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A formal theory of group-level adaptation for obligate eusociality

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Abstract

Darwin argued that natural selection leads organisms to appear as if they are striving to maximize their fitness. This idea is readily recognized at the individual cell or body level, but such adaptive design may also manifest at some higher levels of biological organization. Previous work has formalized the idea that social groups can be viewed as adaptive individuals in their own right—i.e., "superorganisms"—under the assumptions that within-group selection is absent and that there is no class structure. However, the original and most common biological use of the term "superorganism" is in reference to insect colonies in which members exhibit striking class structure in the form of reproductive division of labour. Accordingly, although obligately eusocial colonies are regularly conceptualized as having the capacity for colony-level adaptation, current formalisms are unable to support this idea. Here, we develop a formal theory of group-level adaptation for obligately eusocial colonies by establishing mathematical correspondences that connect the dynamics of natural selection—as described by Price's equation—to the mathematics of optimization—wherein the colony is considered a fitness-maximizing agent—under a range of assumptions as to which members of the colony control its phenotype and the degree to which they are genetically related.

Keywords: adaptation, class structure, division of labour, eusociality, formal Darwinism, group as maximizing agent, group selection, individuality, natural selection, Price equation

Introduction

Darwin (1859) argued that natural selection leads organisms to appear as if they are striving to maximize their fitness. This idea is foundational to the field of behavioural ecology (Alcock, 2009; Davies et al., 2012), and is supported by formal analysis—from Fisher's (1930) "fundamental theorem of natural selection" to Grafen's (2002, 2006b) "formal Darwinism" project. It has been suggested that, in some taxa, social groups may also be viewed as adaptive individuals, i.e., "superorganisms" (Emerson, 1939; Hölldobler & Wilson, 2009; Marais, 1925; Reeve & Hölldobler, 2007; Seeley, 1989, 1997; Sober & Wilson, 1998; Wells et al., 1929; Wheeler, 1911; Wilson & Sober, 1989). Gardner & Grafen (2009) have shown that the same links between the mathematics of selection and optimization that justify individual-level adaptation also hold for group-level adaptation in some specific cases in which within-group selection is completely abolished (Figure 1). In particular, their simple model assumes that all individuals are generic and interchangeable—i.e., there is no class structure (Fisher, 1930; Grafen, 2006a; Taylor, 1990).

However, the original biological use of the term "superorganism" by Wheeler (1911) was in reference to social insect colonies in which members exhibit striking class structure in the form of a reproductive division of labour. Wheeler's "superorganism" echoed and further emphasized Darwin's (1859) and Weismann's (1893) recognition of the evolutionary importance of queen-worker caste differentiation in the biology of these highly social insect colonies, though the term was later confusingly broadened to include any collection of single creatures where between-group selection overwhelms within-group selection (Emerson, 1939; Wilson, 1971, 1975, 1985; Wilson & Sober, 1989; see Boomsma & Gawne, 2018 for a full review, and Table 1 for a glossary of key terms). Boomsma & Gawne (2018) have argued that these latter conceptions of the superorganism have been imprecise in comparison with the original, which stressed strict reproductive division of labour and is analogous to some modern definitions of obligate eusociality—i.e., where colonies are formed by individuals who exhibit and commit to an irreversible caste phenotype, sometimes (but not always) leading to full sterility of one or more castes (Boomsma, 2007, 2009, 2022; Boomsma & Gawne, 2018; Crespi & Yanega, 1995, see also Table 1). This reproductive division of labour is akin to the separation of germline and soma characteristic of obligately multicellular organisms and, in both cases, leads to strict mutual dependence among the lower-level members of higher-level collectives (Bourke, 2011; Fisher, 1930; Queller, 1997, 2000; Weismann, 1893; West et al., 2015; Wheeler, 1902, 1910, 1911, 1928). Indeed, the permanence and irreversibility of organismality and superorganismality are often ascribed to such differentiation within both multicellular bodies and multi-individual colonies (Boomsma, 2022). Accordingly, the neglect of class structure within the analysis of Gardner & Grafen (2009) means that there is a lack of formal support for viewing obligately eusocial colonies with reproductive division of labour as adaptive units.

Here, we provide formal justification for viewing obligately eusocial colonies ("superorganisms", sensu Wheeler) as

