

Reproductive Task Specialisation Through the Lens of Ovarian Groundplan Hypothesis: An Individual-Based Model

Research project report

by

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Abstract

Eusociality presents a fascinating phenomenon observed primarily in insect societies. The Ovarian Groundplan Hypothesis (OGH) posits that eusociality may arise from pleiotropic side effects and contextual shifts in the ovarian cycle of solitary insects. To explore this hypothesis, we developed an individual-based simulation model simulating the evolution of eusociality inspired by OGH. Our model incorporates the notion that the reduction and enlargement of ovary size for foraging and breeding, respectively, incur significant energy and resource costs, thus imposing a survival cost to task switching. Through extensive simulations varying task switching costs, we observed distinct evolutionary trajectories. When there was no cost to task switching, group living emerged, but task specialization did not occur. With a small cost to task switching, altruistic behaviours increased, leading to increased relatedness and enhanced foraging. However, under a higher cost scenario, task specialization emerged, albeit resulting in evolutionary suicide. Our findings provide support for the OGH, suggesting that under certain conditions, altruistic behaviours can evolve, but further refinement and exploration of model parameters are necessary to fully elucidate the mechanisms driving eusocial evolution.

Introduction

Eusociality represents a pinnacle of social organization within certain species, characterized by intricate divisions of labour among individuals. In such societies, distinct castes specialize in one of the tasks essential for colony survival, contributing to the collective success of the group (Nowak et al. 2010). While a majority of examples of eusociality are limited to insects, rare cases such as the naked mole rat are also seen in higher animals, where individuals either forage, defend the colony or reproduce (Burda et al. 2000). Insects like ants, bees, and termites showcase remarkable reproductive and non-reproductive division of labour, with sterile workers supporting their fertile counterparts in tasks essential for colony survival (Anderson 1984). This organizational complexity has independently evolved multiple times, notably within the Hymenoptera order, encompassing ants, bees, and wasps (Linksvayer and Wade 2005).

Eusocial insect colonies are typically defined by three key characteristics: overlapping generations, cooperative care of the young, and division of labour among colony members (West-Eberhard 1987). Task specialization is a hallmark of eusocial societies, and its degree and permanence vary across species, giving rise to a spectrum of eusociality, ranging from solitary insects to facultative eusociality, primitive eusociality, and advanced eusociality as seen in honeybees and certain ants (Hunt 2012). Solitary insects exhibit no social organization, while facultative eusocial species display a flexible social structure, transitioning between solitary and social lifestyles based on environmental conditions (Nonacs and Denton 2023). Primitive eusociality involves simple cooperative behaviours, typically observed in small, family-based groups (West-Eberhard 1987). However, their behaviour can be highly sensitive to environmental cues, suggesting a transition stage in the evolution of eusociality. This culminates in advanced eusociality, characterized by elaborate caste systems and highly cooperative behaviours (Hunt 2012).

Various theoretical frameworks have been suggested explaining the evolution of eusociality. Kin selection theory forms the basis for a large number of eusociality models and emphasizes the role of inclusive fitness in promoting altruistic behaviours among related individuals provided the cost is sufficiently low (Hamilton 1964). While the theory might give various conditions and scenarios in which eusociality may evolve, models based on this often do not explain the developmental processes required for the evolution of distinct castes. Without such a developmental basis, these models often underplay the adaptive nature of facultative eusociality, where the expression of castes is environment-sensitive, and suggest that other mechanisms may be at play here (Kreider and Pen n.d.).

Another hypothesis, the Ovarian Groundplan Hypothesis (OGH), posits that eusociality may arise from pleiotropic side effects and contextual shifts in the ovarian cycle of solitary insects (West-Eberhard 1987). For instance, a solitary life cycle (Fig 1a) with single use of cells may shift to reusing, usurping, adoption of unrelated offspring and abandoning of cells under group living and may give rise to primitive eusociality. In solitary wasps, females follow a simple reproductive cycle, building nests, laying eggs, and provisioning offspring independently. However, slight variations in this cycle may occur if the wasps were to develop group living (Fig 1b). Such group living could evolve through entirely different mechanisms. For example, reusing cells nests may mitigate construction costs, and would result in a push towards group living. Once group living would evolve, primitive behaviours such as adopting unrelated offspring, usurping cells, and domination could represent early steps towards sociality (Fig 1c) (West-Eberhard 1987).

