

Luck can explain the positive link between fecundity and longevity: the Matthew effect in social insects and beyond

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Abstract

The universality of the trade-off between fecundity and longevity in life-history theory is sometimes contested. Social insects present the arguably strongest challenge, as (i) queens not only monopolize reproduction, but also live much longer than workers, and (ii) within a caste, those individuals that lay more eggs are also observed to live longer. Positive fecundity–longevity relationships can appear in observational data even though an underlying trade-off exists, as individual variation in resource acquisition (e.g., variation in habitat quality) can mask the trade-off. Here, we demonstrate theoretically that the fecundity–longevity trade-off in social insects can be easily masked even without differences in individual quality. Demographic stochasticity, caused by variable worker lifespans, leads to self-reinforcing dynamics (equivalent to the well-known Matthew effect), where “lucky” colonies exhibit healthy growth and long-lived, productive queens, while “unlucky” colonies show the opposite combination of traits. Allocation variation between individual queens, if present, can unmask the trade-off in principle, but the trade-off remains commonly concealed not only when measuring fecundity as a cumulative total (a strongly confounded measure as longer-lived queens have more time to produce eggs), but also when measuring fecundity as a rate. Our results help align superorganismal fitness components with general life-history principles, and highlight the necessity of experimental manipulations when making statements regarding trade-offs or the lack thereof.

Keywords: lifespan, life-history theory, trade-offs, Matthew effect, positive feedback, demography, stochasticity, acquisition and allocation of resources

Introduction

Survival and fecundity are a priori selected for: higher values should, all else being equal, lead to higher fitness. Organisms nevertheless do not evolve to be “Darwinian demons”, defined as organisms with infinite fecundity, immediate maturity after birth, and zero mortality (this organism only exists as a thought experiment by Williams, 1966; see also Law, 1979). A demon would fill the entire universe with its copies instantaneously, and since this is clearly impossible, life-history theory must take into account limits to what can be achieved (Shoval et al., 2012).

The impossibility of the demon means that a central quest in life-history theory is to identify trade-offs. A trade-off between reproduction and survival is a key tenet in life-history theory (Stearns, 1992), as reproduction is costly, and the costs often manifest themselves as a shorter lifespan. The underlying idea is that each unit of resources can be spent on reproduction or maintenance of the soma, but not both (Pontzer & McGrosky, 2022; Zera & Harshman, 2001). At first sight, this creates the expectation of negative relationships between measured fecundity and measured lifespan, both in within-species and between-species contexts (Anderson & Gillooly, 2021; Reznick, 1985; Westendorp & Kirkwood, 1998).

Yet the above expectation is not always borne out (Anderson et al., 2011; Cohen et al., 2020; Le Bourg, 2007; Schnebel & Grossfield, 1988; Skibieli et al., 2013). Positive relationships between lifespan and fecundity are commonly observed (Bell, 1984a, 1984b; Cayuela et al., 2024; Chang et

al., 2024; Glazier, 1999; Haave-Audet et al., 2022; Meitern & Hörak, 2024; Meitern et al., 2024; Smith, 1981; Wit et al., 2013), and the role of trade-offs as a driver of lifespan-related phenomena, such as ageing, has recently been questioned as a whole (Cohen et al., 2020). Part of the solution is that organismal fitness has more components than just two; hence, there may be further trade-offs, e.g., between the size and the number of offspring produced (visible even in fossil records; Ou et al., 2020), and such additional trade-offs can make the relationship between fecundity and longevity look positive. Nevertheless, the most fundamental answer to the puzzle has been explained with great clarity by van Noordwijk & de Jong (1986) (see also de Jong & van Noordwijk, 1992; Flatt & Partridge, 2018; Metcalf, 2016; Reznick et al., 2000). The situation is analogous to the observation that expensive cars tend to be parked in front of large, expensive houses, which by no means disproves the existence of a strict trade-off that the same euro (or dollar) that is spent on buying a bigger house cannot be spent on buying a bigger car. This analogy explains why a trade-off, which is due to the allocation of resources to conflicting functions, can be masked by differences in resource acquisition between organisms (van Noordwijk & de Jong, 1986), which makes it difficult to detect an underlying trade-off unless experiments are conducted. Experimentally increasing or decreasing reproductive effort is a far more effective method to detect trade-offs than observational studies

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Table 1. Studies that investigate fecundity–longevity relationships comparing individual queens of social insects.

	Lifetime egg production	Egg production per time interval
Total eggs	Heinze and Schrempf (2012): <i>Cardiocondyla obscurior</i> Heinze et al. (2013): <i>C. itsukii</i> Kramer et al. (2015): <i>C. obscurior</i>	Fuessl et al. (2015): <i>C. tjobodana</i> Kramer et al. (2015): <i>C. obscurior</i> Schrempf et al. (2017): <i>C. obscurior</i>
Sexual eggs	Schrempf and Heinze (2008): <i>C. obscurior</i> Lopez-Vaamonde et al. (2009): <i>Bombus terrestris</i> Heinze et al. (2013): <i>C. itsukii</i>	

Note. All studies report positive relationships.

can be (Boonekamp et al., 2020; Canal et al., 2021; Daan et al., 1996; Glazier, 1999; Winder et al., 2025), making it difficult to provide good estimates for measuring this trade-off whenever experimentation is hard (or ethically impossible, as is the case for life-history studies on humans, Bolund, 2020; but see Hukkanen et al., 2024 for a recent twin study, with a gist that comes close to experimentation).

There is an interesting case where an underlying trade-off can be particularly hard to investigate, but which also offers opportunities to link the resource acquisition–allocation question with the role of luck (e.g., in the form of initially minute differences growing into significant inequalities in success; Snyder & Ellner, 2024; Strauss & Shizuka, 2022) as we shall explain in detail below. Queens of social insects (as well as kings in termites) are often emphasized to have reversed the fecundity–longevity relationship to an unexpected positive one (Heinze & Schrempf, 2008; Keller & Genoud, 1997; Korb, 2016; Lin et al., 2021; Negroni et al., 2016; Parker, 2010; Rau et al., 2023; Rodrigues & Flatt, 2016; Rueppell et al., 2015, 2016; Séguret et al., 2016, 2021; Tasaki et al., 2021; von Wyszczetki et al., 2015). This makes them represent a particularly strong challenge to the life-history trade-off view.

The statement that social insects have reversed the fecundity–longevity trade-off takes two different forms. First, one can make a queen–worker contrast: queens not only produce a vast number of eggs, but also live considerably longer than non-reproductive workers, and in this sense the positive fecundity–longevity correlation is very stark (though not all workers in all species are sterile; Carmona-Aldana et al., 2024). The first case is, however, also unsurprising, as sterile workers are simply interpretable as the “soma” of a superorganism (Kramer & Schaible, 2013; Kramer et al., 2022). This makes the second context more important and more challenging to understand: the apparent reversal of the fecundity–longevity trade-off also applies within the queen caste, such that those queens that are observed to be very productive are also the most long-lived ones. We particularly focus on the second context of the reversal statement, though our model also includes the first, unsurprising one.

