



Reproductive inefficiency and increased behavioral variation are associated with large group size in the orchid bee, *Euglossa dilemma*

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Abstract

Orchid bees are the only corbiculate bee lineage that is not obligately eusocial. However, multiple species of orchid bee show facultative sociality, with reproductive division of labor and a social hierarchy effectively enforced by oophagy. Orchid bee species differ in the degree of reproductive skew in social groups, as well as the rigidity of social roles. In the orchid bee *Euglossa dilemma*, previous observation of social groups of two or three individuals found that reproductive skew was complete, with one clear dominant individual that ate and replaced each subordinate laid egg. Here, we compare patterns of egg laying and egg-replacement between typical social nests of 2–3 individuals and larger social nests of 4–5 individuals. We find a striking difference in the reproductive behavior of colonies of varying group size; larger nests exhibit more reproductive inefficiency and conflict over the dominant social position, characterized by repeated oophagy and slower egg replacement. Our findings are consistent with the hypothesis that group size in *E. dilemma* may be limited by the ability of dominant bees to keep up with egg replacement. We discuss the possible causes and consequences of observed behavioral variation and its implications for understanding social behavior in orchid bees.

Keywords Orchid bees · *Euglossa* · Facultatively social · Oophagy · Reproductive conflict

Introduction

Social insects that form small or facultatively social affiliations may be especially useful as model systems for understanding the emergence of reproductive division of labor, a defining characteristic of eusocial species (Brahma et al., 2018; Shell & Rehan, 2018). The orchid bees (Euglossini) are the only tribe in the corbiculate bees (which includes honey bees, bumblebees, and stingless bees), which is not obligately eusocial, instead exhibiting solitary or

facultatively social life-histories, where females may form small, cooperatively breeding groups (Saleh et al., 2022). In orchid bee species within the genus *Euglossa*, social groups may consist of 2–3 females where one individual is a dominant reproductive and nest guard, and one or two individuals serve as subordinate foragers (Cocom Pech et al., 2008). Although these social groups show features typical of eusociality, including overlapping generations, cooperative brood care, and reproductive division of labor, they lack non-reproductive workers. Instead, they effectively achieve an indirect reproductive division of labor through oophagy, where a queen-like dominant individual eats and replaces eggs previously laid by worker-like subordinates.

Across species of *Euglossa*, there appears to be substantial variation in the rigidity of social role and the degree to which full reproductive skew via oophagy is achieved. In some species, such as *E. cordata*, reproductive skew is complete, with all social groups having a single dominant individual that eats and replaces all subordinate laid eggs in the nest (Freiria et al., 2017). This appears to be the case whether social groups consist of kin or unrelated females (Freiria et al., 2017). In contrast, in *E. melanotricha* social nests, dominant females adjust oophagy rates based on the

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relatedness of nestmates, with dominant females eating only 51% of eggs laid by unrelated subordinates, compared to up to 84% of eggs laid by kin (Andrade et al., 2016). In other species, like *E. annectans* and *E. townsendi*, social roles may be unstable, with individuals transitioning back and forth between dominant and subordinate-like roles, or with multiple dominant individuals vying for reproductive control involving repeated egg replacements among individuals (Augusto & Garófalo, 2004; Boff et al., 2017).

Observation of *E. dilemma* has suggested that reproductive skew in this species is complete, with a sole dominant bee responsible for all reproductive output in a nest, regardless of relatedness to the subordinates (Saleh & Ramírez, 2019; Saleh et al., 2021). Observations in Saleh and Ramírez, 2019 revealed that in *E. dilemma* social groups, each brood cell is first provisioned by a subordinate bee, which then lays an egg and closes the brood cell. The dominant bee then opens the brood cell, eats the subordinate egg, replaces it with her own, and closes the brood cell. Furthermore, these social groups, which typically range in size from 2 to 3 individuals, show highly consistent dominant and subordinate roles, with social hierarchy among nestmates only changing when the dominant individual dies or disappears. However, it was observed that *E. dilemma* group sizes can occasionally grow to 4–5 individuals with groups persisting for several weeks or months (N. Saleh, personal observation).