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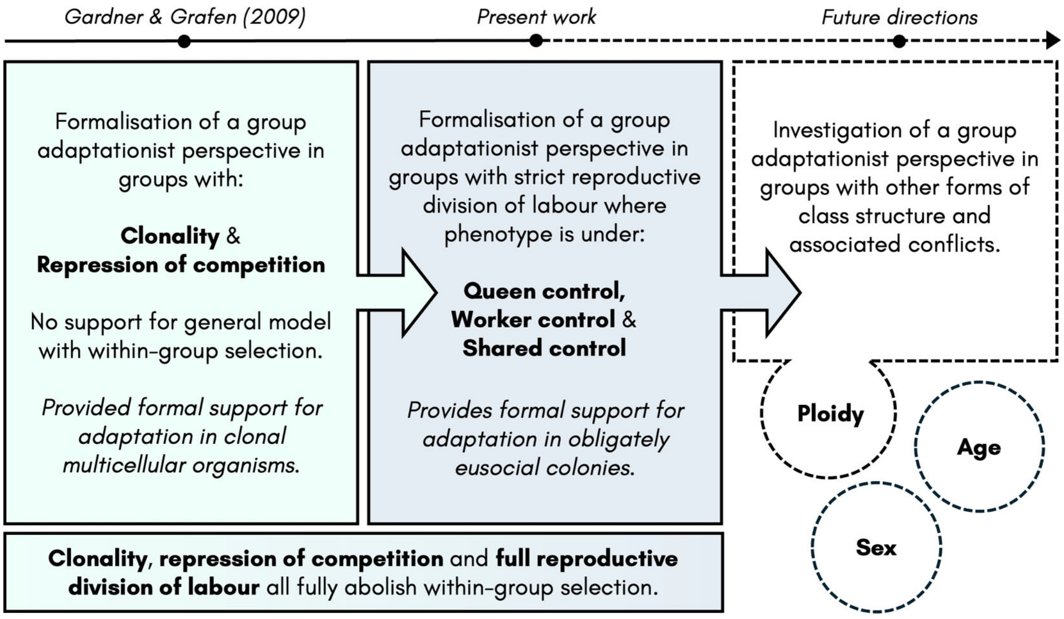

Figure 1. Overview diagram of past, present, and potential future directions of the formal Darwinism approach as applied to group-level adaptation.

fitness-maximizing individuals in their own right. We build upon Gardner & Grafen's (2009) "group as maximizing agent" analysis to consider groups in which individuals belong to separate reproductive versus non-reproductive classes, establishing a series of mathematical correspondences between the dynamics of selection—as described by Price's (1970, 1972) equation—and the maximization of group-fitness—as described by an optimization program. We consider three separate cases: a "queen control" scenario in which the colony's phenotype—being the entirety of its morphology, physiology and behaviour—is fully determined by the queen's genotype; a "worker control" scenario in which the colony's phenotype is fully determined by the workers' genotypes; and a "shared control" scenario in which the colony's phenotype is jointly determined by both queen and worker genotypes. Our aim is not to detail specific predictions concerning particular traits but rather to provide the formal foundations for a group-adaptationist research programme within which testable hypotheses may be formulated and empirically tested.

Methods and results

Population genetics

We consider a large, finite population of individuals with discrete, non-overlapping generations. The population is organized into M groups, or colonies, within which all social interactions take place. Each of these M colonies comprises one reproductive individual—the queen—and N non-reproductive individuals—the workers. Each colony is assigned a unique index $i \in I = \{1, 2, 3. . ., M\}$, and, within each colony, each individual is assigned a unique index $j \in J = \{0, 1, 2. . ., N\}$, where $j = 0$ designates the queen. We do not consider any class structure beyond the basic reproductive division of labour—for example, individuals are not divided into separate age, sex, or ploidy classes. We assume that density-dependent regulation ensures the number of colonies and the number of individuals within each colony at the time of census remains the same in every generation.

We describe an individual's additive genetic value for any character of interest as a linear weighted sum of genic values, or "p-score" (Falconer, 1981; Grafen, 1985; Price, 1970). We denote the p-score for the jth individual in the ith colony as p_{ij}, with p_{i0} representing the queen's p-score. The average p-score of the colony may then be given by $p_i = c_q p_{i0} + c_w \sum_{\hat{J}} p_{ij}/N$, where $\hat{J} = \{1, 2..., N\}$ indexes workers and c_q and c_w are the class reproductive values of queens and workers, respectively—i.e., the probability that a gene chosen at random from the population in the distant future traces its ancestry to each class in the present generation (Fisher, 1930; Grafen, 2006a; Taylor, 1990). Because only queens reproduce, such that $c_q = 1$ and $c_w = 0$, the colony's p-score is equal to that of its queen i.e., $p_i = p_{i0}$. The average p-score of the population is then given by $p = c_q \sum_I p_{i0}/M + c_w \sum_I \sum_{\hat{J}} p_{ij}/(MN) = \Sigma_\mathrm{I} p_{i0}/M$.

We incorporate demographic uncertainty in reproductive success, i.e., an individual's number of offspring surviving to next census, by assigning a unique index $\omega \in \Omega$ for every possible reproductive outcome for the population and by denoting the ith colony's queen's reproductive success under outcome ω as w_{i0}^{ω}. Following Grafen (2002, 2006a), descriptors of the population of individuals (e.g., the group index) are denoted by subscripting, while descriptors of the state of nature (e.g., realizations of the future) are denoted by superscripting. Because only queens reproduce, the colony's reproductive success is given by $w_i^{\omega} = w_{i0}^{\omega}$ and the population's by $w^{\omega} = \Sigma_\mathrm{I} w_{i0}^{\omega}/M$. We denote the probability that outcome ω occurs by q^{ω}. Averaging over uncertainty, the expected reproductive success of the queen is given by $w_{\mathrm{i}0} = \Sigma_\Omega q_\omega w_{i0}^{\omega}$, that for the colony by $w_\mathrm{i} = w_{\mathrm{i}0} = \Sigma_\Omega q_\omega w_{i0}^{\omega}$, and that for the population by $w = \Sigma_\Omega q_\omega \, w^{\omega}$. We assume that density-dependent regulation maintains a constant number of colonies M in each generation, so that $w^{\omega} = w = 1$ for all $\omega \in \Omega$.

