03 ± 0.10 intruders ($n = 31$ observation sessions) entered while the nest was unguarded (Fig. 7b; GLMM: $t = 2.816$, df = 107, $p = 0.03$).

The number of intruders that inspected the nest entrance but did not enter was significantly higher when nests were guarded for solitary (GLMM: $t = 7.70$, df = 104, $p < 0.001$) and for social nests (GLMM: $t = 5.24$, df = 104, $p < 0.001$). In solitary nests 1.54 ± 2.26 ($n = 26$ observation sessions) intruders inspected, but did not enter, the nest per hour while the nest was guarded and 0.43 ± 1.18 ($n = 26$ observation sessions) intruders inspected the nest per hour when the nest was unguarded (Fig. S1a). In social nests, the mean number of intruders that inspected, but did not enter, the nest per hour while the nest was guarded was 1.38 ± 2.82 ($n = 29$ observation sessions) and 0.00 ± 0.03 intruders ($n = 29$ observation sessions) inspected, but did not enter, the nest per hour while the nest was unguarded (Fig. S1b). For full model outputs, see supplementary material S1.

Discussion

Relatively little is known about the importance of the foraging-guarding trade-off for the evolution of sociality (Socias-Martínez and Kappeler 2019). Despite the fact that this trade-off is expected, few studies have empirically tested for it as a potential selective force favouring social life (e.g. Abrams and Eickwort 1981; Hogendoorn and Velthuis 1993). Our study closes this gap by comparing solitary and social nests of the socially polymorphic orchid bee *E. viridissima.* We tested whether sociality might reduce the costs imposed on a solitary life-style by the foraging-guarding trade-off, i.e. whether the threat of intruders and the need to guard the nest favours sociality. We found that social nests were guarded more than solitary nests and that fewer intruders entered social *versus* solitary nests, as also seen in the facultatively social *Xylocopa pubescens* (Hogendoorn and Velthuis 1993). Moreover, we found that subordinates in social nests undertook far longer foraging (provisioning) flights than solitary females, suggesting that solitary females may cut short their flights for brood cell provisions to minimize nest depredation.

Among the intruders we observed were *Melipona* bees, wasps, flies and conspecific *Euglossa* females, wasps and ants, which comprised the vast majority of all intruders. The relatively few intruders that entered social *E. viridissima* nests could be a consequence of their extended nest guarding, where one female was present in the nest most of the time. This result provides direct support for the parasite defence hypothesis for the evolution of sociality.

Sealing the nest entrance is a common strategy of fossorial and cavity-nesting Hymenopterans that helps to avoid intrusion by natural enemies (McCoquordale 1988, Richards 2004; Lienhard et al. 2010). In *E. viridissima*, females seal their nest from within during the brood guarding stage, when brood cell production and provisioning

