Extensive Social Choice and the Measurement of Group Fitness in Biological Hierarchies

Walter Bossert[1], Chloe X. Qi[2], and John A. Weymark[3]

[1] Department of Economics and CIREQ, University of Montreal, P.O. Box 6128, Station Downtown, Montreal QC H3C 3J7, Canada
E-mail: walter.bossert@umontreal.ca
[2] Boston Consulting Group, Exchange Place, 31st Floor, Boston, MA 02109, USA
E-mail: qi.chloe@bcg.com
[3] Department of Economics, Vanderbilt University, VU Station B #35189, 2301 Vanderbilt Place, Nashville, TN 37235-1819, USA
E-mail: john.weymark@vanderbilt.edu

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Abstract: Extensive social choice theory is used to study the problem of measuring group fitness in a two-level biological hierarchy. Both fixed and variable group size are considered. Axioms are identified that imply that the group measure satisfies a form of consequentialism in which group fitness only depends on the viabilities and fecundities of the individuals at the lower level in the hierarchy. This kind of consequentialism can take account of the group fitness advantages of germ-soma specialization, which is not possible with an alternative social choice framework proposed by Okasha, but which is an essential feature of the index of group fitness for a multicellular organism introduced by Michod, Viossat, Solari, Hurand, and Nedelcu to analyze the unicellular-multicellular evolutionary transition. The new framework is also used to analyze the fitness decoupling between levels that takes place during an evolutionary transition.

Keywords: consequentialism, group fitness, evolutionary transitions, fitness decoupling, multilevel selection, social choice.

1 Introduction

According to the theory of Darwinian evolution, if there is variation among a population, some variants produce more offspring than others, and offspring tend to resemble their parents, then natural selection will take place—the more fit variants will tend over time to supplant the less fit. These three properties are the principles of phenotypic variation, differential fitness, and heritability.

It is now widely believed that any entity possessing these properties may be subject to natural selection. For example, selection may take place among cells, organisms, or whole species. Following Godfrey-Smith (2009), we call such an entity a *Darwinian population*.

Darwinian populations form a nested biological hierarchy. The modern theory of *multilevel selection* deals with natural selection that takes place at more than one level in this hierarchy.[1] Multilevel selection theory has been useful in helping to explain phenomena that cannot be satisfactorily explained in terms of selection operating on individual organisms, such as the spread of cancer cells, which are the result of selection operating at the cellular level to the detriment of the higher-level organism.

Multilevel selection theory has also contributed to our understanding of major *evolutionary transitions in individuality* in which a new level in the biological hierarchy emerges. Maynard Smith and Szathmáry (1999) describe a number of such transitions. A familiar example (Margulis, 1998) is the origin of eukaryotic cells (cells with nuclei) by the symbiotic incorporation of bacteria as organelles, such as plastids and mitochondria, into prokarytoic cells (cells without nuclei). A distinguishing feature of such transitions is that biological entities that were capable of surviving and reproducing on their own prior to the transition lose that ability as they combine to form a new, more complex organism.

Fitness has two components—viability and fecundity (Michod, Viossat, Solari, Hurand, and Nedelcu, 2006). *Viability* is a measure of the ability to perform vegetative functions, whereas *fecundity* is a measure of reproductive capacity. There are many complications involved in measuring fitness at different levels when generations overlap and the different levels do not reproduce at the same time (Godfrey-Smith, 2009). When these complications do not arise, the expected number of offspring can be used to measure fitness, in which case viability is the probability of surviving long enough to reproduce and fecundity is the average number of offspring conditional on reproducing. A natural question to ask is: How is the fitness of a Darwinian population related to characteristics of other associated entities in the biological hierarchy? Here, we focus on a two-level hierarchy composed of individuals and groups and ask how group fitness depends on the characteristics of the individuals that form the group.[2]

Group fitness is typically measured by the sum or average of the individual fitnesses. While these may be good measures of fitness for a group that is not well integrated, as Okasha (2009) has observed, there are many reasons why these measures are not, in general, satisfactory. Here, we consider an

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[1] For a good introduction to multilevel selection theory, see Okasha (2006).