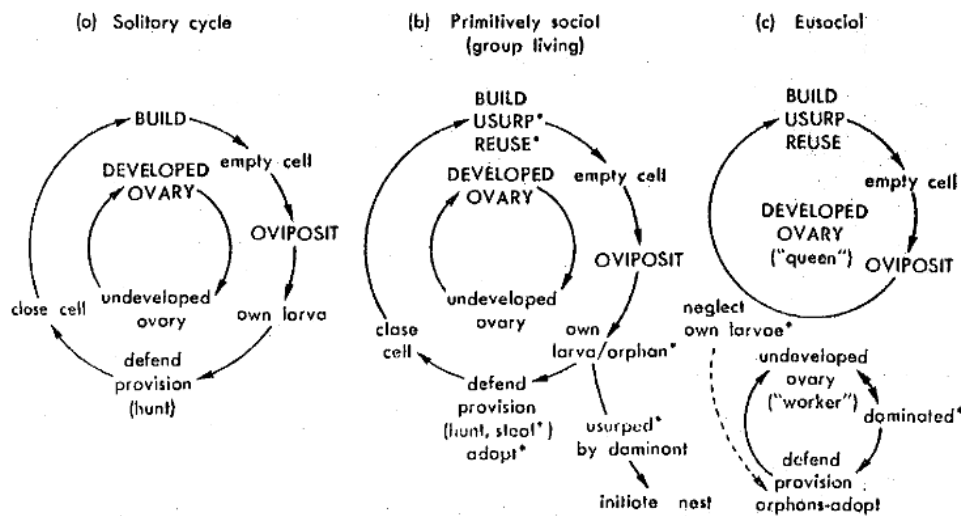


Figure 1: Features of solitary, group living and true eusociality respectively from left to right. Image taken from West-Eberhard 1987. a) Solitary cycle, where an individual alternates between functions related to breeding and has developed ovaries and functions related to defense and foraging, possessing reduced ovaries; b) Primitively social life of *Zethus miniatus*, where new behaviours such as usurpation, abandoning and adoption of larvae, stealing of resources occur, potentially as contextual shifts to group living; c) Eusocial life cycle in *Polistes*, where the breeding and foraging life cycles are completely disjoint. Queens with developed ovaries take care of breeding functions, and workers with reduced ovaries handle the foraging and defense functions.

The eusocial cycle, characterized by cooperative brood care, reproductive division of labour and a complete separation of foraging and breeding cycles may emerge from contextual shifts in said primitive cycle. Empirical support for OGH comes from studies demonstrating physiological and behavioural adaptations linked to ovarian status across eusocial species. For instance, alkali bees follow a solitary cycle and show increased sucrose sensitivity under treatments from juvenile hormone, which increases the size of Dufour's gland (Kapheim and Johnson 2017). Secretions from the Dufour's gland fulfil multiple roles, including contributing to nest construction materials and larval nutrition, as well as serving various communicative functions such as marking hosts, recognizing nests and nestmates, distinguishing kin, signaling fertility, acting as a trail pheromone, and functioning as a sex pheromone. The conserved reproductive nature of Dufour's gland in bees suggest linkage between reproductive status and foraging status, quite adjacent to OGH (Kapheim and Johnson 2017).

Experimental evolution of true eusociality from more primitive versions is certainly unfeasible owing to the extremely large periods of time required for such experiments. Hence theoretical models and

computational confirmation become key for exploration of the field. In this study, we employ an individual-based simulation to model the evolution of eusociality inspired by the ovarian groundplan hypothesis. Our model simulates haplodiploid organisms, where we observe the evolution of a population comprising of finite multiple nests. The organisms can disperse between nests, and we start the evolution of dispersal from the solitary scenario where individuals have to find a nest almost always. We assume a linear relation between larval signalling for food and their numbers in the nest. Thus, females in our model can sense the number of larvae in their nest and make a task choice between breeding or foraging depending on their foraging probability reaction norms. These reaction norms are evolvable, and we started the simulations with equal propensity to forage and breed irrespective of the larval numbers. The adult females on successful foraging trips feed a random larva from the nest, which then may mature if they cross a resource threshold. We implement principles of OGH by introducing a survival cost to task switching under the assumption that reduction and enlargement of ovaries between tasks would be an energy intensive process. By varying key parameters and letting the population evolve over large time scales, we explore conditions under which group living and further task specialisation may occur.

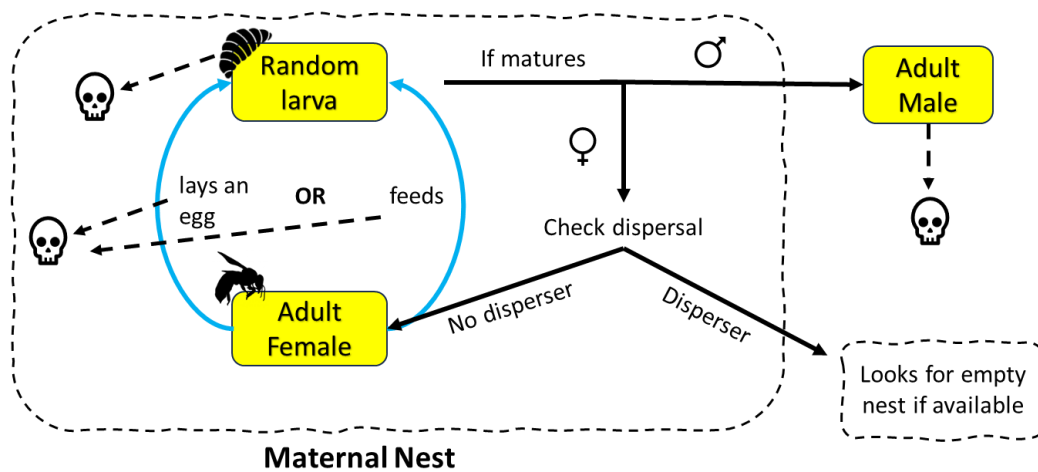


Figure 2: Basic schematic for our model; depicts the life cycle for a female individual and the subsequent development of the associated larva. At every update point, an adult female senses the number of larvae in the nest and makes a choice whether to lay an egg or feed an existing larvae based on its foraging propensity. Females can perish during tasks and task switching. A larva dies if it is not fed enough resources in its predetermined lifespan and matures otherwise. Each mature male has a predetermined lifespan, in which a female can choose it for mating. Once a female matures, it mates with a random male if available, and settles within the maternal nest if it is not a disperser. If the mature female is a disperser, it sets out to find an empty nest and perishes otherwise.