Because group adaptation manifests in a colony's phenotype, we develop an explicit model of colony phenotypes and their relation to genotypes and reproductive success. We denote the set of all possible individual genotypes by G and we

Table 1. Glossary of terms (as used in this paper).

Superorganism: a term originally used by Wheeler (1911) to describe insect colonies in which members belonged to morphologically distinct castes; the prefix "super-" is intended to emphasize that they represent a distinct domain of social evolution beyond metazoan multicellularity (Boomsma & Gawne, 2018). Later, the term was confusingly broadened to capture any collection of single creatures where between-group selection overwhelms within-group selection (e.g., Wilson & Sober, 1989).
Obligate eusociality: social groups in which caste is irreversibly determined early in development such that no individuals in predestined worker castes retain the behavioural, and often physiological, option to disperse and found their own colonies independently (Boomsma, 2009).
Kin selection: a theory originally conceived by Darwin (1859), developed by Hamilton (1964), and named by Maynard Smith (1964), describing how natural selection can operate through the reproductive success of relatives (Frank, 1998).
Group selection: the portion of natural selection that operates at the between-group level (Hamilton, 1975; Price, 1972).
Group-level adaptation: the quality of groups exhibiting adaptive individuality in their own right (Gardner & Grafen, 2009).
Price equation: an equation describing overall evolutionary change as the change in the average value of some character of interest that occurs between two assemblages, conventionally termed "parents" and "offspring" (Price, 1970, 1972; Gardner, 2020). The Price equation expresses this overall evolutionary change as the sum of two terms: a "selection" term and a "transmission" term, providing general definitions of these two processes.
Formal Darwinism: a project pursued by Alan Grafen and colleagues to formalize and justify ideas of fitness optimization originating from Darwin and used by behavioural ecologists, including by linking the mathematics of change described by the Price equation and the mathematics of optimization (Grafen, 1999, 2000, 2002, 2006a,b, 2007, 2014; Gardner & Grafen, 2009; Gardner & Welch, 2011).
Optimization program: a mathematical device often used in economics and control theory that describes an objective and the means by which that objective may be pursued. The optimization program provides a formal mathematical definition of purpose and optimality, without implying that the latter is achievable (Grafen, 2002).
Group-as-maximizing-agent (GMA) analogy: an optimization program where a social group is described as a purposeful agent with its own agenda in pursuit of some objective—both in Gardner & Grafen (2009) and in the present analysis that objective is to maximize its expected reproductive success.

denote the genotype of the jth individual in the ith colony by g_{ij}. The set of all possible colony genotypes, made up of the member's individual genotypes, is Γ and the genotype of the ith colony is denoted as γ_i. Similarly, the set of all possible colony phenotypes is Π and the phenotype of the ith colony is denoted as π_i. We assume that the phenotype is fully specified by the genotype, i.e., $\pi_i = P(\gamma_i)$, where P is the phenotype function. Finally, we assume that the relationship between a colony's phenotype and its expected reproductive success is given by $w_i = W(\pi_i)/\overline{W}$, where $W(\pi_i)$ is the fitness function and $\overline{W} = \Sigma_I W(\pi_i)/M$. That is, except for the scaling factor $\overline{W}$ that is applied equally to all colonies to ensure constancy of population size across generations, a colony's expected fitness depends only on its own phenotype—i.e., there is no social interaction between colonies. This density regulation is assumed purely for mathematical convenience and has no impact on allele frequency change relative to a population that is allowed to exhibit unrestricted growth.

Using Price's (1970, 1972) theorem, the change in average p-score for a colony due to the action of natural selection is given by

$$\Delta_{NS} p = Cov_{i \in I}\left(w_i, p_i\right), \tag{1}$$

i.e., the covariance of a colony's expected fitness and its p-score (see *Appendix* for derivation). Note that, as a consequence of the queen being the only colony member capable of reproduction, natural selection acts wholly at the between-colony level and there is no selection at the within-colony level.

Optimization program

Following Grafen (2002), we capture ideas of biological adaptation and design by adopting the concept of a maximizing agent whose circumstances are framed within an optimization program. An optimization program is a mathematical device made up of three elements: (1) the employed strategy σ, (2) the set of all possible strategies S; and (3) the objective function, or maximand $F(\sigma)$ defined for all $\sigma \in S$, that describes how well the employed strategy σ realizes the agent's objective, i.e., better strategies return a higher value of the objective function. The optimization program can be written as

$$\sigma \max_{\sigma \epsilon S} F\left(\sigma\right). \tag{2}$$

The optimization program formalizes the concept of optimality. An optimal strategy $\sigma^* \in S$ is defined as satisfying $F(\alpha) \leq F(\sigma^*)$ for all $\alpha \in S$, i.e., it maximizes the objective function. A suboptimal strategy $\sigma^\circ \in S$ is defined by the existence of different strategy $\alpha \in S$ such that $F(\alpha) > F(\sigma^\circ)$, i.e., it does not maximize the objective function.