In order to explain a positive correlation between fecundity and longevity, the classic results of van Noordwijk and de Jong (1986) suggest looking for differences in resource acquisition, e.g., as a result of individual heterogeneity or other aspects of “quality” (e.g., differences in habitat quality) (Forsythe et al., 2021; Wilson & Nussey, 2010; Winder et al., 2025). If strong enough, between-individual differences in resource acquisition (and hence in total budget to be allocated) are predicted to override the effects of allocation differences. Our study addresses an even more fundamental question: can a positive relationship between fecundity and longevity arise even in the

absence of predefined individual differences? By means of simple simulations, we show that individual stochasticity (“luck”) alone (i.e., without inherent differences in trait expression or resource availability) produces a so-called Matthew effect, which is sufficient to mask the underlying trade-off between fecundity and longevity. The Matthew effect, with its biblical etymology (“For to everyone who has will more be given, and he will have abundance; but from him who has not, even what he has will be taken away”; Matthew 25:29), refers to a self-reinforcing accumulation of wealth or other advantages, exaggerating minute initial differences (Bol et al., 2018; DiPrete & Eirich, 2006; Huber et al., 2022; Merton, 1968; Perc, 2014; Rigney, 2010).

As we will show, the “luck” axis is sufficient to mask an underlying trade-off between egg production and queen lifespan. We show this with two model variants, where colony growth (the ergonomic phase; Oster & Wilson, 1978) is followed by the production of sexuals using either colony size, or age, as the decision cue. We call the former the size-dependent model, and present the second, age-dependent model in the [Supplementary Results, Section 2](#). For both model variants, we derive results assuming either evolutionarily optimal or suboptimal decisions of queens regarding investment into egg production. This allows us to examine how easily the unmasking occurs: if queens make suboptimal allocation decisions, the underlying trade-off may be unmasked, potentially shining through the data in an empirically observable manner. Also, to aid communication between theory and empirical work, we will depict our results using several metrics that have been used when making statements about positive covariation of fecundity and lifespan in social insect queens.

Methods

Empirical patterns: positive covariation is the norm

We first searched the literature for studies that investigated fecundity–longevity relationships comparing individual queens. Interestingly, all studies that met this requirement reported positive relationships (Table 1). These studies can be categorized depending on (1) whether egg count was measured as a cumulative total (not correcting for the queen’s lifespan) or as a rate (e.g., eggs per week), and (2) whether the number of total eggs or sexual eggs was counted.

The first distinction is important because, if only lifetime fecundity is measured, a positive association with longevity can arise simply because longer-lived queens have more time for reproduction than their unlucky competitors that died young. However, if this was the sole reason for the positive covariation, there would be no entries in the second column of Table 1, where in reality several studies have quantified positive covariation patterns between the egg production *rate* and the

Table 2. Symbols used.

General parameters	
n	Number of workers in a colony (workforce size)
x	Proportion of resources allocated to reproduction (the complementary proportion $1 - x$ is allocated to somatic maintenance)
y	Threshold workforce size above which the queen produces sexuals (sexual threshold)
Queen variables	
W	Queen fitness (lifetime number of sexuals produced)
μ_Q	Queen mortality
b	Queen productivity (rate by which a new individual is produced)
Species characteristics	
μ_{Q0}	Queen baseline mortality
μ_W	Worker mortality
a_1	Parameter adjusting how important help by workers is to keep the queen alive
a_2	Parameter adjusting how many workers are needed to create a significant shift towards a longer-lived queen
a_3	Parameter describing the strength of the positive effect of a large workforce on queen productivity

ultimate lifespan of queens (Table 1 also has an empty cell, see below for its significance).

The second distinction is important because the lifetime number of sexuals produced can be seen as the ultimate measure of queen fitness (since only sexuals reproduce and transmit genes to the next generation; Keller, 1993), while the number of workers is a means to that end. Using lifetime reproductive success as a fitness measure is appropriate if one assumes a constant global population size and regulation at the colony founding stage, with each sexual offspring having equally good chances to reproduce (Brommer, 2000; Mylius & Diekmann, 1995). Interestingly, we could only find reports of a positive covariation between the number of sexuals and queen lifespan that use cumulative total (sexual) egg counts as a metric; no studies opted to report the production of sexuals as a rate. Thus, the strongest conceivable evidence for a positive covariation—a situation where queens that live longest would also produce sexuals at a higher rate—has not been documented in nature, conceivably due to the strong temporal variation in the production of sexuals. In social insects, sexuals are produced typically only late in the colony life cycle, following the ergonomic stage of colony growth (Oster & Wilson, 1978).

Since the production of sexuals sometimes overlaps with the production of workers, selecting a relevant time period for specifying rates for a comparison between individuals is not trivial. In our examples, whenever we report fecundity as a rate, we go for the simplest measure: the cumulative egg count of each queen (total eggs or sexual eggs), divided by the queen's realized lifespan. For queens who died before commencing the production of sexual offspring, this measure is zero.

Model

Overview

We use stochastic simulations to model the life cycle of a social insect colony. We consider a monogynous, independent-founding social insect species (i.e., one queen per colony), and we track each mated queen from her first day of founding a colony to the end of her life. However, time is not divided into days or any other fixed unit, but flows as a continuous variable (Kokko, 2024) with an algorithm that tracks the time between two eggs laid. Higher productivity is represented as a shorter time interval between each egg laid. During this interval, deaths may also have happened in the colony: either that

of one or more workers, or that of the queen itself. Queen death marks the end of the focal colony's life cycle.

The aims of this study are twofold. First, we wish to examine how easily an existing trade-off between queen productivity and her lifespan is masked by variation in resource acquisition, created by the Matthew effect. In our model, variation in resource acquisition is determined by the number of workers, n , which we track dynamically (Table 2 lists all symbols used). The more workers there are in a colony, the higher the level of resources that can be acquired, which can mask the trade-off. Second, we aim to examine how easily this effect can be “unmasked” by variation in two crucial life-history decisions faced by a colony, which we now briefly discuss.

The first decision concerns resource allocation, which is controlled by x , the proportion of resources allocated into reproduction, as opposed to soma. This variable is used by both model variants (size-dependent and age-dependent). All else being equal (i.e., same n), a queen that spends a larger proportion x of her budget on reproduction has a higher egg production rate, but this occurs at the expense of her somatic maintenance. Thus, we assume a fecundity–longevity trade-off but allow it to be potentially masked by variations in n .