Methods

Model Overview

The evolutionary individual-based simulation models a population of haplodiploid organisms, where females are diploid and males haploid over 1,000,000 arbitrary time units. Each simulation commences with N identical solitary breeding females ($N = 1000$, considered as nests). Throughout their adult life, each individual undergoes updates independently, wherein they choose between foraging and breeding tasks at every update point after assessing the number of larvae in its nest.

Life cycle

Each simulation initiates with N mated, solitary foundresses. When an individual undergoes an update, it completes its previous task and then decides between foraging and breeding for the next update. Adult females have survival probabilities, ϕ_{breeding} and ϕ_{foraging} , for each instance of breeding and foraging, respectively (survival parameter values in figure captions).

If the current task is breeding, a larva is added to the female's nest at the subsequent update time if the individual survives the task. The larvae are produced at a constant sex ratio of 0.5. If foraging, a random larva from the nest is chosen and fed upon the individual's return to the nest, provided it survived the foraging trip. The resources allocated after a successful foraging trip is a positive value sampled from a normal distribution (μ_{foraging} , σ_{foraging}). Breeding and foraging take t_{breeding} and t_{foraging} time steps respectively.

To implement cost of transition that may occur due to physiological changes occurring in ovaries of the individuals, a mortality risk was assigned to task switching. Whenever an individual switches task from foraging to breeding or vice versa, it has a survival probability η .

Each larva is assigned a lifespan sampled from an exponential distribution with parameter λ_{larva} . If larvae are fed within their lifespan and their resource value exceeds the maturation threshold (α_{mat}), they mature. Mature males are assigned lifespans from an exponential distribution with parameter λ_{male} . Mature females choose whether to disperse or stay in the maternal nest, a decision influenced by their genetically determined dispersal probability. Females are monogamous and choose a male at random from the available pool when they mature for mating. If a male is not available, unmated females lay haploid eggs till a male is available for mating.

Dispersal

Upon maturation, each female larva decides whether to disperse in search of an empty nest or remain in the maternal nest for the rest of its life. This decision relies on the phenotypic dispersal value, which, when logistically transformed, yields the dispersal probability. All simulations start with the genetic dispersal value of -5. This value is then logistically transformed with to give us the phenotypic dispersal probability of 0.98, hence initiating simulations with solitary breeding prevalent across individuals. If a disperser fails to find an empty nest among the existing N nest instances, it perishes.

Task Choice

We assume a highly flexible cubic natural spline function (further explained in Supplement) whose shape is determined by 5 evolvable gene values to model the propensity of choosing the task of foraging as a function of total larvae in the individual's nest. This propensity is logistically transformed to obtain the foraging probability. Each simulation starts with a constant spline function with a value 0.5 unless stated otherwise, allowing for an equally probable random choice between foraging and breeding for all larval values.

Relatedness

When exploring task specialization and altruistic behaviours, it's important to look at the genetic relatedness of the individuals because kin selection theory predicts that altruistic behaviours can only evolve if genetic relatedness is sufficiently high. To quantify relatedness between adult females and larvae from the same nest, we designate a selectively neutral gene for every individual, following the same recombination and mutation dynamics as dispersal and task choice traits. Intra-nest relatedness is defined as a function of female neutral gene values array (F_{ng}) and larval neutral gene values array (L_{ng}), where the arrays contain a random female and larva from each nest respectively in order. Relatedness is calculated as:

$$r = \frac{Cov(F_{ng}, L_{ng})}{Sd(F_{ng}) * Sd(L_{ng})}$$

Genetics and mutation

Individuals have haplodiploid sex determination, where each female carries two sets of seven genes. Each set contains five genes that determine the spline functions for task choice, a single gene codes for dispersal propensity and a single selectively neutral gene. Males carry only one such set of genes. The model allows for non-additive expression of genes where the genetic trait values from one of the gene sets in a female are randomly chosen as the phenotypic trait values. Recombination during gene transmission to offspring occurs with a rate of 0.5. The model allows for complete linkage between task choice genes enabling the dispersal gene, task choice genes and the neutral gene to recombine independently.

Mutation can occur at each locus when an egg is laid, with a constant per-locus mutation rate (μ). If a locus undergoes mutation, a mutational effect is drawn from a normal distribution (μ_{mut}, σ_{mut}), modifying gene values accordingly. Genes are expressed in females, with males acting as gene carriers.

Individual state update

Given that individual task update is a pivotal feature of our model, we maintain a priority queue of individuals. This queue, a data structure in the C++ *std* library, prioritizes adult females, ensuring the individual with the immediate next action time is at the top. Consequently, at every update step, we dequeue the individual at the top, update its task or death status, revise its next action time, and enqueue it back into the queue.

Model Analysis

The model was implemented in C++ and compiled with g++ 8.5.0. Relevant data, such as average gene values, standard deviation of gene values, relatedness, larval and adult population size, and average colony sizes, were stored during the simulation. Details, like fraction of time spent foraging and number of total choices for a fraction of individuals chosen randomly that died during the simulation, was also stored.