"Group as maximizing agent" analogy

Here, we link our population genetical model to the optimization program to form a "group as maximizing agent" analogy. We identify the agent as the colony—and, as there are M colonies in our model, we describe M agents with their own optimization program, indexed using the subscript $i \in I = \{1, 2, 3\ldots, M\}$. We identify the ith agent's strategy as the ith colony's phenotype, i.e., $\sigma_i = \pi_i$, and the strategy set as the set of all possible colony phenotypes, i.e., $S = \Pi$. Lastly, we identify the objective function as the fitness function, i.e., $F(\sigma) = W(\pi_i)$. This analogy can be summarized in the form of an optimization program, i.e.,

$$\pi_i \max_{\pi_i \epsilon \Pi} W\left(\pi_i\right). \tag{3}$$

This formalizes the use of optimality language in relation to colony phenotypes. An optimal colony phenotype $\pi_i{}^* \in \Pi$ satisfies $W(\phi) \leq W(\pi_i{}^*)$ for all other colony phenotypes $\phi \in \Pi$, i.e., it maximizes the colony's fitness. A suboptimal colony phenotype $\pi_i{}^\circ$ is defined by the existence of another phenotype $\phi \in \Pi$ such that $W(\phi) > W(\pi_i{}^\circ)$, i.e., it does not maximize the colony's fitness.

Gardner & Grafen (2009; see also Grafen, 2002) formed a similar "group as maximizing agent" analogy and showed that—in the context of clonal groups—six mathematical correspondences exist between the optimization program and Price's theorem. These correspondences relate the scenarios concerning the optimality or suboptimality of group phenotypes to scenarios concerning the action of natural selection, and vice versa, and may be summarized as follows:

Table 2. Group-level adaptation.

Correspondence	Queen control	Worker control	Shared control
*I. If all agents behave optimally, then there is no scope for selection (*i.e., *no expected change in any gene frequency).*	✓	✓	✓
*II. If all agents behave optimally, then there is no potential for positive selection (*i.e., *no introduced genetic variant is favoured when rare).*	✓	✓	✓
III. If all agents behave sub-optimally, but equally so, then there is no scope for selection.	✓	✓	✓
*IV. If all agents behave sub-optimally, but equally so, then there is potential for positive selection (*i.e., *at least one introduced genetic variant will be favoured when rare).*	✓	✓	✓
V. If agents vary in their optimality, then there is scope for selection, and the expected change in all gene frequencies and in the additive genetic component of every trait is given by its covariance with the agent's relative maximand value.	✓	✓*	✓*
VI. If there is no scope for selection and no potential for positive selection, then every agent behaves optimally.	✓	✓	✓

Summary of mathematical correspondences between the dynamics of natural selection in the context of a population genetical model of obligate eusociality—expression (1)—and the "group as maximizing agent" analogy—expression (3)—across three scenarios: queen control, worker control, and shared control. An asterisk (*) indicates that non-zero relatedness between queen and workers is required for there to be a guarantee that correspondence V holds in a non-trivial way (see *Appendix* for full derivation).

I. If all agents behave optimally, then there is no scope for selection (i.e., no expected change in any gene frequency).
II. If all agents behave optimally, then there is no potential for positive selection (i.e., no introduced genetic variant is favoured when rare).
III. If all agents behave sub-optimally, but equally so, then there is no scope for selection.
IV. If all agents behave sub-optimally, but equally so, then there is potential for positive selection (i.e., at least one introduced genetic variant is favoured when rare).
V. If agents vary in their optimality, then there is scope for selection, and the expected change in all gene frequencies and in the additive genetic component of every trait is given by its covariance with the agent's relative maximand value.
VI. If there is no scope for selection and no potential for positive selection, then every agent behaves optimally.

The first five correspondences translate the mathematics of optimality into the mathematics of selection. Correspondences I and III together provide an equilibrium condition: if all group-level agents have the same degree of optimality or suboptimality (i.e., the same expected fitness), then there is no expected change in any gene's frequency, because natural selection does not operate in the absence of variation in expected fitness. Correspondences II and IV together provide a stability condition: if all agents are optimal, then no genetic variant introduced at low frequency can invade the population; whereas if all agents behave sub-optimally, but equally so, then the population is vulnerable to such an invasion, because the rare variant enjoys higher fitness than the resident. Correspondence V describes how within-population differences in optimality (i.e., variation in expected fitness) relate to the action of selection when the population is not at equilibrium, i.e., the selective change is given by Price's theorem. The sixth correspondence translates the mathematics of selection into the mathematics of optimality: correspondence VI reveals that if there is neither scope nor potential for selection, then all group-level agents must be acting optimally; were they not all acting optimally, then there would be some scope or potential for selection to occur. Together, the correspondences provide formal justification for viewing clonal groups as fitness-maximizing agents.