The second life-history decision for which variation is able to unmask the trade-off concerns the sexual threshold y . This variable is only needed in the size-dependent model (for details of the age-dependent model, see Supplementary Results, Section 2). The size-dependent model uses y as the colony size (number of workers) above which the colony switches from the production of workers to that of sexuals (transitioning from the ergonomic stage to the reproductive stage; Oster & Wilson, 1978). Importantly, we assume a temporal dynamic that can make the colony produce both workers and sexuals after first reaching the reproductive stage: should worker mortality make the colony size drop below y , the next eggs will develop as workers until the colony reaches size y again (Figure 1; see also Supplementary Figure S1 for a comparison between the life cycle of a lucky and an unlucky colony). We use the size-dependent model in the main text, and report the findings based on the age-dependent model (which uses a specific time t_s to commence the production of sexuals) in the Supplementary Results, Section 2.

We expect variation in the allocation decision x or the sexual threshold y to at least potentially unmask the trade-off. This follows general principles from the allocation–acquisition literature (van Noordwijk & de Jong, 1986): varying trait values imply strongly varying allocation (high x and

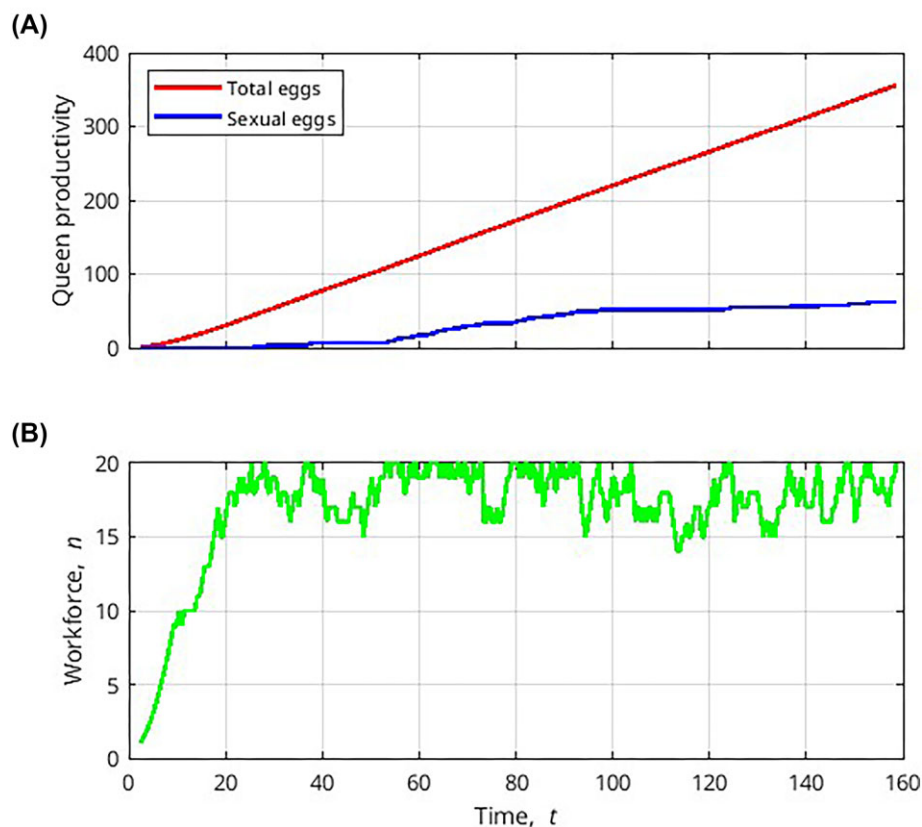


Figure 1. Example of the temporal dynamics of a colony life cycle. Shown are queen productivity, both for total and sexual eggs (A), and workforce size n (B). Note that the sexual threshold y works as an upper bound for n (in this example, $y = 20$). No sexual eggs are produced when $n < y$. The colony life cycle ends with queen death, which here occurs around time $t = 160$. Other parameter values are $x = 0.5$, $\mu_W = 0.1$, $\mu_{Q0} = 0.005$, $a_1 = a_2 = a_3 = 1$.

low y mean high investment in reproduction as opposed to building the “soma” of a superorganism), while the “soma,” i.e., the workforce of the colony, impacts acquisition. Trade-offs might thus be exposed if x and/or y vary greatly, but since their values impact both allocation (directly) and acquisition (via impacting the future workforce), this statement requires scrutiny in the form of actual model results. Also note that, for the argument we are making, it is inconsequential whether queens or workers are in control of these variables (particularly y); the important feature of the model is that the total budget that the queen can “play with” is strongly impacted by the size of her current workforce, n . Lastly, note that the scale of the two traits is different: $0 \leq x \leq 1$ and $y \geq 1$, with y an integer.

Determining queen lifespan and productivity

Since we assume independent colony foundation, a queen begins her colony life without workers, and adds workers through reproduction; we denote her current number of workers (workforce) as n . In the following, we describe in detail how we model queen lifespan and productivity, and how both variables depend on n , x , and other parameters.

We assume that being cared for by many workers has the advantage of reducing queen mortality. This may be due not only to the queen receiving less or lower-quality food in smaller colonies, but also to the fact that smaller colonies have a lower survival rate because they suffer more from competition with larger colonies, including open attacks, and are less able to fend off environmental challenges such as infec-

tions (Gordon & Kulig, 1996; Jerome et al., 1998; Leclerc & Detrain, 2018). Here, we model workforce-dependent queen mortality as a continuous-time hazard. However, the benefits of an increased workforce often show diminishing returns in reality (Kramer et al., 2014), and therefore, we do not assume that a linear increase in workforce translates into linear increases in lifespan. For the queen mortality hazard μ_Q , we use the function

$$\mu_Q = \mu_{Q0} (1 + a_1 e^{-a_2(1-x)n}) \quad (1)$$

where μ_{Q0} is the queen’s baseline mortality, a_1 is a parameter that adjusts how important help by workers is to keep the queen alive (higher a_1 means higher μ_Q), and a_2 scales how many workers are needed to create a significant shift towards a longer-lived queen (higher a_2 associates with efficient workers). Equation (1) implies that the expectation for the lifespan of a queen has an upper limit $1/\mu_{Q0}$. This expectation can only be achieved if she is always very well cared for (very large n leads to $\mu_Q \approx \mu_{Q0}$ unless she completely neglects her soma maintenance, $x = 1$, or if we prevent workers from having any positive effect by choosing $a_2 = 0$). Note though that realized lifespans of individual queens can also exceed the expectation due to luck (mortality strikes later than the statistical expectation). The low expectation, achieved without any workforce, is $\frac{1}{1+a_1} \cdot \frac{1}{\mu_{Q0}}$.