These observations raise questions about how social group size may affect reproductive interactions and whether larger social groups show the same consistent patterns of complete reproductive skew and stable dominance hierarchies seen in smaller groups (2–3 individuals). In addition, it seems plausible that the oophagy and egg replacement behavior displayed by the dominant female may become inefficient with increasing group size, though this remains unexplored. Finally, it is not known whether these larger social groups consist of a single dominant individual with additional foragers, multiple individuals competing for

dominance in addition to one or two foragers, or some other undescribed combination of behaviors. Here, using continuous video monitoring of behavior and reproduction in social nests of varying group size, we evaluated the possible effects of group size on reproductive strategies in *E. dilemma* nests.

Methods

Euglossa dilemma nesting behavior was observed in Broward County, Florida, USA, where *E. dilemma* was accidentally introduced approximately 20 years ago (Skov & Wiley, 2005). Active nests were monitored at the University of Florida, Fort Lauderdale Research and Education Center, where trap nests have been maintained since 2015. Each wooden trap nest box (3.5" × 2.5" × 3") had one 5/8" hole drilled into one side to serve as an entrance/exit. In addition, all boxes had a red plexiglass lid placed on top to facilitate video recordings. These boxes were placed outside on the eaves of a covered structure so that the boxes were shielded from the rain and wind. Nests were initiated by the bees in available nest boxes without any human intervention, by bees from the locally established population.

For nest observation, we used infrared CCTV cameras placed on top of the red plexiglass lids, which allowed us to continuously record video to an attached digital video recorder. Video recordings were downloaded from the digital video recorder for later analysis. Recording of nests was done opportunistically on available nests year-round, which may have been active for multiple generations before observation began. Nests were chosen for inclusion in the study post-hoc based on the availability of long-term video recordings required for confirming consistent nest membership. Each nest included in the dataset was observed continuously for at least one month, with some observed up to eight months (Table 1).

Table 1 Data summary for nests used in reproductive observations of *E. dilemma*

Nest ID	Dates observed	Days observed	Brood cells completed	Egg laid	Nest size
2	05/19/2016 – 06/20/2016	32	9	20	Small
21_1	10/19/2021 – 06/13/2022	237	18	37	Small
21_50	12/01/2021 – 1/06/2022	36	9	18	Small
21_10	03/17/2022 – 05/26/2022	70	9	18	Small
21_12	06/12/2022 – 08/28/2022	77	9	22	Small
21_14	09/08/2022 – 11/12/2022	66	5	10	Small
8_47	07/03/2019 – 08/24/2019	52	12	43	Large
18_79	12/07/2021 – 08/07/2022	243	25	98	Large
P1	03/01/2022 – 05/29/2022	89	21	82	Large
21_44	04/01/2022 – 05/30/2022	59	11	31	Large
21_13	06/12/2022 – 08/28/2022	77	10	31	Large

Video files were viewed using VLC media player (VideoLan, 2006), which allowed for high-speed playback of video in between brood cell construction and completion. All recorded videos were time-stamped by the digital video recorder, so that information containing Nest ID, date, and time are displayed on the recordings (see Fig. 1 and Figs. S1, S2, S3, S4 and S5, for representative screenshots). When a particular brood cell under observation neared completion, playback was slowed to 2× speed, to identify the timing of specific reproductive events. The time and dates of all completed egg laying, egg eating, and egg replacement events for each brood cell were recorded as well as the identity of involved individuals (Table S1, electronic supplementary material). To track individual identity, bees were marked with small plastic numbered discs glued to the thorax with cyanoacrylate glue.