We now investigate whether these same mathematical correspondences hold between our statement of the action of natural selection in the context of a population genetical model of obligate eusociality—expression (1)—and our "group as maximizing agent" analogy—expression (3)—to determine whether colonies with a reproductive division of labour may similarly be viewed as adaptive units. We consider three separate scenarios, in which the colony's phenotype is: (i) fully determined by the queen's genotype (queen control); (ii) fully determined by the workers' genotypes (worker control); or (iii) determined by both the queen and worker genotypes (shared control) (see Table 2 for summary of results).

Queen control—If the colony's phenotype is fully determined by the queen's genotype g_{i0}, then we may write $\gamma_i = g_{i0}$ for all $i \in I$ and hence $\pi_i = P(g_{i0})$. In this queen control scenario, we find that all six of the above mathematical correspondences hold (see *Appendix* for derivations). If all group-level agents, here colonies, behave optimally—i.e., all achieve the maximum expected fitness—then the absence of variation in expected fitness means there is no scope for selection (correspondence I), and as no introduced genetic variant can achieve higher fitness, there is no potential for positive selection (correspondence II). If all group-level agents behave equally sub-optimally, there is again no variation in expected fitness and thus there is no scope for selection (correspondence III), but there exists at least one genotype that would achieve greater expected fitness if introduced into the population and thus there is potential for positive selection (correspondence IV). If group-level agents vary in their optimality, then there is variation in expected fitness and scope for selection and—from expression (1)—the expected change in every gene's frequency will be given by its covariance with the fitness maximand (correspondence V). It then also follows that, if there is neither scope for selection nor potential for positive selection, all group-level agents must be behaving optimally (correspondence VI). There is therefore formal justification for viewing an obligately eusocial colony as a fitness-maximizing agent in the queen-control scenario.

Worker control—If the colony's phenotype is determined by a non-ordered list of worker genotypes $\hat{g}_i$, we may write γ_i

= $\hat{g}_i$ for all $i \in I$ and hence $\pi_i = P(\hat{g}_i)$. In this worker control scenario, we also find that all six mathematical correspondences hold (see *Appendix* for derivations). Because the queen is the only individual in the colony who can reproduce, within-colony selection is abolished, and the response to natural selection is modulated entirely by colony-level fitness. If all group-level agents behave optimally then, for the same reasons as in the queen control scenario, there is no scope for selection (correspondence 1) and no potential for positive selection (correspondence II). Similarly, if all group-level agents behave sub-optimally then, for the same reasons as in the queen-control scenario, there is no scope for selection (correspondence III), and there exists at least one genotype that would achieve greater expected fitness if introduced into the population, and thus there is potential for positive selection (correspondence IV). If group-level agents very in their optimality, there will be variation in expected fitness and scope for selection, with the expected change in every gene's frequency being given by its covariance with the fitness maximand (correspondence V). However, this correspondence holds only trivially—i.e., there can be no action of natural selection (Grafen, 2014)—unless the queen is genetically related to the workers: if she is not, then the worker genes that underpin an improved colony-level phenotype may not be passed onto future generations via the queen's reproductive success. Conversely, positive relatedness (even if very low) between the queen and workers will allow for genes that are expressed in the workers to be passed on by the queen, and thus, to be acted upon by natural selection. Lastly, as in the queen-control scenario, if there is neither scope for selection nor potential for positive selection, then all group-level agents must be behaving optimally (correspondence VI). Overall, then, there is also formal justification for viewing an obligately eusocial colony as a fitness-maximizing agent in the worker-control scenario.

Shared control—If the colony's phenotype is jointly determined by both the queen's genotype and a non-ordered list of worker genotypes, we may write $\gamma_i = \{g_{i0,\hat{g}_i}\}$and $\pi_i = P(\{g_{i0}, \hat{g}_i\})$ for all $i \in I$. Because reproductive division of labour still ensures no within-colony selection, we may use the same logic from both the queen-control and worker-control scenarios to find that all six mathematical correspondences hold in this shared-control scenario but that, again, natural selection can only act on the workers' contribution to the group phenotype if there is genetic relatedness between the queen and the workers (see *Appendix* for derivations). We therefore also obtain formal justification for viewing obligately eusocial colonies wherein the queen and workers share control over the phenotype as a fitness-maximizing agent.