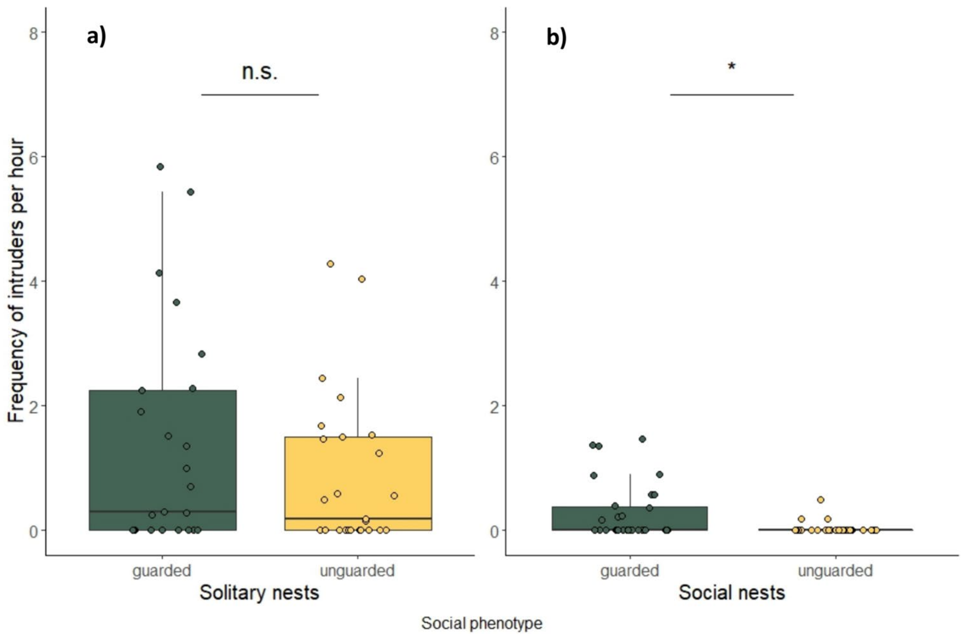

Fig. 7 **a** Number of intruders entering solitary nests and **b** social nests, when the nests were either guarded (green, left), i.e. when at least one female was present inside the nest, or when the nests were unguarded (yellow, right), i.e. when no bee was present inside the nest box. Boxplots show the median, the 25th and 75th quartiles and 1.5 * IQR, dots represent independent observation events. The number of intruders was not different when the female was absent from a solitary nest compared to when a female was inside the nest (GLMM: $p = 0.78$) but there were fewer intruders in unguarded social nests compared to guarded social nests (GLMM: $p = 0.03$). The figure shows the proportion of intruders with respect to observation time (statistical modelling used observation time as an offset variable). In solitary nests, 0.58 (median; minimum: 0.00, maximum: 10.32, $n = 26$ observation sessions) intruders entered per hour while the nest was guarded and 0.33 (median; minimum: 0.00, maximum: 9.89, $n = 26$ observation sessions) intruders entered per hour when the nest was unguarded (Fig. 7a). In social nests, the median number of intruders that entered while the nest was guarded was 0.00 (minimum: 0.00, maximum: 1.47, $n = 31$ observation sessions) versus 0.00 intruders (minimum: 0.00, maximum: 0.49; $n = 31$ observation sessions) entered while the nest was unguarded (Fig. 7b)

is complete, after which a female waits inside the nest for offspring emergence. During the brood provisioning phase while the female is foraging, however, the entrance usually remains open. Sociality could help to reduce intrusion by retaining a guarding female in the nest during the brood provisioning phase (Zammit et al. 2008; Rehan et al. 2011). Abrams and Eickwort (1981) found that communal nests of *Agapostemon virescens*, in which a female almost continuously guarded the nest entrance, were less vulnerable to intrusion than solitary nests because the female present in the nest could actively prevent intruders from entering. Boff et al. (2015) described the presence of a temporary guarding caste in *E. viridissima* during times of resource shortage, which prevented non-nestmate conspecifics from stealing nesting material. In other orchid bee species, the unguarded nests faced a higher number of attacks by natural enemies than nests in which females were present (Otero 2001; Soucy et al. 2003; Nogueira et al. 2019), though the opposite has also been found e.g. in some halictid bees (Packer 1986, 1988).

The number of intruders in solitary nests was not significantly different between guarded or unguarded nests, which was contrary to our expectation of a higher number of intruders when a nest is left unguarded. In social nests, we even observed higher intrusion rates when nests were guarded than when they were unguarded (though social nests suffered overall low rates of intrusion). We found the same trends when examining intruders that inspected the nest entrance, without entering nest, both for solitary and social nests. These results are surprising, because if the mere presence of a bee in the nest had been sufficient to ward off intruders, we would have expected to see less intruders when nests were guarded (Daly et al. 1967; Sick et al. 1994). We observe the opposite pattern (more intruders when guarded) and at the same time found reduced intrusion in social nests compared to solitary nests (see Fig. 7a, b for intruders that entered nests and SM2, Fig. S1a, b for intruders that inspected nest entrances without entering) suggests that social females might actively protect their nests against intruders using additional mechanisms. The stingless bee *Tetragonula carbonaria*, for example, deposits plant-derived products at the nest entrance, the chemical properties of which have been shown to act as a successful barrier for ants (Wang et al. 2018). The search for, application and maintenance of such products could be more easily achieved in a social environment, when tasks such as foraging and guarding can be divided among two or more individuals.

An explanation for finding more intruders and inspectors in guarded nests compared to unguarded nests could be that intruders locate their host nest by observing or following the movement or odour of a host female (Cane 1983; Münster-Swendsen and Calabuig 2000; Litman 2019), yet the preferred strategy of an intruder is still likely to be waiting for the nest to be unguarded (Cane 1983; Rosenheim 1987, Sick et al. 1994, Münster-Swendsen and Calabuig 2000, Litman 2019). The latter would also apply to solitary nests, yet we observed intruders entering guarded and unguarded nests at similar rates. Another possible explanation for the increased pressure of intruders in guarded nests is that intruders are not directly attracted to the resources inside the nest, but to physical or chemical signals emitted by their hosts (Batra 1965; Vinson 1976; Rosenheim 1987; Ostwald et al. 2019; Broder et al. 2022). With a guard at the nest entrance, a putative host cue, e.g. an odour, could be stronger, which could help explain why nests were more often intruded when a host bee was present. Alternatively, the nests might be guarded when they emit more cues, i.e. when they are also more sensitive to intrusion. When intruders and bees are attracted by the same cues to enter a nest (Müller and Robert 2001), this could result in guarded nests being more frequently visited by intruders. The reduced intrusion in social nests compared to solitary nests, regardless of whether they were guarded or unguarded, supports our hypothesis that sociality can help reduce the foraging-guarding trade-off through better protection of the nest against intruders. Still, it is not possible to exclude observer bias towards nests when they were guarded, compared to unguarded, as we might have been more attentive to a nest when bees were present in it.