We also need to specify queen productivity. Workers help the queen not only to live longer, but also to reproduce: the queen produces a new individual (worker or sexual) at a rate

$$b = \ln(1 + a_3 x (1 + n)) \quad (2)$$

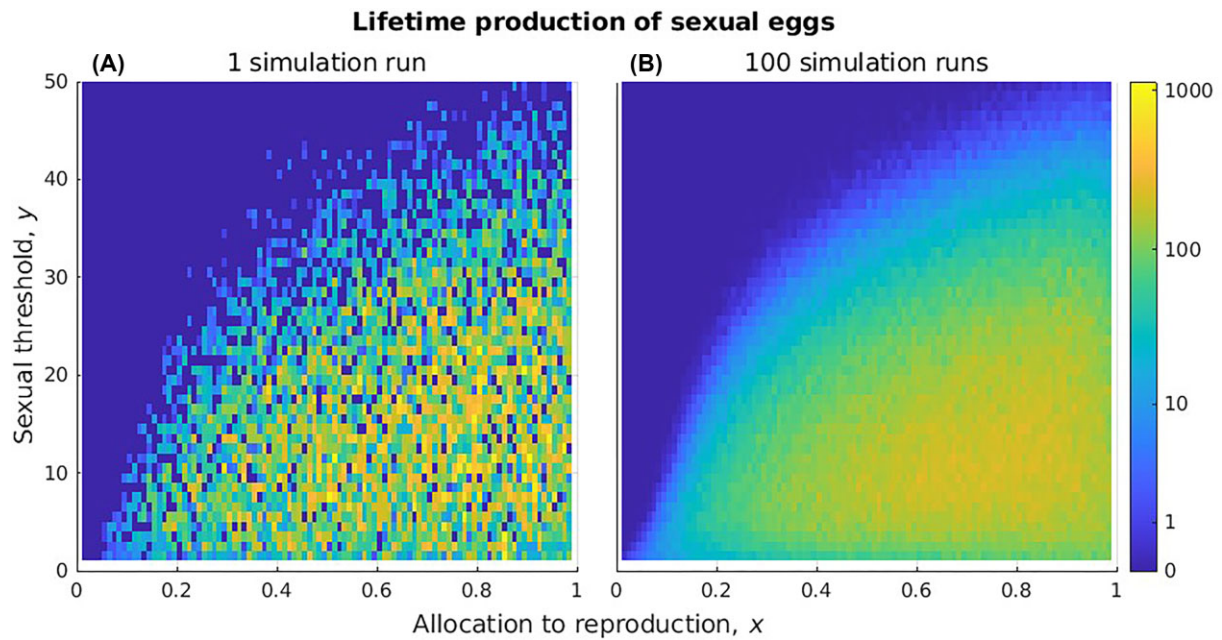


Figure 2. Lifetime production of sexual eggs as a function of the proportion of resources allocated into reproduction, x , and the sexual threshold, y , for 1 simulation run (A) and 100 simulation runs (B). The number of eggs produced is colour-coded: the warmer the colour, the more eggs are produced (note that the colour bar has a logarithmic scale). Lifetime production of sexual eggs can be viewed as a measure of queen fitness and is highest for relatively high x values and relatively low y values. Note that, in panel A, even favourable $\{x, y\}$ combinations can yield low or even zero fitness, due to stochasticity (visible as blue spots in the favourable $\{x, y\}$ region). Parameter values are $\mu_W = 0.1$, $\mu_Q = 0.005$, $a_1 = a_2 = a_3 = 1$.

where a_3 describes the strength of the positive effect of a large workforce on queen productivity, and the 1 in the term $(1 + n)$ allows a queen to be reproductively active at the very beginning of her life, when she has no workers yet. Equation (2) implies that the production rate b increases with workforce size n but does so with diminishing returns.

Modelling the colony life cycle in continuous time

We use queen productivity b as a “pacemaker” for all the other events in the colony, quantifying all the changes that occur in the time interval of length $1/b$ (smaller steps for more productive colonies, as there is more “action” per time unit). Each interval ends with the increase of the colony size by 1 if the individual produced is a worker (in colonies of size $n < y$), or with an increase by 1 in the sexual production tally if the colony has reached the reproductive stage (colony size $n \geq y$). We equate the production of sexuals with ultimate queen fitness, which implicitly assumes that the sex ratio decisions are optimal, such that it does not matter if the sexual was a haploid male or a diploid female; all sexual offspring contribute equivalently to queen fitness.

While the increases of colony size and fitness, respectively, that come with productivity are easy to tally, demographic processes that diminish colony size require more care since time intervals between events vary in length (see Kokko, 2024 for extensive tutorials for continuous-time methods). To keep the bookkeeping consistent, the model quantifies the deaths that occurred since the last reproduction event. For workers, we assume the simplest possible mortality rate: a constant hazard μ_W (hence a worker’s average lifespan is $1/\mu_W$). Constant hazards translate into an exponentially declining probability that an individual is still alive, thus the probability that an individual has died, when a time $t = 1/b$ has passed, is an increasing function of t and, thus, a decreasing function of

b : $P_{\text{death}} = 1 - e^{-\mu_W t} = 1 - e^{-\frac{\mu_W}{b}}$. When the current colony is of size n , the number of workers that have died in the time span $1/b$ is binomially distributed, $n_{\text{death}} \sim \text{Bin}(n, 1 - e^{-\frac{\mu_W}{b}})$. The queen herself dies in this time span with the probability $1 - e^{-\frac{\mu_Q}{b}}$, with μ_Q following Equation (1). We note that the randomness associated with worker mortality is the critical source of demographic stochasticity that enables Matthew effect-like dynamics.

Thus, the simulation implements the following procedure for one queen, from colony founding (first time point $t_1 = 0$) to death:

Update time from t_i to $t_{i+1} = t_i + 1/b$, and during this time

- change workforce n by $1 - n_{\text{death}}$ if $n < y$ (here one worker has been produced, and n_{death} workers have died), otherwise add 1 to queen fitness W and subtract n_{death} from the workforce n . Note that the colony grows if $n < y$ and $n_{\text{death}} = 0$, otherwise it stays at constant size or shrinks. Highly productive colonies (high b) that are in the ergonomic stage ($n < y$) are more likely to grow than to shrink, because events that add workers to the colony are frequent (occur at intervals $1/b$) and the intervals, being short, are unlikely to contain death events.
- check if the queen is still alive; she survives with probability $e^{-\frac{\mu_Q}{b}}$.