Discussion

The concept of adaptation should be employed only when it is properly justified (Grafen, 2003; Williams, 1966). Gardner & Grafen (2009) established links between the mathematics of selection and optimization to justify the application of group-adaptationist thinking in some limited cases where there is no within-group selection and all group members are generic and interchangeable—i.e., when the group exhibits no class structure (Fisher, 1930; Grafen, 2006a; Taylor, 1990). Here, we have extended their theory of group-level adaptation to include multiple classes in order to capture Wheeler's (1911) original "superorganisms" (Figure 1). We have modelled an obligately eusocial colony with two classes of individuals—a reproductive queen and non-reproductive workers—and considered it acting as a purposeful agent striving to maximize its reproductive success. We have then established mathematical links between this optimization view and the dynamics of gene-frequency change to formalize this conception of colony-level adaptation. We have obtained formal justification for group-level adaptation for obligately eusocial colonies in three cases: a "queen control" scenario, wherein the colony's phenotype is fully determined by the queen's genotype; a "worker control" scenario, wherein the colony's phenotype is fully determined by the workers' genotypes; and a "shared control" scenario, wherein the colony's phenotype is jointly determined by both queen and worker genotypes. The justification in the latter two scenarios highlighted an important role for relatedness on the action of natural selection in obligate eusociality when non-reproductive individuals influence a colony's phenotype.

We have assumed full reproductive division of labour, such that the queen is the only member of the colony who is able to reproduce and pass on her genetic material. In the queen-control scenario, the queen is also the only individual in the colony whose genes have an influence upon the colony's phenotype. Accordingly, our having obtained formal justification for the group-as-maximizing-agent analogy in the queen-control scenario effectively recovers Grafen's (2002) formal justification for the individual-as-maximizing-agent analogy: here, the workers can be considered a mere extension of the queen's phenotype (Dawkins, 1982). Nowak et al. (2010) conceptualized workers in this way, without agency and with their properties controlled entirely by the queen's genotype, but our inclusion of this special case in our analysis is done simply for the purpose of exploring the underlying logic, and we do not intend for this toy model to be taken literally as a realistic model of obligately eusocial organization.

We also obtained formal justification for group-level adaptation in scenarios with worker-control or shared queen and worker control of the colony's phenotype, and, in doing so, revealed a central role for genetic relatedness between queen and workers. Worker genes contribute to shaping the colony's phenotype in these two scenarios, yet workers—being incapable of reproduction—cannot directly transmit their genes to future generations. Accordingly, unless the queen—who can reproduce—also shares copies of these same genes then it may be that better-adapted colony phenotypes are possible, but these phenotypes are unable to be worked upon by natural selection as the underlying genes cannot be passed on. One of the formal correspondence between group-level optimization and the dynamics of selection—in particular, correspondence V—continues to hold in the absence of such relatedness, but only trivially: i.e., a group-level formulation of Price's equation correctly describes the action of natural selection, even if this is equal to zero (cf. overdominance and heterozygotes in Grafen, 2014). Relatedness does not feature in the queen-control scenario because the queen has sole genetic control over the colony's phenotype and is able to transmit these genes to future generations via her own reproductive success. Relatedness also did not feature explicitly in Gardner & Grafen's (2009) analysis of the group-as-maximizing-agent analogy, but was implicit in their clonal-groups scenario, with clonality serving to both abolish within-group selection and also ensure that the genes underlying the group's phenotype are passed on if any group member reproduces. Moreover, Gardner & Grafen's (2009) repression-of-competition scenario did not require relatedness because all group members are assured the same expected reproductive success—i.e., all genes may be passed on to future generations.

One of the formal correspondences between the optimization view of fitness-maximizing agents and the dynamics of natural selection—in particular, correspondence IV—concerns the potential for positive selection in a scenario in which all agents are behaving sub-optimally but equally so. Grafen's (2002) treatment of the individual-as-maximizing-agent analogy assessed the potential for positive selection by introducing rare genetic variant individuals into the population at vanishingly low frequency and establishing whether any could invade under the action of natural selection, and Gardner & Grafen's (2009) treatment of the group-as-maximizing-agent analogy employed this same procedure. This resulted in a failure of correspondence IV (and hence also correspondence VI) in Gardner & Grafen's repression-of-competition scenario, as there was no guarantee that introduced variant individuals would be correctly arranged into groups in such a way as to produce an improved group phenotype—and hence no potential for positive selection under their interpretation. Here, we have taken a slightly different approach, introducing rare genetic variant groups into the population, such that if an improved group phenotype is possible then it can be introduced fully formed—for example, by migration from elsewhere (McGlynn, 2012)—and experience positive selection. We suggest that this approach might yield full formal justification for group adaptationism in Gardner & Grafen's (2009) repression-of-competition scenario.

In reality, insect societies in which reproductive potential is fully monopolized by a single queen are rare—this has only been described in some stingless bees and some ant species (Bueno et al., 2023; Holldobler & Wilson, 2009). In many social *Hymenoptera* taxa, workers retain the capacity to lay male eggs, and it is relatively common to find several reproductive queens in ant colonies (Keller & Reeve, 1994). Our justification for group-level adaptation in class-structured superorganisms relies on sterility of the worker class and the presence of only one reproductive queen in each colony. Relaxing these assumptions would introduce within-colony selection into our model, causing all six correspondences to fail. This is because an analysis based solely on the group's expected reproductive success captures only between-group selection and therefore cannot correctly predict the overall dynamics of selection when within-colony selection is also operating (Gardner & Grafen, 2009).