The initial $N = 1000$ colonies simulated for 1,000,000 time steps will be referred to as the “main simulation”, where we observe the traits evolving during this period. Once this period is over due to population extinction or end of experiment, the larval brood was sampled for 25 individuals, and these foundresses started a colony each. The colony size was recorded for 30,000 time steps or earlier in case the colonies went extinct. Mutation step size was 0 for this final round of colonies. This will be referred to as “post simulation” as it reflects the stable results post evolution, where we record the population and colony dynamics. 10 replicates were done for each set of unique parameters.

In our parameter exploration, η was the focal parameter varied to have representative values 1.0 (no cost to task switching), 0.94 (small cost to task switching) and 0.92 (large cost to task switching). Other values for $\eta \in [0.8, 1.0]$ in intervals of 0.01 were also explored, but population extinction occurred for $\eta < 0.90$ and no exceptional behaviour was seen for other values at this resolution.

The parameters $\mu_{foraging}$ was also varied for values $\{0.5, 1.0\}$. A low value of 0.5 indicates that most larvae need to be fed multiple times for them to mature, a phenomenon largely observed in solitary insects, and these are the results reported here. Varying environmental stochasticity by varying $\sigma_{foraging}$ did not show any effect on evolutionary dynamics (results not shown).

All data analysis and plotting were performed in R v4.2.2 using R packages *ggplot2* v3.4.2, *tidyverse* v2.0.0, *ggpubr* v0.6.0, *gridExtra* v2.3, *ddplyr* v1.1.0 and *tidyr* v2.0.0

Table 1: List of model parameters, their descriptions, and values

Parameter	Description	Value
N	Total number of available nests during evolution of traits	1000
ϕ_{breeding}	Survival probability during breeding task	0.99
ϕ_{foraging}	Survival probability during foraging task	0.99
t_{breeding}	Time taken to successfully finish breeding task	4.0
t_{foraging}	Time taken to successfully finish foraging task	4.0
η	Survival probability during task switching	Variable
μ_{foraging}	Mean of normal distribution resources delivered by an adult foraging female is sampled from	0.5*
σ_{foraging}	Standard deviation of normal distribution resources delivered by an adult foraging female is sampled from	0.5
α_{mat}	Maturation threshold for larva, mature if resources cross this value	1.0
λ_{larva}	Parameter for exponential distribution larval lifespans are sampled from	0.01
λ_{male}	Parameter for exponential distribution adult male lifespans are sampled from	0.01
μ	Mutation rate	0.03
μ_{mut}	Mean of normal distribution mutation effect is sampled from	0
σ_{mut}	Standard deviation of normal distribution mutation effect is sampled from	0.04

Results

Low dispersal and selfish behaviour evolve under no cost to task switching.

We start with a simulation where there is no cost to task switching and individuals live solitarily. In the solitary phase where dispersal probability is high, individuals spent slightly more time foraging than breeding, which is justified by the multiple rounds of foraging trips required for a single larva to mature. Over simulation time, individuals evolve low dispersal and hence group living emerges (Fig 3a). Once group living evolves, individuals spend most of their time reproducing rather than foraging (Fig 3b,c). This can be understood as selfish behaviour where individuals in nests with large number of larvae rely on other nestmates to feed their larval offspring randomly, breeding themselves and increasing their reproductive success. This behaviour is reflected in the evolved reaction norm, where individuals breed more as larval numbers in the nest increase, relying on others increasingly to feed their larvae (Fig 3d). Task specialisation may not evolve under group living here due to low relatedness between individuals (Fig 3e), as altruistic behaviours under low relatedness would exact huge costs to the altruist. As group living evolves, we see an initial dip in relatedness due to the increase of number of females per nest. However, next the females evolve to spent more time breeding than foraging and caring for larvae, which causes a decrease in overall larval survival. This leads to a stabilisation of the number of females per nest and a slight increase in relatedness. Overall, under the given set of parameters and no cost to task switching, specialisation doesn't occur.