Once the queen is dead, her total lifespan is the final value of t_i , and the above procedure has yielded a value for her fitness, i.e., the total tally of sexual eggs produced. If the queen died before the colony ever reached the reproductive stage, her fitness remains 0 (the lifespan is typically still positive). While the number of total eggs increases continuously with time, the cumulative tally of sexual eggs only increases during

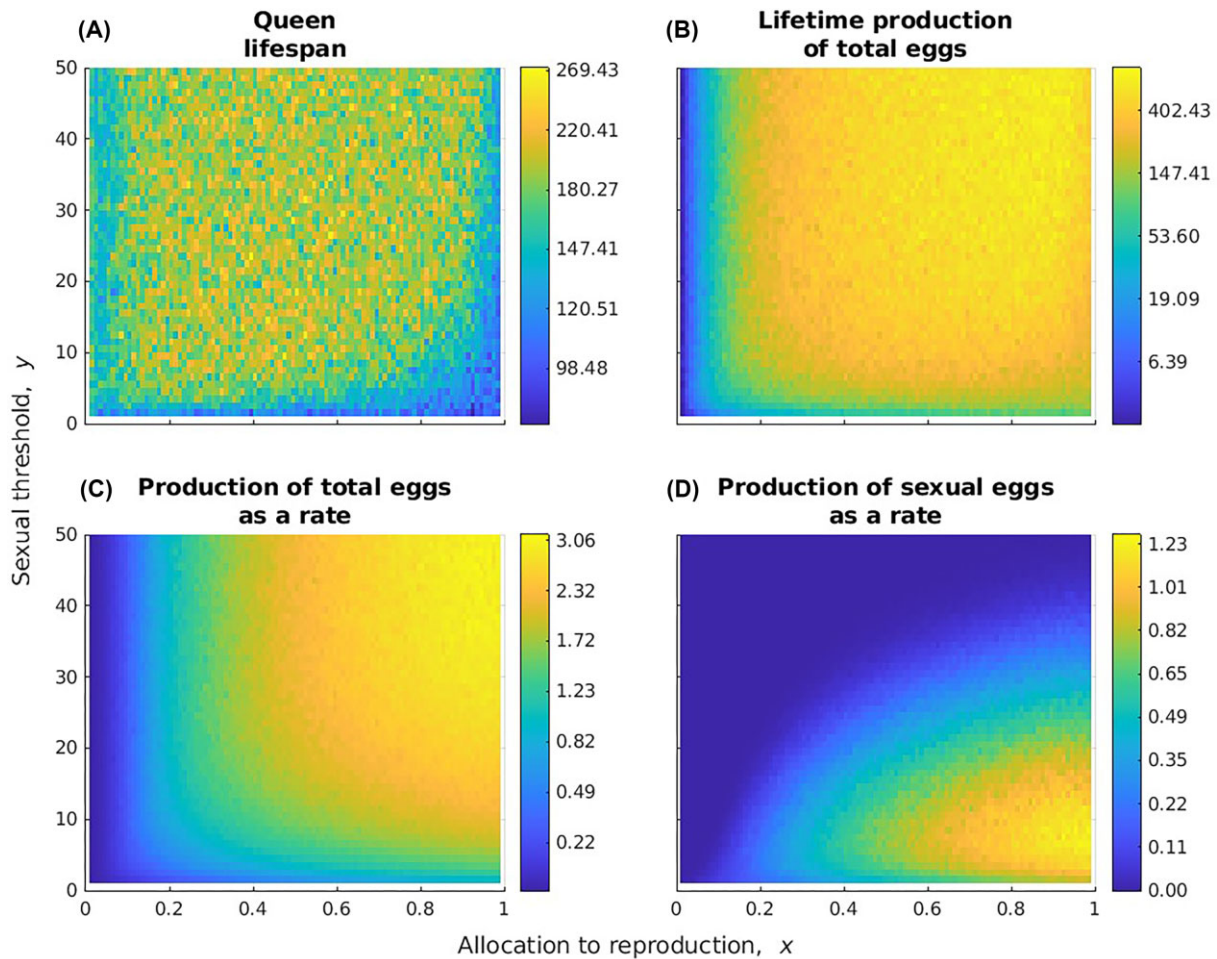


Figure 3. Queen lifespan (A), lifetime production of total eggs (B), production of total eggs as a rate (C), and production of sexual eggs as a rate (D) as a function of the proportion of resources allocated into reproduction, x , and the sexual threshold, y , for 100 simulation runs. Results are colour-coded: the warmer the colour, the longer the lifespan of the queen (A), and the more eggs she produces (B–D), respectively; also note that colour bars have a logarithmic scale. Parameter values are $\mu_W = 0.1$, $\mu_{Q0} = 0.005$, $a_1 = a_2 = a_3 = 1$.

times when the workforce size n is equal to or larger than the sexual threshold y (Figure 1).

Determining the optimal life-history strategy

Each value of x and y yields expectations of queen fitness (lifetime production of sexual eggs). Intuitively, one expects that an intermediate x is optimal, since too sluggish reproductive rates fail to build a colony and the reproductive stage will never be reached, while $x = 1$ totally neglects the maintenance of the queen's soma. A similar argument can be made for y : too early production of sexuals (low y) fails to take advantage of large colony sizes, too late (very large y) means that the colony is likely to still be in the ergonomic stage when the queen dies. However, due to the stochastic nature of the colony's demography, a single run of a queen's fate for each value of x and y is not sufficient to determine the optimum. Some queens experience "bad luck," while others enjoy a better trajectory early in life, translating into a long productive life (Matthew effect; Supplementary Figure S1). This stochasticity is responsible for the mosaic nature of Figure 2A. Expectations thus need to be based on multiple simulations for each $\{x, y\}$ combination (Figure 2B).

We then fitted a smoothing spline surface to the data on expected queen fitness to find the $\{x^*, y^*\}$ combination that

maximizes queen fitness (in other words, the optimal $\{x^*, y^*\}$ combination).

Data collection on hypothetical species: 4 × 4 ways to investigate the situation

While we use the total lifetime production of sexuals as the queen's fitness measure, other researchers may use different fecundity measures. Therefore, we always report relationships between queen lifespan and fecundity using (1) total eggs per lifetime, (2) sexual eggs per lifetime, (3) total eggs as a rate, and (4) sexual eggs as a rate. In addition, following our rationale (see the *Overview* section in the Model description) that variation in x and/or y might unmask the trade-off, we assume that x , y , or both may vary across colonies. This requires us to choose what to assume about variation, since a deviation from an optimal decision $\{x^*, y^*\}$ is, by definition, suboptimal. However, the penalty in fitness is not necessarily very strong if x and/or y deviate from the strict optimum (Figure 2). A relatively flat fitness surface makes it unlikely that very precise optimization occurs in nature, and we may instead expect a range of $\{x, y\}$ combinations to exist in nature. Still, combinations that yield very poor fitness are unlikely to persist in nature. Thus, we model suboptimal variation in x and y in a way that reflects the above considerations: we assume one or