We have considered a scenario in which obligate eusociality has already become established, and hence our analysis does not address the evolutionary origins of obligate eusociality. It is now widely accepted that obligate eusociality has only ever arisen in lineages characterized by singly mated queens (Hughes et al., 2008), whereby strict lifetime female monogamy has resulted in maximal relatedness (Boomsma, 2009, 2022). Our analysis does help to explain how obligately eusocial taxa have often subsequently evolved female promiscuity (Boomsma & Ratnieks, 1996; Crozier & Fjerdingstad, 2001) by showing that once obligate eusociality is attained there is no requirement for queen-worker relatedness to remain high and that—so long as relatedness is nonzero—the action of natural selection will continue to correspond to the principle of fitness maximization at the colony level. That is, so long as female promiscuity serves to increase colony fitness—for example, by enabling the queen to overcome the limitations of sperm storage and produce a larger workforce—then this will be evolutionarily favoured. The present analysis equally applies to multicellular organismal adaptation, since germ–soma specialization also imposes a strict reproductive division of labour, and here too our results are consistent with the view that obligate multicellularity has only ever arisen in a clonal context (Fisher et al., 2013; Twyman & Gardner, 2025) as they concern the consequences rather than the origins of obligate multicellularity.

Our biological model considers the key form of class structure that defines obligate eusociality—reproductive division of labour. However, obligately eusocial taxa often exhibit other forms of class structure that are not considered in the present analysis, including in relation to sex, ploidy, and age (Hölldobler & Wilson, 2009). The consequences of these additional forms of class structure for group-level adaptation remain obscure. For example, the haplodiploid genetics of the Hymenoptera (ants, bees, and wasps) yield relatedness asymmetries within colonies that can drive conflicts of interest between queen and workers over sex allocation (Hamilton, 1972; Trivers & Hare, 1976), and such conflicts have the potential to drive substantial colony-level maladaptation, including in relation to aspects of the group's phenotype that are not under contention (Rautiala & Gardner, 2023). The assumption of non-overlapping generations—e.g., an annual life-history—is likely more benign, but it does eliminate age-differences between colonies, which could potentially modulate within-colony conflicts. Incorporating these additional forms of class structure into the group-as-maximizing-agent analogy represents an intriguing avenue for future investigation.

Data availability

No data were used in this paper.

Author contributions

Kalyani Z. Twyman (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Project administration [equal], Writing — original draft [lead], Writing — review & editing [equal]), and Andy Gardner (Conceptualization [equal], Formal analysis [equal], Funding acquisition [lead], Investigation [equal], Methodology [equal], Supervision [lead], Writing — review & editing [equal])

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Conflicts of interest

We declare we have no competing interests.

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APPENDIX

Price's equation under uncertainty

From Price's (1970, 1972) theorem, the change in average p-score in one generation for a colony under outcome ω can be expressed as

$$\Delta p^{\omega} = Cov_{i\in I}\left(w_{i0}^{\omega}, p_{i0}\right) + E_{i\in I}\left(w_{i0}^{\omega}\Delta p_{i0}\right), \qquad \text{(A1)}$$

where $Cov(x, y)$ denotes a covariance and $E(x)$ denotes an expectation or arithmetic average. The first term on the right hand side describes change due to selection, and the second describes change due to transmission—i.e., non-Darwinian processes that tend to erode adaptation (Fisher, 1930; Gardner & Welch, 2011; Grafen, 2003; Price, 1972). From this, we can define a statement of selection as

$$\Delta_S p^{\omega} = Cov_{i\in I}\left(w_{i0}^{\omega}, p_{i0}\right). \qquad \text{(A2)}$$

By including future uncertainty in expression (A2), we retain the effect of random genetic drift (Grafen, 2000). Averaging over this uncertainty yields a statement of the effect of natural selection only, which is given by

$$E_{\omega\in\Omega}\left(\Delta_S p^{\omega}\right) = Cov_{i\in I}\left(w_{i0}, p_{i0}\right), \qquad \text{(A3)}$$

and as a group's fitness and p-score are equivalent to its queen's fitness and p-score, this may also be written as expression (1) of the main text, where $E_{\omega\in\Omega}(\Delta_S p^{\omega}) = \Delta_{NS} p$.

Derivation of mathematical correspondences

Here, we prove the six mathematical correspondences (see Table 1) between the action of natural selection—expression (1)—and the group-as-maximizing agent (GMA) analogy—expression (3)—in the queen control, worker control, and shared control scenarios.

I. If all agents behave optimally, then there is no scope for selection (i.e., no expected change in any gene frequency).

Queen control, worker control, and shared control—If all colonies behave optimally, we have $W(\pi_i) = \overline{W}$ for all $i \in I$ such that $w_i = \overline{W}/\overline{W} = 1$ for all $i \in I$. Substituting this into expression (1) obtains $\Delta_{NS} p = Cov_{i\in I}(1, p_i) = 0$.

II. If all agents behave optimally, then there is no potential for positive selection (i.e., no introduced genetic variant is favoured when rare).