Nests were classified as “social” if more than one individual was present for multiple complete brood cell provisioning and egg laying processes, as solitary nests were not included in this study. Social nests were further classified as “small,” if 2–3 individuals were consistently observed over multiple brood cell provisioning and egg laying processes. Nests were classified as “large” nests if at least 4 individuals were consistently observed for multiple brood cell provisioning and egg laying processes over the span of at least two weeks. In this study, six “small” nests and five “large” nests were used.

All statistical analyses were conducted with R (R Core Team, 2023). Due to consistent deviations from normality and heteroscedasticity in the data, we used Mann Whitney U tests to compare reproductive differences based on egg laying and egg replacement behaviors between “small” and “large” group size nests.



Fig. 1 Representative screen shot from video recordings of a “large” nest (21_44) of five tagged individuals. Date and time (lower right corner) stamps are shown on videos. The nest entrance is shown in the top center of the image, with the cluster of brood cells shown just inside. The debris scattered around the nest floor and walls consists primarily of resin collected by the bees

Results

Across all nests, we observed 410 eggs laid in 138 brood cells, spanning over 1000 days of continuous video recording (Table 1). Consistent with previously published data for *E. dilemma* and other *Euglossa* species, we found that subordinate egg laying occurred primarily in the early afternoon, with dominant replacement occurring most frequently around 3.5–4 h after subordinate egg laying, though egg replacement was also observed overnight and into the morning (Fig. 2). Of the 138 brood cells, a dominant bee laid the final egg in 136, or about 98.6%, of these brood cells. Of the two subordinate eggs that were not replaced, one was in a nest of three individuals (“small”), and one was in a nest of four individuals (“large”).

Individual behavior in social groups

We sought to classify individual behavior in social groups to determine whether reproductive division of labor or other individual behaviors differ between groups of varying size (Table 2). We observed three broad categories of behavior across all nests. As expected from previous studies, we observed subordinate foragers, which collected pollen and resin and laid the first egg in brood cells. We also observed dominant females, which primarily remained in the nest without foraging and replaced eggs laid by other bees. Finally, in several large nests, we observed an additional category of behavior that we term “stay-and-wait,” in which females were present in nests for multiple weeks without foraging or egg-laying, with these behaviors sometimes initiated after a turnover in nest membership. In “small” group nests, all individuals could be clearly categorized as “dominant” or “subordinate,” with all “small” groups having one dominant bee and one or two subordinate bees. No “stay-and-wait” females were observed in small nests.

The additional members of “large” social groups expressed several combinations of the three broad behavioral roles, thus elevating the number of nestmates compared to “small” groups. For example, in 2/5 “large” group nests, three subordinate foragers were simultaneously present along with at least one dominant. In 4/5 “large” nests, two dominant egg laying individuals were simultaneously present in the nest, with at least one of these corresponding to a bee that did not emerge from the focal nest and was not the foundress. In one case, the second dominant bee to join an existing social nest was formerly the dominant bee in a nearby nest, which had recently lost its subordinates and had no remaining live brood. In most cases, the two dominant bees persisted over time without