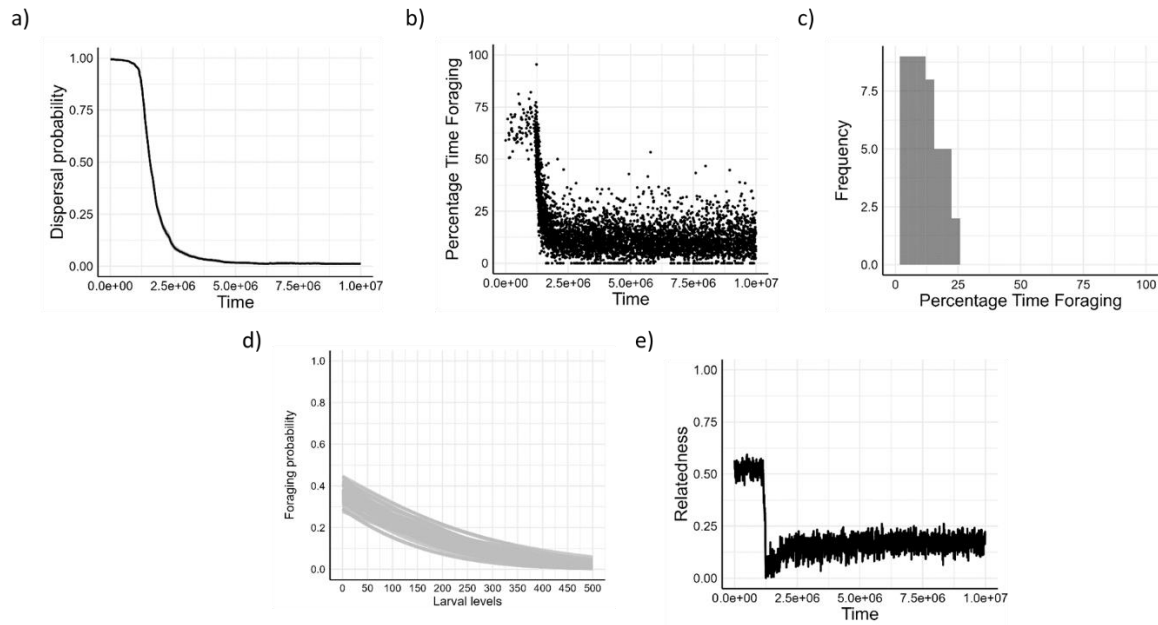


Figure 3: Results from representative replicate for no cost to task switching ($\eta = 1$):
a) Average dispersal probability of the population versus time during simulation;
b) Percentage time foraging for randomly sampled individuals at their death versus time during simulation;
c) Histogram of percentage time foraging for dead individuals in the last 100,000 time units during simulation;
d) Representative evolved reaction norms of 25 foundresses during post simulation;
e) Relatedness between random female and larva in the same nest versus time during simulation.

Small transition cost result in increased foraging and relatedness.

When we added a small cost to task switching, individuals evolve group living albeit with a higher stable dispersal value than earlier (Fig 4a compared to Fig 3a). Once group living evolves, a larger fraction of individuals spent more time foraging compared to the “no-cost-scenario”, suggesting an increase in altruistic behaviour where some individuals spend a larger time foraging for their nestmate’s larvae (Fig 4b, c). Some individuals evolve to specialise 100% of their time in reproduction but there is no clear bimodality in the proportion of time spent on the tasks, indicating an absence of clear division of labour, although some individuals also spent large amounts of their time foraging and feeding larvae (Fig 4c). This reduction in selfish behaviour can also be observed via the evolved reaction norms, where the foraging probability at lower larval numbers is higher compared to the “no-cost-scenario”, aiding the rise of altruists that majorly forage (Fig 4d). Individuals have higher relatedness within nests (Fig 4e), which increases the frequency of altruistic behaviour as the cost to a majorly foraging altruist is lower. A majority of individuals still increases their own reproductive success by breeding more and relying on others for foraging. Post simulation, colonies are rather short-lived, which is probably due to higher net mortality imparted by increased task switching morality (Fig S1).

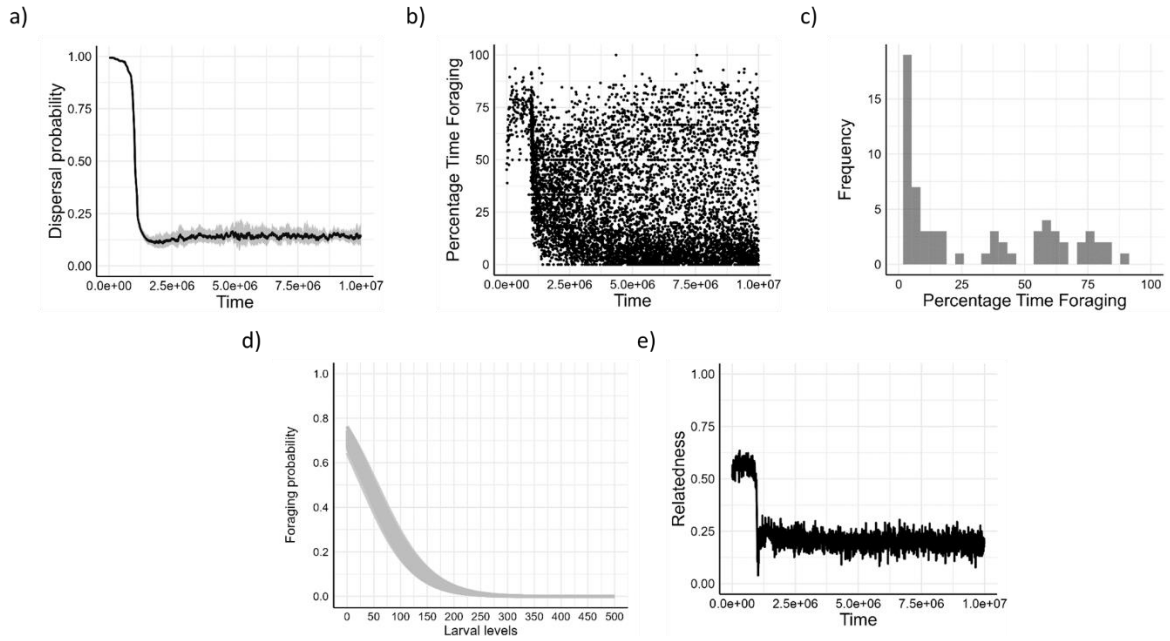


Figure 4: Results from representative replicate for small cost to task switching ($\eta = 0.94$:

- a) Average dispersal probability of the population versus time during simulation;*
- b) Percentage time foraging for randomly sampled individuals at their death versus time during simulation;*
- c) Histogram of percentage time foraging for dead individuals in the last 100,000 time units during simulation;*
- e) Representative evolved reaction norms of 25 foundresses during post simulation;*
- d) Relatedness between random female and larva in the same nest versus time during simulation.*

Large transition cost result in task specialisation and evolutionary suicide.