Nest protection, defined here as at least one female being present in the nest, was indeed higher in social nests than in solitary nests. This suggests that solitary females are more impacted by the foraging-guarding trade-off (Soucy et al. 2003; Ohkubo et al. 2018). During the time that the solitary female leaves her nest to forage for brood provisions, her nest and the brood are unguarded, which leaves them potentially more vulnerable. The risk of the nest being depredated increases with the time that the nest is unguarded (Goodell 2003; Seidelmann 2006; Zurbuchen et al. 2010). But in nests with more than one bee present, females can cooperate and divide the tasks of foraging for brood provisions and guarding such that one bee is always present in the nest while the other is foraging. Our results suggest that, in social nests of *E. viridissima*, females are indeed released from the foraging-guarding trade-off. The dominant female only occasionally left the nest for short trips (maximally once per day), on return from which she was never observed to carry pollen in her corbiculae. We assume that she was collecting food for herself rather than collecting brood provisions. Besides these short periods of absence from the nest, the dominant female stayed inside the nest while the subordinate female often undertook multiple brood provision flights per day. This could be an indication for active cooperation and division of labour, rather than a passive side effect of nest sharing (McCorquodale 1988, see Ostwald et al. 2022). To clarify this potential cooperation, it would help to understand the genetic relationship between the two social partners.

In social species, or those with guards, constraints on foraging are relaxed and foraging females can optimize their foraging time i.e. undertake longer provisioning trips (Prager 2014; Mikát et al. 2017) to maximize their return of brood cell provisions to the nest. Solitary females, on the other hand, are bound to the foraging-guarding trade-off and cannot, therefore, optimize their foraging time to maximize the return of provisions to the nest but rather to maximize brood production as a function of foraging duration and brood survival. Indeed, foraging trips of solitary *E. viridissima* females were shorter that those of subordinate females in social nests. Our results suggest that sociality may indeed mitigate the foraging-guarding trade-off. On theoretical grounds, solitary females should reduce the time spent out of the nest to avoid intruders and potential natural enemies that depredate the brood and nesting material. Hogendoorn and Velthuis (1993) have found that foragers in social nests of *X. pubescens* perform longer foraging trips when the nest is guarded by another bee. Despite being expected, no such pattern in foraging behaviour has been seen in a variety of other socially polymorphic bee species (e.g. Vogel and Kukuk 1994; Prager 2014); such a pattern might also be dependent on the kind of intruder or natural enemy.

Our results demonstrate that social nesting is a benefit in terms of nest protection against intruders. Though we did not quantify reproductive success in terms of offspring production in our observed solitary and social nests, we have evidence that brood survival in *E. viridissima* is markedly improved by the presence of a guarding female (Friedel et al. in press 2024). Similar results have been reported for other facultatively social bees (Smith et al. 2003, 2007; Zammit et al. 2008, Rehan et al 2011). It has long been argued that cooperative behaviour may have evolved as an adaptation to the selective pressure imposed by natural enemies (Lin 1964; Lin and Michener 1972, Hogendoorn and Velthuis 1993; Evans 2009; Socias-Martínez and Kappeler 2019, Hearn et al. 2022). However, the benefits of guarding might also be associated with assured fitness returns (Smith et al. 2003); if one female dies, her direct or indirect fitness investment can be realized by the remaining female through her continuing protection of the dead female's offspring or collateral kin

(Smith et al. 2017). Assured fitness returns could account for sociality and for why subordinates undertake potentially risky foraging even in social systems with weakly related or unrelated nestmate females if both females contribute to offspring production in the nest, as in *Euglossa melanotricha* (Andrade et al. 2016).

Conditions that favour group nesting, such as predation pressure and resource availability, can fluctuate seasonally or inter-annually (Soucy et al. 2003, Smith et al 2019, Rehan et al 2011), making helping sometimes more beneficial and at other times less beneficial (Stark 1992, Hogendoorn and Velthuis 1993). Sociality might then be favoured when conditions beyond parasitism are harsh or very variable (Socias-Martínez and Kappeler 2019). However, the opposite is observed for halictid bees (see e.g. Field et al. 2012). The seasonal differences in adult survival, e.g. through changes in foraging effort, and in nest productivity might influence the costs and benefits of sociality (Smith et al 2019). Even though social nesting provides obvious benefits in terms of nest protection and assured fitness returns, the fitness benefits through individual (solitary) nesting might be higher than the indirect fitness benefits of being a helper (Smith et al. 2019); sociality might be seasonally dependent on survival benefits and increased nest productivity (Smith et al 2019, Rehan et al 2011). The social polymorphism in *E. viridissima* might then result from temporally fluctuating selection: females in social groups might be in a better position to bridge unfavourable environmental conditions, and then start solitary reproduction when conditions are favourable again for (solitary) brood provisioning or nest protection, making the social polymorphism a bet hedging strategy (Rehan et al. 2011; Kennedy et al. 2018; Smith et al. 2019). Social subordinate *E. viridissima* females might eventually disperse and become solitary foundresses, thus potentially accruing indirect fitness benefits as helpers and direct fitness benefits as foundresses. This would be an interesting topic for further exploration of the costs and benefits of sociality in this species.

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Data availability All the data are contained in the Supplementary Material 1 (xlsx).

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval Not applicable.

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