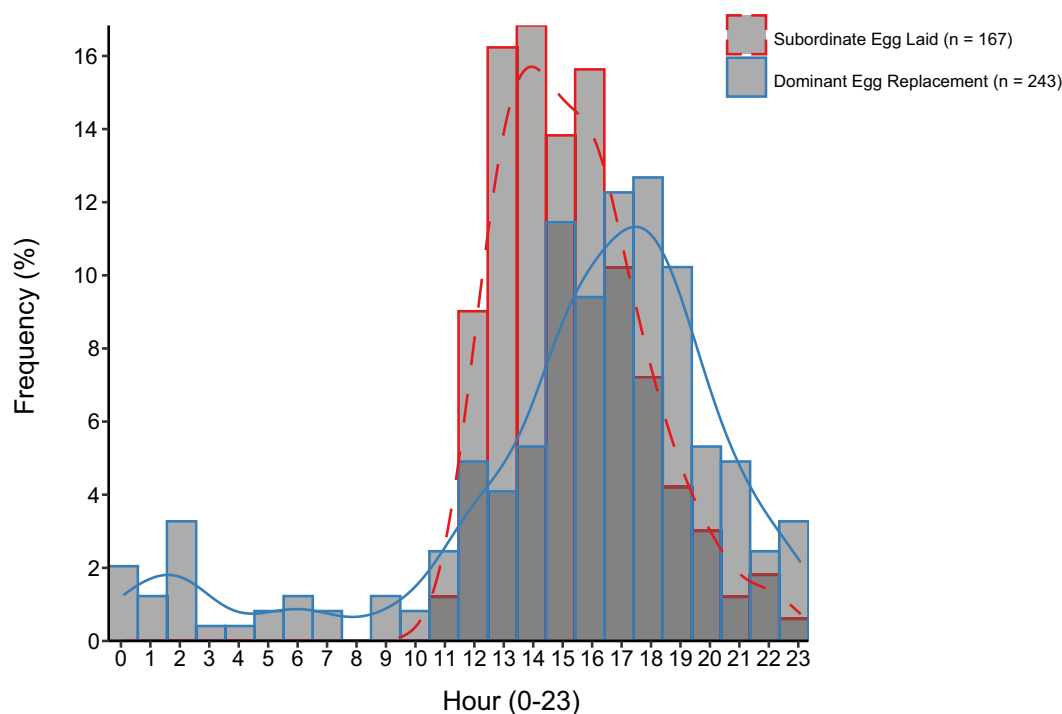


Fig. 2 Circadian rhythm of subordinate egg laying and dominant egg replacement. A density histogram is shown, with the X-axis showing hours from 0 to 23, with “0” representing midnight. The Y-Axis shows the frequency of observations falling into a particular hour,

with each bar representing the percent of observations at that time. Subordinate eggs laid and dominant egg replacement frequencies were calculated from the total number of eggs laid

Table 2 Summary of behavioral roles observed in small and large nests

Behavior	Observed at least once in “small” nests	Observed at least once in “large” nests
One dominant and one or more subordinates	6/6	5/5
Two dominants with one or more subordinates	0/6	4/5
Three provisioning subordinates	0/6	2/5
“Stay-and-wait” female(s)	0/6	3/5
Primary oophagy	6/6	5/5
Secondary oophagy	3/6 (7/136 events)	5/5 (129/136 events)

obvious aggression. However, in one case, after a period of approximately three weeks in the same nest, one dominant bee became highly aggressive, stinging the other dominant bee until it died. We did not observe any other event where aggression between individuals led immediately to mortality.

In 3/5 large nests, “stay-and-wait” females were observed. “Stay-and-wait” females differed substantially from one another in their duration in the nest and in the individual behaviors they exhibited. For example, in one nest, two “stay-and-wait” bees were simultaneously present for over four months before any foraging or reproductive activity was observed from these individuals. In this case, upon disappearance of the active dominant and subordinate pair, these

two “stay-and-wait” females transitioned to behavior typical of a standard dominant and subordinate bee, with one “stay-and-wait” female initiating foraging while the other remained in the nest and replaced eggs. In another nest, one “stay-and-wait” female showed no foraging or reproductive activity for over one month, until she replaced two subordinate laid eggs and disappeared from the nest.

Egg replacement, oophagy, and brood cell completion

Next, we sought to evaluate possible deviations from expected egg replacement patterns in “small” versus “large” social nests. Considering the ratio of eggs laid per brood cell

completed, we expect to see two eggs per brood cell—one first laid by the subordinate and one replacement egg laid by the dominant following oophagy (Saleh and Ramírez, 2019). In “large” nests, we see an elevated ratio of eggs laid per brood cell compared to “small” nests (mean: 3.26 vs. 2.12 eggs per brood cell per nest, median: 3.58 vs. 2.03, “large” nest $n = 5$, “small” nest $n = 6$, Mann–Whitney U , $p < 0.01$, Fig. 3A). No nest of either category had a ratio below two. We also saw differences in the timing of egg replacement by dominant bees between “small” and “large” nests, with dominant bees taking longer to replace eggs in “large” nests relative to “small” nests (mean: 9.42 vs. 3.60 h, median: 3.78 vs. 2.41 h, “large” nest $n = 94$, “small” nest $n = 59$, Mann–Whitney U , $p < 0.001$, Fig. 3B).