Out of the 10 replicates for high cost condition ($\eta = 0.92$), task specialisation emerges in just one replicate. A representative replicate where task specialisation is not observed is given in Fig S2.

Imparting a higher cost of transition to the simulations and thus further strengthening the OGH nature of the model results in task specialization once group living evolves. Clear distinction exists between the breeders and foragers in terms of time spent foraging (Fig 5a). While strict task specialisation where uniquely 100% and 0% foraging occurs is not seen, a clear bimodality is seen in the fraction of time spent foraging by individuals (Fig 5b).

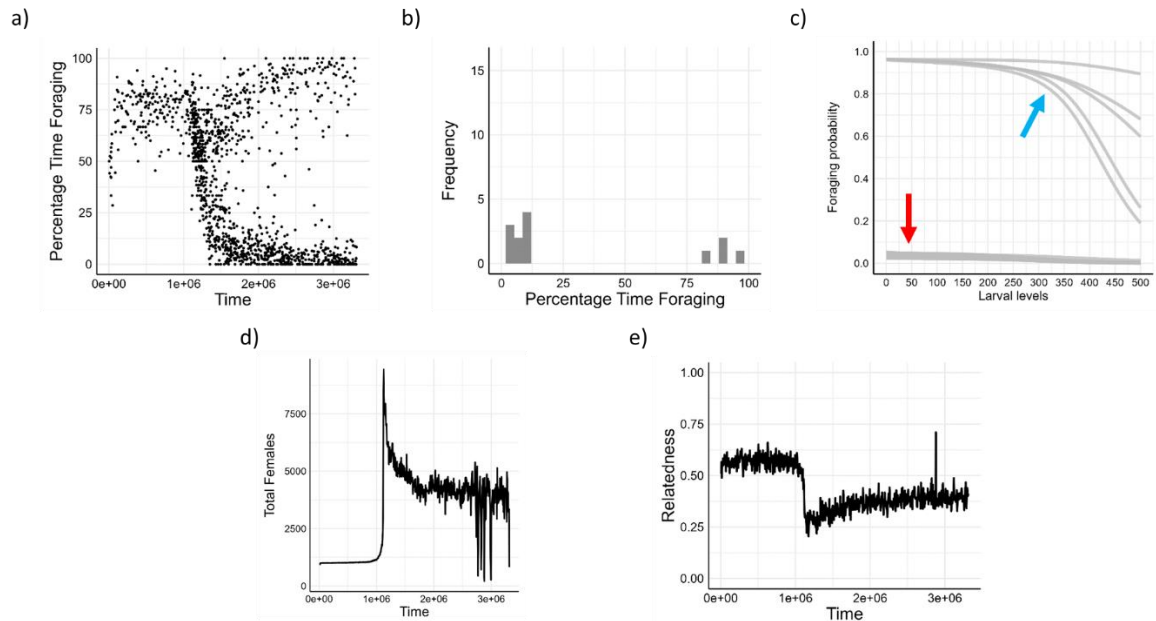


Figure 5: Results from the replicate simulation where task specialisation is observed for a large cost to task switching ($\eta = 0.92$):

- a) Percentage time foraging for randomly sampled individuals at their death versus time during simulation;*
- b) Histogram of percentage time foraging for dead individuals in the last 100,000 time units during simulation;*
- c) Representative evolved reaction norms of sampled individuals at the end of evolution during simulation. Red and blue arrows represent breeders and foragers respectively;*
- d) Total female population versus time during simulation;*
- e) Relatedness between random female and larva in the same nest versus time during simulation.*

Two distinct evolved reaction norms are seen, one corresponding to breeders and another to foragers (Fig 5c). This genetic polymorphism is probably carried distinctly in the two sets of genes carried by females but eventually dooms the populations. The population dies out eventually, as a new foundress expresses only one consistent phenotype in her lifespan, and thus is unfit to start a new colony (Fig 5d). If the foundress is a breeder, foraging happens rarely and the larvae rarely mature due to increasing competition amongst them and random selection. If the foundress is a forager, breeding rarely happens and the population goes extinct due to insufficient number of larvae in the nest.

A higher relatedness is seen under group living compared to earlier scenarios (Fig 5e); however, the resultant altruism causes evolutionary suicide.

Discussion

In this study, we introduced an evolutionary individual-based simulation model adapted from the ovarian groundplan hypothesis (OGH), representing the first known attempt to translate the verbal model into a computational framework (West-Eberhard 1987). Our model incorporates the notion that the reduction and enlargement of ovary size for foraging and breeding, respectively, incur significant energy and resource costs. We operationalize this concept by imposing a survival cost to task switching. Our findings indicate that distinct task specialization emerges when there is a high cost associated with task switching, providing support for the OGH. However, it's important to note that task-specialized individuals are ultimately unfit to sustain colonies in our model.

Across all scenarios, we observe the evolution of group living from a solitary life cycle. Dispersal probabilities consistently decrease, with higher costs of task switching associated with higher evolved dispersal values. We hypothesize that the increased dispersal under scenarios with higher task switching costs may be driven by the potential for higher reproductive fitness among disperser individuals in altruistic scenarios. In such cases, a successful foundress would have higher reproductive success than an adult that stays in the maternal nest. However, our results do not directly confirm this hypothesis, warranting further model analysis to establish causality.