[2] In multilevel selection theory, "individuals" and "groups" are used relatively to denote a lower and higher level in the biological hierarchy, respectively. What is considered to be an individual in one context may be considered to be a group in another.

argument advanced by Michod, Viossat, Solari, Hurand, and Nedelcu (2006). As we have noted, in an evolutionary transition, individuals may lose their ability to survive and reproduce on their own. For example, in the transition from unicellular to multicellular organisms, some cells specialize in survival-enhancing vegetative functions (soma cells) and others in reproduction (germ cells). When the transition is complete, cells are completely specialized in one of these two tasks. As a consequence, the fitness of each individual cell is zero and, hence, group fitness as measured by the sum or average of the individual fitnesses is also zero. However, during this transition, the group emerges as more than the sum of its parts, with group fitness being enhanced as the transition progresses. In other words, there is a *decoupling* of the individual and group fitnesses (Michod and Nedelcu, 2003; Michod, 2005; Okasha, 2006).

Michod *et al.* (2006) have introduced an index of group fitness for a two-level biological hierarchy that can be used to analyze group fitness during an evolutionary transition. Their index of group fitness, henceforth referred to as the *MVSHN index*, is the product of indices of group viability and group fecundity, which in turn are equal to the sum of the individual viabilities and fecundities, respectively. In the case of a multicellular organism, unlike with total or average individual fitness, the MVSHN index can be positive if there is complete germ-soma specialization.

Recently, Okasha (2009) has used social choice theory to model the construction of a group fitness index and has applied his methodology to analyze the MVSHN index. Specifically, he has reinterpreted the concept of a social welfare functional introduced by Sen (1970) so as to apply to the problem of measuring group fitness. In Sen's approach, each person in a group of individuals has a *utility function* that assigns a number to each alternative in some set. An individual's utility function may be thought of as being a function that denotes how well off this person is with each of the alternatives. A *social welfare functional* determines a social (i.e., group) ranking of the set of alternatives as a function of the individual utility functions. Sen's social welfare functionals permit the social choice procedure to take account of intra- and interpersonal comparisons of utility. Different assumptions concerning the measurability and interpersonal comparabilty of utility can be formalized by requiring the social ranking of the alternatives to be invariant to certain transformations of the utility functions. For example, if levels of utility are intra- and interpersonally comparable, but no other kinds of utility comparisons are meaningful, then the social ranking is required to be invariant to any common increasing transform of the individual utility functions.[3]

In Okasha's reinterpretation of this framework, an alternative describes all aspects of the state of the world relevant to the biological group being considered and its constituent individuals. For example, an alternative includes descriptions of what nutrients are available to the individuals and of

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[3] For an in-depth survey of the literature that employs social welfare functionals, see Bossert and Weymark (2004).

how tasks are allocated among them. The analogue of a utility function is a *fitness function* that specifies how fit an individual is with each alternative. Okasha reinterprets a social welfare functional as a *group fitness functional* that determines a ranking of the alternatives in terms of overall group fitness as a function of the individual fitness functions. A *group fitness index* is a numerical representation of such a ranking. In principle, any way of aggregating the individual fitness functions can be employed, not just taking their sum or average.

Because Okasha's group fitness functionals use the fitness functions of the individuals in the group as their only inputs in determining the group fitness ranking, they are ill-equipped to deal with germ-soma specialization when applied to a multicellular organism. As is the case with using the sum or average of the individual fitnesses to measure group fitness, Okasha's approach cannot capture the gains that accrue from the specialization of vegetative and reproductive functions.

There is a natural analogy between utility and fitness that has been explored by Okasha (2011), among many others. In economics, individual decision-making is modeled as a problem in utility maximization subject to some constraints. Analogously, in evolutionary biology, biological entities are regarded as behaving as if they are maximizing fitness subject to the constraints imposed by their environment. The analogy between utility and fitness that Okasha (2009) draws on is different. He exploits the analogy between the social choice problem of determining a group ranking of a set of alternatives based on the individual utilities with the biological problem of determining a group fitness ranking based on the individual fitnesses.