In addition, we examined patterns of oophagy between “small” and “large” nests. Typically, as observed in “small” nests, the first instance of oophagy in a brood cell is done by a dominant bee eating a subordinate’s egg, except in cases where the provisioning subordinate has disappeared before the brood cell was completed. In these cases, dominant bees laid eggs directly onto the available provision. Beyond the first occurrence of oophagy (primary oophagy), we observed 136 instances of secondary oophagy across all nests, where at least one additional round of oophagy occurred. These instances were divided into three categories of oophagy: “self-oophagy,” where a dominant bee ate her own egg,

“dominant oophagy,” where a dominant bee ate the egg of another dominant egg-layer in the nest, and “subordinate oophagy,” where the dominant bee ate an egg laid by a subordinate bee an additional time after the first subordinate laid egg. In these “subordinate oophagy” cases, primary oophagy was not immediately followed by a dominant bee laying an egg, and this delay resulted in the subordinate restarting brood cell provisioning in the open brood cell and then laying another egg in that brood cell. This egg was subsequently eaten by a dominant bee.

Of the 136 instances of secondary oophagy, seven occurred in “small” nests and 129 occurred in “large” nests. Of the seven instances in “small” nests, three of these consisted of “self-oophagy” by the dominant bee and four of these were categorized as “dominant oophagy.” These seven instances of secondary oophagy were observed across three of the six “small” nests. In three of the four cases of “dominant oophagy,” outside bees, present in the nest for a period less than a day, opportunistically laid an egg in an open brood cell or replaced a recently laid egg, which was then replaced by the resident dominant bee. Although we categorize these three cases as “dominant oophagy,” based on the egg eating/replacement behavior, we note that these individuals are distinct from typical dominant bees, as they are not participating any further in the social group. In the fourth case, an outside bee ate an egg that was