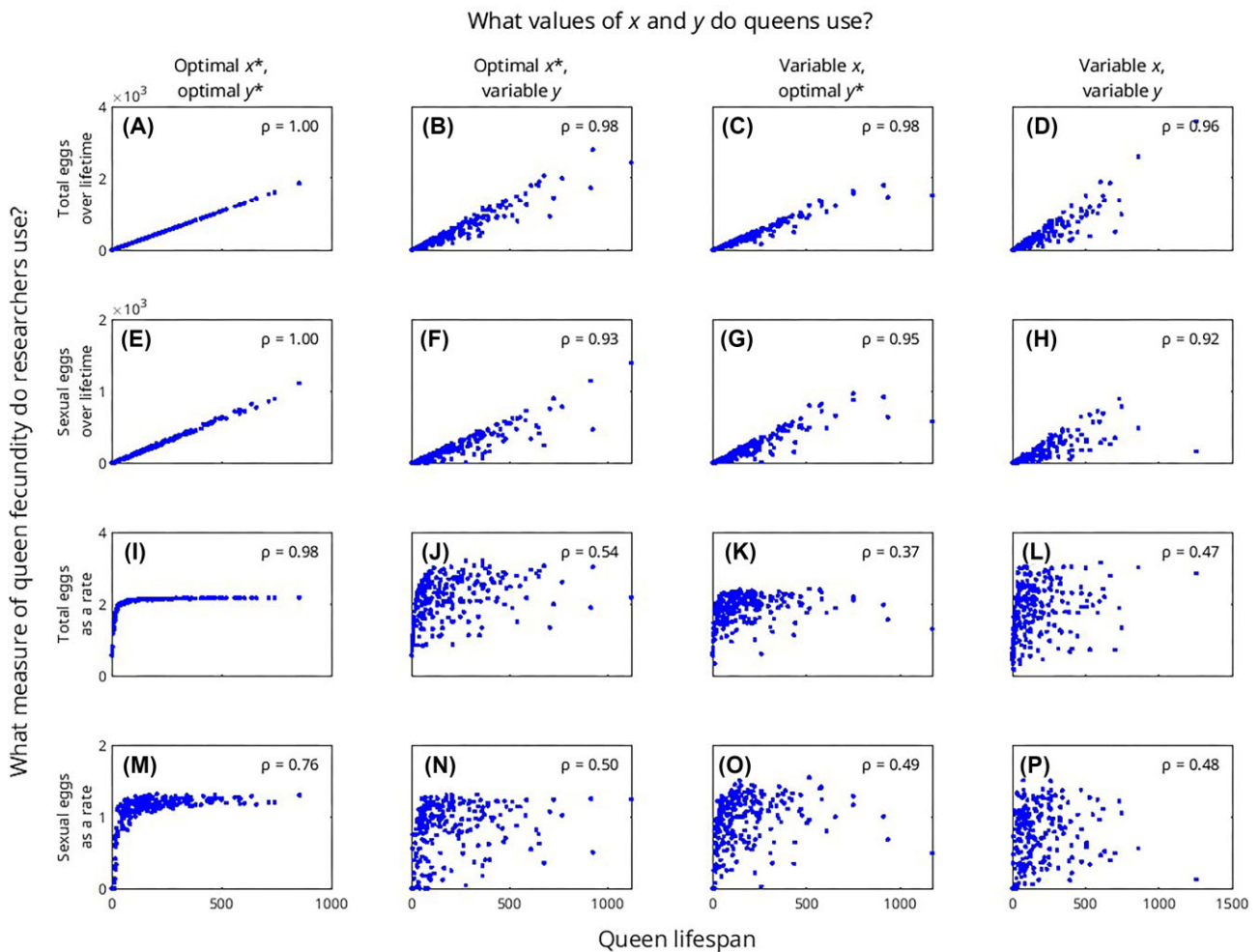


Figure 4. Correlation between queen lifespan and fecundity, shown for different measures of queen fecundity (rows) and different (x, y) combinations used by queens (columns), based on 250 colonies in each of the 16 subplots, for 100 simulation runs. In each subplot, the Spearman correlation coefficient ρ is shown. Parameter values are $\mu_W = 0.1$, $\mu_{Q0} = 0.005$, $a_1 = a_2 = a_3 = 1$.

both traits to occur with a frequency distribution that matches in shape its fitness surface. Trait values that are p times as successful as the optimal value ($p < 1$) occur with relative frequency p in the population of queens that form the simulated colonies.

We use four different variation patterns in allocation decisions x and y : (1) optimal x^* and y^* , (2) optimal x^* , variable y , (3) variable x , optimal y^* , and (4) variable x and y . Each setting was run for 250 colonies, and the results were plotted for the four different fecundity measures a researcher might use. As the resulting fecundity–lifespan plots were often non-linear (Figure 4), we used the Spearman correlation coefficient ρ as a statistic to summarize an entire subplot with a single number (values are given in each subplot of Figure 4). Whenever the correlation is positive, then luck has masked the underlying trade-off; whenever it is negative, the trade-off has been unmasked, and we expect this to be a potential outcome if allocation decisions are allowed to vary (van Noordwijk & de Jong, 1986).

The above procedure leads to $4 \times 4 = 16$ different covariation estimates, and thus 16 different subplots. We then repeated the entire exercise (16 estimates, each based on 250 colonies) to extend our analysis to 50 different “species” (Figure 5), defined as parameter combinations that are unique

to each species (Table 2, “Species characteristics”). We did this by generating 50 random numbers from exponential distributions with mean 0.1 for μ_W , mean 0.005 for μ_{Q0} , and mean 1 for a_1 , a_2 , and a_3 , respectively.

Results

Resilience: suboptimal decisions do not immediately decrease fitness

Even if fitness is ultimately determined by the total number of sexual eggs (Figure 2), it is of interest to quantify differences between the surfaces derived using each fecundity measure. For example, production of total vs. sexual eggs is maximized for different y values. The results are intuitive, since high y means that the queen invests in colony growth for longer, before any sexuals are produced. As another example, queen lifespan drops dramatically if x is very high (right end of the heatmap in Figure 3A). This in itself is unsurprising, given the assumed trade-off between x and somatic maintenance; however, queen fitness (Figure 2B) does not diminish nearly as radically. The resilience of queen fitness at suboptimally high x values becomes explicable by noting that high- x queens compensate for their short lifespan through a rapid pace of reproduction. This allows them to capitalize on a “live fast die