Evolved relatedness between adults and larvae in a nest also increases as task switching cost increases. This is in line with kin selection as altruists now bear a lower cost for their behaviour. Under high cost to task specialisation ($\eta = 0.92$), task specialisation via genetic polymorphism emerges. Such an evolved system results in evolutionary suicide though as the population dies out. Two gene sets corresponding to breeders and foragers are present through the population, however a foundress can express only one of these through her life. This is obviously not realistic, as foundresses in true eusocial insects often perform all the colony functions when establishing a nest, and subsequently settles in to the role of queen when a worker force has been established (Peeters and Ito 2001). This is not reflected in our model. More so, a disperser in our model may not have both the gene sets corresponding to forager and breeder, and hence the resultant larval population would not have task specialization. Future iterations of the models could address these issues, and we may observe sustainable task specialization arise in such conditions. Allowing for multiple foundresses in the model, as observed in primitive eusocial insects may also mitigate for this (da Silva 2021). Multiple foundresses could sustain new colonies as division of labour is now possible, and all colony functions could occur collectively. Such a scenario could also decrease the relatedness though, and further modifications and analyses are needed to confirm this prediction.

The evolved reaction norms from our models are counter-intuitive to natural examples. We observe that individuals tend to forage when the nest larval number is low instead of breeding and tend to breed when the larval numbers are high instead of foraging. This is the selfish behaviour mentioned earlier, where an individual relies on others to feed it's larvae and focuses on reproduction. In natural settings larvae often beg for resources (Kaptein et al. 2005), something that is not an explicit feature of our model, although we assume a linear scaling of the larval signals with the number of larvae, which the adult females in our model can detect. Incorporating such explicit larval signalling in future iterations of the model could help select against such a selfish behaviour.

Furthermore, our exploration focused primarily on task switching costs as the focal parameter, while other parameters remained constant. This could restrict us to a small subset of possible results, and extensive parameter exploration is still required. Parameters such as survival costs during breeding and foraging tasks are important to explore, as for now both have the same value. Foraging and breeding are quite distinct tasks, thus the survival costs for the two are also different. Similarly, the task switching costs for breeding to foraging, and vice versa would be different in a more realistic scenario. Inspiration for asymmetric values of task survival costs could be taken from wild examples and analysing the solitary life cycle.

Improvements on the population architecture of the model can also be made. For now, no density dependence exists in the model, which allows for nests that can virtually have infinite size. Introducing density dependence, maybe via regular nest removal imitating natural calamities could yield interesting results. Such an addition could positively select for dispersal combined with flexible expression of traits in foundresses could also result in sustainable task specialization.

In summary, our model represents an initial step towards building realistic simulations of the ovarian groundplan hypothesis. Our findings suggest that under group living conditions, the ovarian groundplan may give rise to altruistic behaviours. However, further refinement and exploration of the model parameters are necessary to fully elucidate the underlying mechanisms driving eusocial evolution.

Supplementary

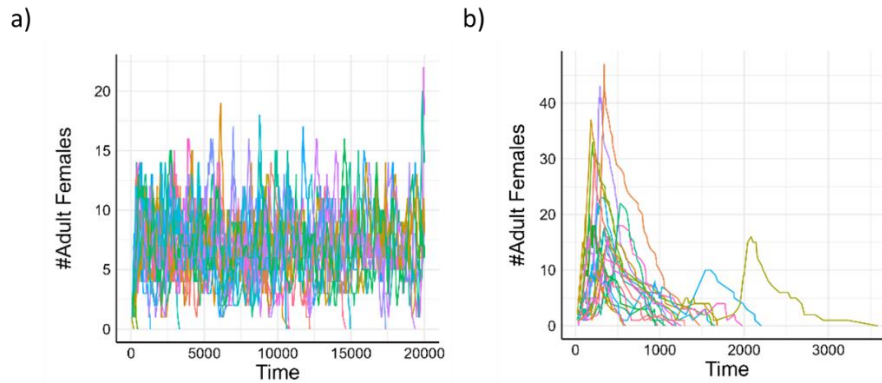


Figure S1: Colony size in terms of number of adult females versus time for a) no cost to task switching ($\eta = 1$) and, b) small cost to task switching ($\eta = 0.94$). Results are for 25 colonies post simulation.