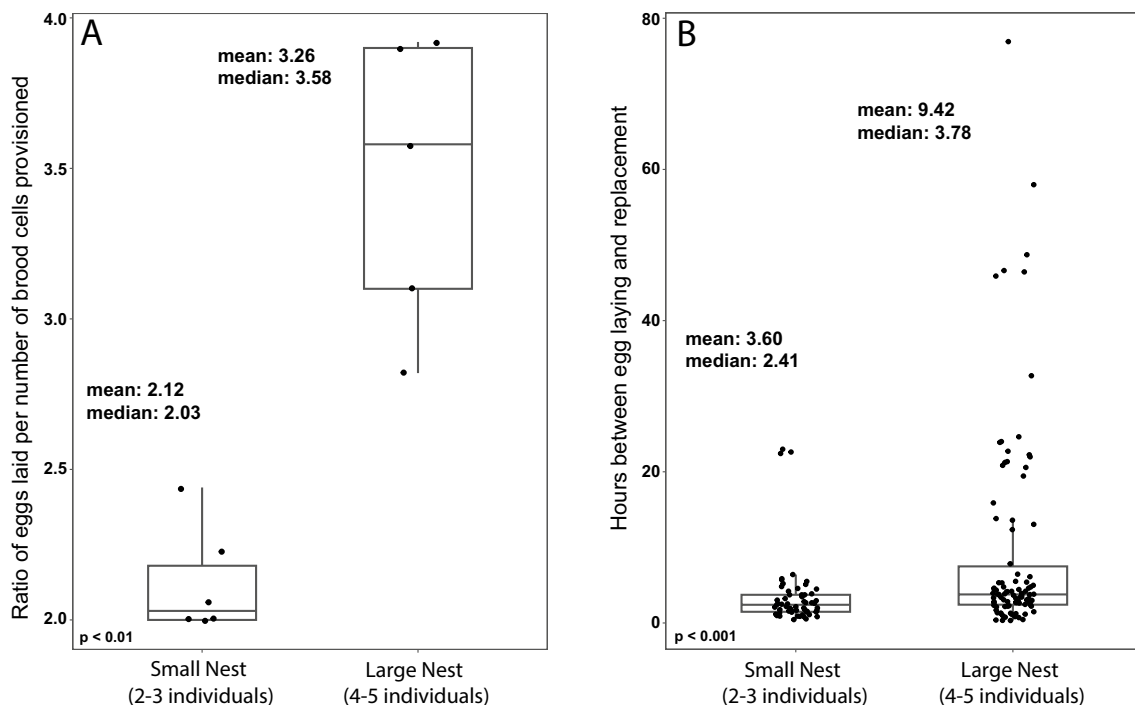


Fig. 3 Comparison of “small” nests and “large” nests based on (A) the ratio of eggs laid per number of brood cells provisioned in each nest and (B) the time between egg laying by a subordinate and egg

laying of the corresponding replacement egg by a dominant. In Both A and B, the difference between the “small” nests and “large” nests is statistically significant in a Mann–Whitney U test

laid by the resident dominant bee, which had disappeared approximately three days prior. The new bee then assumed the vacant dominant position, while the two subordinates in this “small” nest continued foraging. Of the 129 instances of secondary oophagy observed in large nests, 29/129 (22.5%) were “subordinate oophagy,” 37/129 (28.7%) were “dominant oophagy,” and 62/128 (48.8%) were “self-oophagy.” Secondary oophagy was observed in all five “large” nests. Ultimately, this increased rate of secondary oophagy in large nests contributed directly to the higher number of eggs laid per brood cell in large nests (Table 1 and Fig. 3A). We also note that secondary oophagy was not obviously associated with sustained disruptions to social behavior and it occurred within the context of seemingly typical provisioning and reproductive behaviors.

Finally, we assessed the rate of brood cell completion between “large” and “small” nests, to evaluate possible effects of group size on productivity. To do this, we summarized productivity in each nest by dividing the number of days in a reproductive period (when foraging and egg laying were occurring) by the number of brood cells completed during that period. We found no significant differences in the rate of brood cell production between “large” and “small” nests (mean: 4.48 vs. 4.42 days per brood cell, Mann–Whitney U , $p=0.93$), suggesting that the per-capita productivity is marginally lower in “large” nests compared to “small” nests. In other words, brood cell production was not faster in “large” nests, despite the presence of additional individuals.

Discussion

Here, we examine reproductive behavior in social groups of *E. dilemma*, comparing typical “small” groups of 2–3 individuals and “large” groups of 4–5 individuals. Across all social groups, regardless of group size, dominant bees were responsible for almost all the reproductive output of social nests, achieving nearly complete reproductive skew relative to subordinates. However, our observations revealed distinct behavior associated with group size, with larger groups displaying a higher number of eggs laid per brood cell, slower egg replacement by dominant bees, and increased occurrence of secondary oophagy. In addition, large group size was associated with previously unreported behavioral variation, including activity by three simultaneous foragers (instead of the usual 1 or 2), multiple dominant egg laying females within a single nest, and the presence of “stay-and-wait” females.