Queen control, worker control, and shared control—We introduce a fully-formed variant group genotype from another homogenous population into our population through a process like migration. We assign this and every other group a special p-score, $p_i^{\,v}$, to designate them as variant ($p_i^{\,v} = 1$) or resident ($p_i^{\,v} = 0$). From expression (1), the expected change in the population frequency of the variant group genotype can be given by

$$\Delta_{NS} p^{v} = Cov_{i\in I}\left(w_i, p_i^{v}\right) = p^{v}\left(1 - p^{v}\right)\left(w^{V} - w^{R}\right), \qquad \text{(A4)}$$

where $w^V = \overline{W}^v/\overline{W}$ and $w^R = \overline{W}^R/\overline{W}$. If all resident agents act optimally, $w^R = w^*$ and $w^V \le w^*$ such that $w^V - w^R \le 0$, so from expression (A4) we have $\Delta_{NS} p^v \le 0$.

III. If all agents behave sub-optimally, but equally so, then there is no scope for selection.

Queen control, worker control, and shared control—If all colonies behave sub-optimally but equally so, we have $W(\pi_i) = \overline{W}$ for all $i \in I$ such that $w_i = \overline{W}/\overline{W} = 1$ for all $i \in I$. Substituting this into expression (1) obtains $\Delta_{NS} p = Cov_{i\in I}(1, p_i) = 0$.

IV. If all agents behave sub-optimally, but equally so, then there is potential for positive selection (i.e., at least one introduced genetic variant will be favoured when rare).

Queen control, worker control, and shared control—If all resident agents act sub-optimally, $w^R = w^{\circ}$, where w° is some submaximal fitness, and there exists some variant group genotype that can introduced into the population that produces an optimal phenotype such that $w^V = w^*$. Because $w^* > w^{\circ}$, then $w^V - w^R > 0$, and from expression (A4) we have $\Delta_{NS} p^v > 0$.

V. If agents vary in their optimality, then there is scope for selection, and the expected change in all gene frequencies and in the additive genetic component of every trait is given by its covariance with the agent's relative maximand value.

Queen control—From expression (1), the expected change in gene frequency under the action of natural selection is given by $\Delta p = Cov_{i \in I}(w_i, p_i)$, and making the substitution $w_i = W(\pi_i)/\overline{W}$, we obtain $\Delta_{NS} p = Cov_{i \in I}(\frac{W(\pi_i)}{\bar{W}}, p_i)$.

Worker control—The expected change in gene frequency under the action of natural selection is again given by $\Delta p = Cov_{i \in I}(w_i, p_i)$, and making the substitution $w_i = W(\pi_i)/\overline{W}$, we obtain $\Delta_{NS} p = Cov_{i \in I}(\frac{W(\pi_i)}{\bar{W}}, p_i)$. Moreover, using the fact that $Cov(x, y) = \beta(x, y)\ Cov(x, x)$, where $\beta(x, y)$ is the least-squares linear regression of y on x, $Cov_{i \in I}(w_i, p_i) = \beta_{i \in I}(w_i, p_{\hat{i}}) \beta_{i \in I}(p_{\hat{i}}, p_{i0}) Cov_{i \in I}(p_{i0}, p_{i0})$, where $p_{\hat{i}}$ is a non-ordered list of worker p-scores and $\beta_{i \in I}(p_{\hat{i}}, p_{i0})$ defines the kin selection coefficient of relatedness between the queen and workers, and which is normally between zero and unity in standard scenarios (Frank, 1998). Thus, even though the phenotype of the group is fully controlled by the worker's genotype in this scenario, selection may occur when there is relatedness between the queen and workers.

Shared control—The expected change in gene frequency under the action of natural selection is again given by $\Delta p = Cov_{i \in I}(w_i, p_i)$, and making the substitution $w_i = W(\pi_i)/\overline{W}$, we obtain $\Delta_{NS} p = Cov_{i \in I}(\frac{W(\pi_i)}{\bar{W}}, p_i)$. Moreover, $Cov_{i \in I}(w_i, p_i) = Cov_{i \in I}(p_{i0}, p_{i0})(\beta_{i \in I}(w_i, p_{i0} | \hat{p}_i) + \beta_{i \in I}(p_{\hat{i}}, p_{i0})\ \beta_{i \in I}(w_i, \hat{p}_i | p_{i0}))$, where $\beta_{i \in I}(p_{\hat{i}}, p_{i0})$ again defines the kin selection coefficient of relatedness between the queen and workers. Thus, for selection to be guaranteed—i.e., for selection to be able to act on both the workers and queen's genotypes—there must be relatedness between the queen and workers.

VI. If there is no scope for selection and no potential for positive selection, then every agent behaves optimally.

Queen control, worker control, and shared control—Per correspondence V, if colonies vary in their optimality, there is scope for selection. It follows logically, that if there is no scope for selection, colonies cannot vary in their optimality. And per correspondence IV, if all colonies are equally sub-optimal, there is potential for positive selection. Hence, if there is no scope for selection and no potential for positive selection, all colonies must be acting optimally.

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