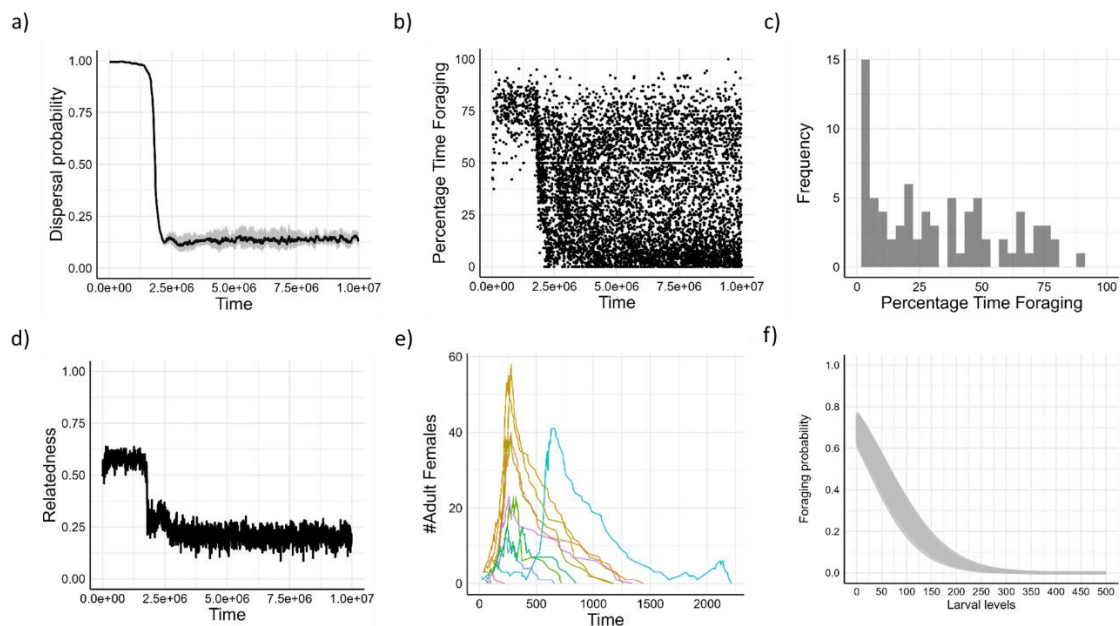


Figure S2: Results from representative replicate for large cost to task switching ($\eta = 0.92$) where task specialisation does NOT evolve:

- a) Average dispersal probability of the population versus time during simulation;
- b) Percentage time foraging for randomly sampled individuals at their death versus time during simulation;
- c) Histogram of percentage time foraging for dead individuals in the last 100,000 time units during simulation;
- d) Relatedness between random female and larva in the same nest versus time during simulation;
- e) Colony sizes in terms of number of adult females versus time for 25 colonies post simulation;
- f) Representative evolved reaction norms of 25 foundresses post simulation.

Modelling reaction norms with natural cubic spline functions

We model flexible smooth reaction norms with natural cubic spline functions as done by Lagos-Oviedo et al (Lagos-Oviedo et al. 2023). These functions consist of connected cubic polynomials but they are linear on both tail ends. We follow the definition of a natural (or restricted) cubic spline function by Harrell (Harrell 2001). A natural cubic spline function has k knots, which are the connection locations of the cubic polynomials with respect to x (in the main manuscript, we set $k = 5$). The knot locations of the k knots are t_1, \dots, t_k . The natural cubic spline function, consisting of the basis functions B_i , is then given by:

$$f(x) = \beta_0 B_0 + \beta_1 B_1 + \beta_2 B_2 + \dots + \beta_{k-1} B_{k-1}, \quad (1)$$

where $B_0 = 1$ and $B_1 = x$. The remaining terms B_2, \dots, B_{k-1} are calculated by iterating over $j = 1, \dots, k - 2$ according to

$$B_{j+1} = (x - t_j)_+^3 - \frac{(x - t_{k-1})_+^3 (t_k - t_j)}{t_k - t_{k-1}} + \frac{(x - t_k)_+^3 (t_{k-1} - t_j)}{t_k - t_{k-1}}, \quad (2)$$

where $(\dots)_+$ indicates that a term is set to 0 when it evaluates to a number below 0. The natural cubic spline function can also be written in matrix notation.

$$f(x_i) = \begin{bmatrix} B_0(x_1) & B_1(x_1) & B_2(x_1) & \dots & B_{k-1}(x_1) \\ B_0(x_2) & B_1(x_2) & B_2(x_2) & \dots & B_{k-1}(x_2) \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ B_0(x_n) & B_1(x_n) & B_2(x_n) & \dots & B_{k-1}(x_n) \end{bmatrix}_i \begin{bmatrix} \beta_0 \\ \beta_1 \\ \beta_2 \\ \vdots \\ \beta_{k-1} \end{bmatrix} \quad (3)$$

Here, the matrix is a so-called basis matrix of the natural cubic spline function. The column vector β contains the parameters $\beta_0, \dots, \beta_{k-1}$ for the natural cubic spline function. The basis matrix subscript i signifies that the i -th row of the basis matrix is used for the multiplication with the column vector β . In our simulations, we assume that the knot locations are evenly distributed within the range of x . The basis matrix is precalculated on equally-spaced intervals at locations x_i at initialisation for a given resolution of the natural cubic spline function for a given range of x (in the main manuscript, we set the resolution to 1000). The number of larvae based on which the spline is evaluated in our model ranges from $X_{\min} > 0.0$ and $X_{\max} = 500.0$, which we normalise to range from 0.0 to 1.0 before it enters the spline evaluation, i.e., x ranges from 0.0 to 1.0.

The natural cubic spline function parameters in column vector β are the evolving gene values. In the reaction norm for dispersal, we initialised all β with 0. Consequently, all females have an equal probability of choosing foraging or breeding a task at all larval values. When evaluating the reaction norm for individual female, we identify the two closest prespecified x_i to the body size X of the individual and select one of these. Subsequently, we multiply the column vector β with the i -th row of the basis matrix. This yields a single value, which is the phenotypic value (in this case, the foraging propensity) for a particular value of x . To arrive at a foraging probability, we logistically transform the foraging propensity.

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