Reproductive inefficiency in large groups

Across social insects, group size has an inconsistent relationship with reproductive efficiency and productivity,

varying from species to species (Dornhaus et al., 2012). In *E. dilemma*, we find evidence of a relative reproductive inefficiency in large groups. Despite a net higher number of eggs laid per brood cell, nest reproductive output was not improved in large groups when compared to small groups. Notably, slower egg replacement by dominants, and higher rates of secondary oophagy were observed in large groups compared to small groups. In addition, larger groups produced brood cells at the same rate as small groups, despite the extra individual(s), leading to lower per capita productivity. In most of the large nests we observed (3/5), larger group size was not driven by the presence of additional subordinate foragers, which could be expected to improve reproductive efficiency and/or productivity through additional brood cell production. Instead, the presence of an additional dominant egg-layer (4/5 large nests) and “stay-and-wait,” females (3/5 large nests), appears to have decreased efficiency and per capita productivity through repeated egg-replacement or lack of involvement in foraging and reproduction. In *E. townsendii* and *E. carolina*, nest productivity was correlated with the number of foraging individuals in the nest, though per capita brood cell production decreased with an increasing number of females, due to the presence of non-foraging, dominant or dominant-like females (Augusto & Garófalo, 2004; Augusto & Garófalo, 2010). In *E. dilemma*, it is difficult to disentangle the direct effects of individual behaviors on reproduction in the nest, as behavioral composition and patterns of individual turnover varied from nest to nest. Our observations of multiple dominant females are reminiscent of descriptions of simultaneous “egg-laying females,” in *E. townsendii*, which repeatedly ate and replaced each other’s eggs. However, in *E. townsendii*, these “egg-laying females,” also occasionally transitioned back to foraging behavior, which we did not observe in *E. dilemma* dominant females. In addition, *E. townsendii* nests with multiple egg-laying females consisted of individuals that likely emerged from the same brood cells (or the original foundress). In our observations of *E. dilemma* nests with two dominant females, one dominant female was already present in the nest and joined by a second dominant female from outside of the focal nest. Given this, different pressures may be acting on *E. dilemma* resulting in reproductive conflict between two dominant females.

Self-oophagy was the most common form of secondary oophagy, occurring across all large nests regardless of the behavioral composition of these nests. Although oophagy is a typical feature of euglossine social groups, extensive self-oophagy has been rarely reported. Self-oophagy has been recorded in *E. dilemma* sister species, *E. viridissima*, where a dominant female replaced her own egg after briefly leaving the nest (Cocom Pech et al., 2008). Social behavior may impose unique cognitive challenges, due to the importance of social learning and individual recognition on

colony function (Chittka & Rossi, 2022). It is possible that the high rate of self-oophagy and the longer egg replacement times we observe in *E. dilemma* “large” nests are partially driven by difficulty in keeping track of egg laying among an increased number of nestmates, lack of chemical cues that facilitate recognition involved in oophagy, or the disruption of such a signaling system. In *E. dilemma*, dominant status is associated with specific CHC changes (Saleh et al., 2021). In the social burying beetle *Nicrophorus vespilloides*, CHCs encode the breeding status of adults, but not individual identity (Steiger & Stöckl, 2017). It may be that in *E. dilemma*, where social groups commonly have a single dominant individual, that the presence of multiple dominant bees in the nest may obscure or confuse typically consistent chemical cues left by the dominant bee to track their own behavior. Little is known about the interplay between sensory cues, cognition, and oophagy in orchid bees; further experiments are needed to better understand how dominant bees are identifying brood cells for egg replacement and/or if they can keep track of specific nestmate identity and activity within the nest.

Barriers to eusociality and increased group size

Euglossine bees are the only corbiculate bee tribe that has not evolved eusocial behavior characterized by physiologically distinct queens and workers (Soucy et al., 2003). However, in *E. dilemma*, dominant bees achieve nearly complete reproductive output (with respect to subordinate reproduction) through behavioral means (oophagy), instead of through physiological control of helpers. In other eusocial species, queen pheromones and/or aggression may inhibit ovary development in workers (Oystaeyen et al., 2014; Saha et al., 2012). Although the behavioral specialization between dominants and subordinates has resulted in an effective reproductive division of labor in orchid bees, this specialization of behavior without correlated physiological change may ultimately constrain further social elaboration and increased group size. Orchid bee ovarian physiology is more typical of solitary bees than eusocial species, having fewer ovarioles per ovary and larger oocytes than eusocial species, slowing down oviposition rate (Augusto & Garófalo, 2010). It has been suggested that this combination of physiology and oophagy behavior places a constraint on group size in *Euglossa*, since dominant bees must keep up with subordinate egg-laying to maintain reproductive control (Augusto & Garófalo, 2010). Our findings, especially the slower replacement rate of subordinate-laid eggs in large nests, are consistent with this hypothesis and could result from limitation in egg laying speed. In addition, in all large nests, we observed instances of secondary, “subordinate” oophagy. This occurred when the dominant bee first ate the subordinate’s egg but did not immediately replace it, instead