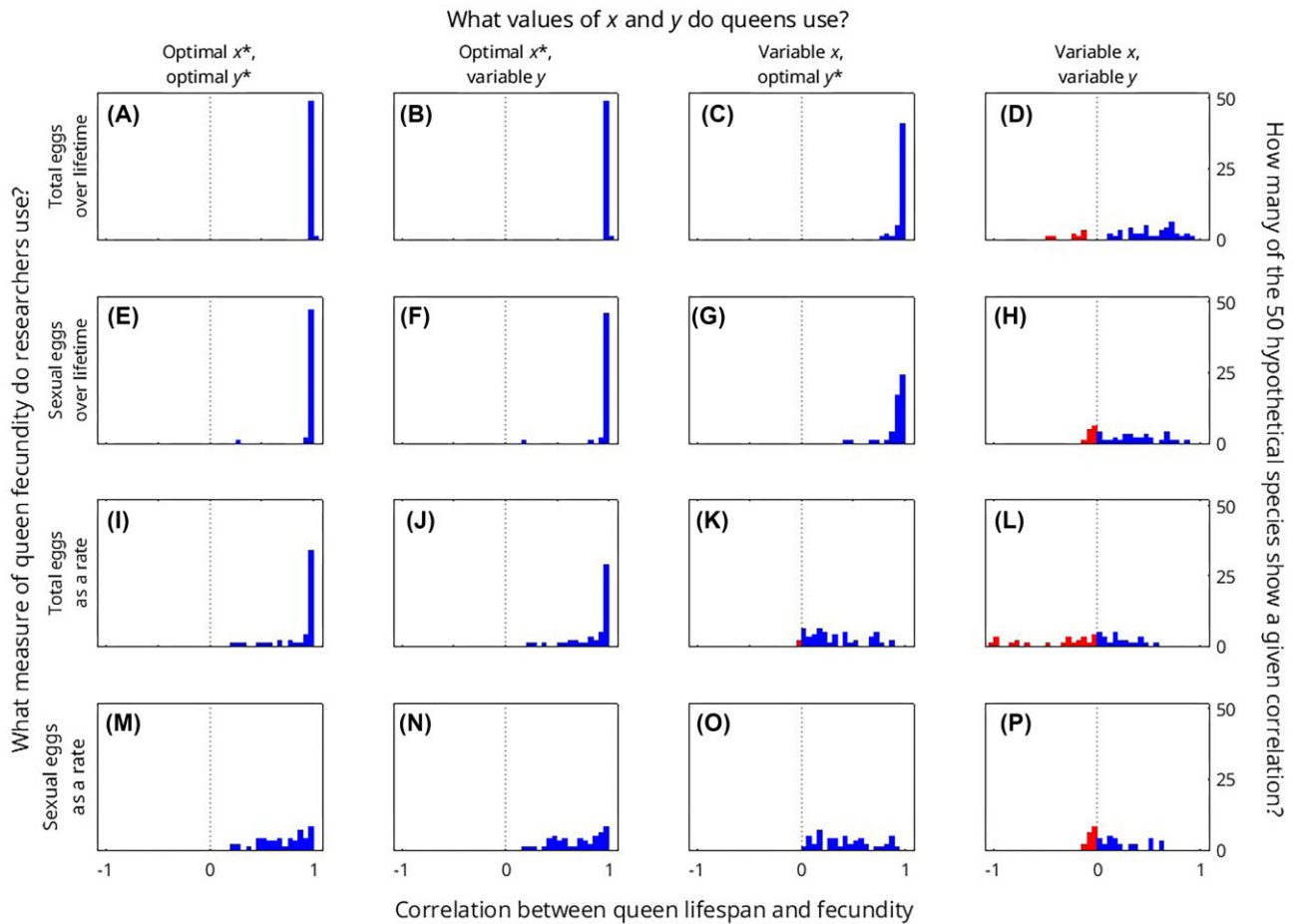


Figure 5. Distribution of correlations (Spearman correlation coefficient ρ) between queen lifespan and fecundity, shown for different measures of queen fecundity (rows) and different $\{x, y\}$ combinations used by queens (columns), based on 250 colonies in each of the 16 subplots, for 50 randomly chosen combinations of values for parameters μ_W , μ_{Q0} , a_1 , a_2 , and a_3 (50 hypothetical species).

young” strategy (Travers et al., 2015), which, in a social insect, comes with an additional benefit: high x also allows for lost workers to be replaced quickly. This reflects the feedback through social life: x is not purely an investment “away from” the soma, it partially enables the queen to keep her own soma intact via the growth of her workforce.

Underlying trade-offs are very easily masked

The relationships between x , y , and queen fitness and its decomposition into fitness components (Figures 2 and 3) is crucial for understanding life-history patterns, yet x is not easy to measure in nature.

We first present a single-species example (Figure 4), before turning to ask whether this particular example is typical. The example uses worker mortality rate of $\mu_W = 0.1$ (average lifetime: $1/\mu_W = 10$ time units), while queens have a baseline mortality rate of $\mu_{Q0} = 0.005$ (thus a well-cared-for queen is expected to live $1/\mu_{Q0} = 200$ time units, but her mortality is higher if not cared for). Also, for simplicity, our first example uses $a_1 = a_2 = a_3 = 1$.

Masking is prevalent in this example (positive covariation patterns in Figure 4), with more positive correlation coefficients if queen fecundity is measured as a lifetime total (Figure 4A–H) than as a rate (Figure 4I–P). If colonies all behave optimally, queen productivity and lifespan are extremely well correlated: lucky queens live longer and have more time to con-

tribute sexuals to the next generation (“to prosper, live long” sensu Snyder & Ellner, 2024; Figure 4E). Their high success does not only reflect a longer lifespan, but also a better average egg production rate (Figure 4I, M) than shortest-lived queens achieve. The short-lived queens spend a larger proportion of their lives in a stage where the workforce is too small to yield a high egg production rate.

As a whole, Figure 4 shows that the trade-off is invariably masked if colonies behave optimally: all variation is due to “luck” and thus observations yield positive correlations between queen lifespan and fecundity (Figure 4, leftmost column), reflecting a strong Matthew effect (see Supplementary Figure S2 for evidence that poor early-life performance is predictive of poor lifetime fitness). The situation becomes somewhat less clear if allocation decisions vary, as now there is a tension between the Matthew effect and real potential for the allocation variation to showcase the trade-off. We thus collected data of the nature depicted in Figure 4 for a total of 50 hypothetical species, collecting the outcome (Spearman correlation coefficients) into histograms (Figure 5).

In principle, variation in allocation decisions is expected to have an unmasking effect (van Noordwijk & de Jong, 1986), and indeed, we found variation to be able to reveal the underlying negative covariation (Figure 5). Negative correlations are most likely to be revealed if there is variation in both the queen’s allocation to reproduction x and the colony’s sexual

threshold y (Figure 5, rightmost column), but this is a best-case scenario—and even then, unmasking occurred in a minority of all runs observed. As a whole, our results thus suggest that the fecundity–longevity trade-off becomes very easily masked by the Matthew effect. In observational data, it is simply difficult for the allocation decisions to vary sufficiently to override the effects of acquisition (sensu van Noordwijk & de Jong, 1986); thus, we do not expect unmasking to be commonplace (see Supplementary Results, Section 1, and Supplementary Figures S3 and S4 for where it is most likely to occur). Taken together, our results emphasize the well-known limitations of observational data (acquisition–allocation interactions) and add strength to the limitations: even if habitats all offer identical acquisition prospects (e.g., food availability), luck due to the Matthew effect can create acquisition differences that easily override the effects of allocation.