leaving the brood cell open for an extended period, until the subordinate began provisioning again. One possibility is that this behavior is due to some refractory period in egg-laying, with dominant bees unable to keep up with oviposition in large nests, giving the opportunity for a subordinate to lay an egg in the same brood cell, which ultimately leads to secondary oophagy events. Although our data are consistent with physiological limitations impeding large group size, group size is a dynamic phenotype shaped by a variety of selective forces. Future study of individual fitness across social behaviors from different groups sizes would be especially powerful in providing context for limits on group size.

Possible causes of large group size and behavioral variation

Based on these observations, it appears that larger group sizes in *E. dilemma* do not provide a reproductive advantage at the dominant individual level. Instead, large groups reduce reproductive efficiency and create a higher degree of reproductive conflict compared to small groups. Why then, do these groups form and persist for weeks or months? One possibility is that some bees join existing nests opportunistically, due to failure in their own nest. For example, in one “large” nest in this study, with two dominant bees, the second dominant bee had previously been observed as a dominant bee in a failed nest, where all subordinates had disappeared, and all remaining brood were dead. Rather than restarting solitary foraging, there may be a greater probability of increasing reproductive output by joining or usurping an existing nest. “Stay-and-wait” females may also be acting opportunistically, waiting either to inherit the nest or gain some share of reproduction without foraging. Unfortunately, we do not know the history of all of these “stay-and-wait” females, so it is unclear if these are females from failed nests or if these are younger females following an alternative life-history strategy. Some carpenter bee species have “tertiary females,” which wait out an entire reproductive season, remaining quiescent in the nest, to have the first opportunity of inheriting the nest the following year (Richards, 2011). The *E. dilemma* “stay-and-wait” females we observe could represent a similar strategy. Resin, the primary nest building material used by many orchid bees, including *E. dilemma*, is expected to be costly to gather, with resin theft from conspecifics occurring commonly in some orchid bee species (Boff et al., 2015). It is possible that costs associated with finding a suitable location for and building a new nest may be steep enough to favor alternative nesting strategies. It is also possible that our observation site had a higher density of nests and/or individuals that artificially encouraged larger group size formation. However, the incorporation of non-kin bees into existing social groups, as well as theft and usurpation by conspecifics, is widely documented across multiple

Euglossa species (Boff et al., 2015; Andrade-Silva & Nascimento, 2015) and consistent with our observations of *E. dilemma*. Further study is needed to disentangle the factors that lead unrelated dominant bees to coexist within a nest over time, despite clear reproductive conflicts.

Conclusions

In this study, we find that “large” social groups in *E. dilemma* show increased signs of reproductive competition and inefficiency. Furthermore, these “large” groups harbor previously undescribed behavioral variation, not seen in typical “small” social groups. Reproductive inefficiency may be driven by the reliance of *E. dilemma* on behavioral rather than physiological control of social reproduction. If this is the case, it is possible that orchid bee social evolution is constrained by the decoupling of ovarian physiology and behavior that is typically present in eusocial species. Additional experiments examining limits on oviposition rate and the sensory cues involved in oophagy are necessary to shed light on the factors that have shaped group size in orchid bees.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00040-024-00967-2>.

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Data availability Observational data taken from video recordings is available in the online supplementary material associated with this study.

Declarations

Conflict of interest The authors declare no competing interests.

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