The age-dependent model (Supplementary Results, Section 2) differs from the above in that it lacks the variable y , and instead, queens commence the production of sexuals at a pre-specified time point, interpretable as the queen having reached a certain age. The age-dependent model produces qualitatively the same results as our size-dependent model (Supplementary Results, Section 2, and Supplementary Figures S5–S9), indicative of our main results being robust.

Discussion

Trade-offs are not easy to detect when investigating observational datasets. The difficulties have even led to claims that costs of reproduction might not be strong drivers of lifespan-related phenomena, such as ageing (Cohen et al., 2020). Social insects present the arguably strongest challenge to the trade-off-based view, as a positive covariation between fecundity and longevity appears to be routinely found in these species, a pattern that we confirm. Therefore, social insect queens have been argued to come closest to hypothetical “Darwinian demons” in the animal kingdom (Schrempf et al., 2017). Here, we developed a simple model to address this riddle. We show how initially minute within-queen differences in resource budgets, based purely on luck, grow larger during the life cycle of a colony, due to positive feedback between workforce size and queen fecundity. The consequently accumulating advantage (Matthew effect) very easily masks the fecundity–longevity trade-off. The masking can in principle be undone if allocation decisions vary greatly; however, in the cases that we study, masking remains the most frequently observed outcome even if colonies vary in the allocation patterns. In other words, even if social insect colonies experience fundamental life-history trade-offs in how queens reproduce and stay alive, it requires very well-designed experiments to unmask them.

Our model involves two important assumptions: (1) worker and queen lifespans are stochastic, and (2) queens with more workers have a larger resource budget than queens with fewer workers. Both assumptions are crucial for the emergence of the self-reinforcing dynamics disproportionately benefiting lucky queens. The first assumption seems obvious, as death events are intrinsically stochastic. Also, one might think that queen lifespan is much more important in our model than worker lifespan; however, this is not the case: there is evidence for worker longevity being a key determinant of colony size and growth rate (Carey, 2001).

The second assumption, that a larger workforce ultimately enhances queen fecundity, is likewise backed by empirical ev-

idence, as the rate of colony growth during the ergonomic stage, which is a measure of queen fecundity, is determined primarily by the size of the active workforce (Oster & Wilson, 1978). Also, experimentally limiting the queen’s access to workers has been found to reduce queen fecundity (Negroni et al., 2021).

Even so, our model is of course a simplification of reality. For example, time lags between investment into an egg and workforce accumulation, or between a workforce size and its estimation by the queen, are not accounted for, but we consider it unlikely that lags would diminish the role of luck: if anything, they would create longer-lasting effects of lucky and unlucky situations. Due to the individual-based nature of our simulation, we also were not able to extend our model to the upper end of colony sizes found in nature. Indirectly, at least, we can suspect that the Matthew effect can operate in species with large colonies, too, since Table 1 is not restricted to species with small colonies. In our simulated species, we found no evidence that unmasking occurs more easily with parameter combinations that produce large colonies (Supplementary Figure S10).

The idea of a positive feedback between colony size and queen fecundity has been used in theoretical models outside ours, particularly in models of optimal resource allocation. While these models have a different focus than the fecundity–longevity trade-off, such as the optimal allocation between production of workers and sexuals (Macevicz & Oster, 1976; Poitrineau et al., 2009), queen–worker conflict over sex allocation (Avila et al., 2019), and competition between overlapping generations (Johansson et al., 2023), they align with our view that positive feedbacks play a major role in shaping the life history of colonies.

Our finding that the Matthew effect easily masks the fecundity–longevity trade-off makes it very difficult to detect the trade-off by observation alone. Therefore, experimental manipulation of trade-off variables is crucial to detect any trade-offs (Korb, 2016), and recent studies that experimentally manipulated reproductive efforts have been able to suggest the presence of a fecundity–longevity trade-off in queens (Blacher et al., 2017; Collins et al., 2023). Here, it is of interest to note that, in our model, colonies that use suboptimal $\{x, y\}$ values can be thought of as “experimenting” with their own reproductive efforts. That unmasking does not immediately happen in our model means that experimentalists probably need to use strong manipulations to reveal trade-offs that can be said to resist unmasking efforts quite strongly (Winder et al., 2025); the success of Blacher et al. (2017) and Collins et al. (2023) is therefore remarkable, strengthening the case for trade-offs underlying social insect colony life.

The association between long lifespans and high fecundity is a characteristic trait of animals living in social groups (Downing et al., 2021; Korb & Heinze, 2021; Lucas & Keller, 2020). Group living is also a prerequisite for the emergence of the self-reinforcing dynamics described in this paper. Therefore, we expect such dynamics to lead to positive fecundity–longevity correlations not only in social insects, but also in other eusocial organisms. In several mole-rat species, breeders of both sexes live significantly longer than their non-breeding colony mates (Dammann & Burda, 2006; Dammann et al., 2011; Ruby et al., 2018; Schmidt et al., 2013). It would thus be interesting to know whether they also follow Matthew effect-like patterns, where luck makes some breeders both live longer and be more fecund than other, less lucky breeders.

It is often assumed that much of the between-individual variation in life-history traits, such as lifetime reproductive success, can be explained by variation in individual traits or quality (“individual heterogeneity”) (Forsythe et al., 2021; Wilson & Nussey, 2010). In contrast, an increasing body of literature is identifying luck (“individual stochasticity”) as an important cause of variance in life-history outcomes, often trumping the contribution of individual heterogeneity (Caswell, 2009; Hartemink & Caswell, 2018; Hartemink et al., 2017; Hernández et al., 2024; Snyder & Ellner, 2016, 2018, 2024; Snyder et al., 2021; van Daalen & Caswell, 2020). Our theoretical work adds to this literature by showing that luck alone (i.e., without individual quality differences) is sufficient to mask the fecundity–longevity trade-off in social insect queens and probably beyond.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

All Matlab files are available at <https://doi.org/10.5281/zenodo.15910469>.

Author contributions

Roman Zug (Conceptualization [equal], Formal analysis [equal], Writing—original draft [equal], Writing—review & editing [equal]), Susanne Foitzik (Funding acquisition [equal], Writing—review & editing [equal]), and Hanna Kokko (Conceptualization [lead], Formal analysis [equal], Funding acquisition [equal], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

None declared.

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