Okasha is right to draw the analogy between the social choice and group fitness problems. He is also right when he argues that social choice theory can shed light on the problem of measuring group fitness. However, a social welfare functional is not the right tool to use for this purpose. A more appropriate tool is an extensive social welfare functional. Extensive social welfare functionals were introduced by Roberts (1995) and later systematically explored by Ooghe and Lauwers (2005). In extensive social choice theory, intra- and interpersonal utility comparisons are made by outside evaluators. Different evaluators may have different opinions about these comparisons. To allow for this possibility, an *extensive social welfare functional* determines a social ranking of the alternatives as a function of the utility functions attributed to each of the individuals by each evaluator. When there is only one evaluator, an extensive social welfare functional is simply a social welfare functional.

We propose a biological reinterpretation of a two-evaluator version of this framework that can be used to construct indices of group fitness. Corresponding to the two evaluators are the two characteristics of the biological individuals that are considered when determining group fitness. Specifically, for each individual there is a *viability function* and a *fecundity function* that specify the viability and fecundity, respectively, of this individual with each alternative. An *extensive group fitness functional* uses these functions as inputs

to determine the group fitness ranking. Because this approach takes account of the two components of individual fitness, not just the fitness itself, the group fitness ranking can reflect the gains from the germ-soma specialization observed in many multicellular organisms.

Okasha's group fitness functionals and our extensive group fitness functionals are used to determine group fitness rankings for a fixed number of individuals. However, as Michod and Nedelcu (2003) and Michod (2005) have emphasized, group size is an important factor in the emergence of germ-soma specialization in cells, with larger groups being associated with greater specialization. In order to take group size into account, we extend the definition of an extensive group fitness functional so as to allow for a variable number of individuals in the group. In social choice theory, the analogous extension of a social welfare functional is used to rank alternatives in which the population size is variable (Blackorby and Donaldson, 1984; Blackorby, Bossert, and Donaldson, 2005).

A social welfare functional is *welfarist* if the social ranking of any two alternatives only depends on the individual utilities obtained with them. Welfarism is a form of consequentialism in which the social evaluation of alternatives only takes account of utility consequences. Okasha (2009) considers the analogue of welfarism for group fitness functionals, what we call *fitness consequentialism*. With fitness consequentialism, the group fitness ranking only depends on the individual fitnesses. In particular, it does not depend on the individual viabilities and fecundities. As Okasha notes, the MVSHN index of group fitness does not satisfy this form of consequentialism. He argues that this observation can be used to help explain the decoupling of individual and group fitnesses in an evolutionary transition from unicellular to multicellular organisms.

We believe that Okasha's identification of the source of this decoupling is misplaced. As we argue, Okasha's approach to constructing a group fitness ranking ignores vital information about the individuals in the group, namely, their viabilities and fecundities. The ranking of alternatives by the MVSHN index only depends on the individual viabilities and fecundities, so it also satisfies a form of consequentialism, what we call *viability-fecundity consequentialism*. However, fitness decoupling is not inherently linked to whether the group fitness index satisfies this form of consequentialism. Rather, or so we argue, it has to do with the functional form of the extensive group fitness functional.

2 Biological Preliminaries

Natural selection can be viewed as a constrained optimization problem in which a Darwinian population behaves as if it is maximizing fitness (or, at least, it behaves as if it is seeking to increase its fitness) subject to the constraints imposed on it by its environment (Grafen, 2007; Michod *et al.*, 2006). These constraints identify the trade-offs that are possible between viability

and fecundity. A Darwinian population that uses more of the resources available to it for reproductive purposes will have fewer resources available for enhancing its survival, and vice versa. Michod *et al.* (2006) have used this optimization framework to help understand the germ-soma specialization that occurs when a multicellular organism emerges from its unicellular ancestor.

A great deal of what is known about the transitions to multicellularity has been obtained from the study of the family of volvocine green algae. These algae are a good model system for investigating the unicellular-multicellular transition for a number of reasons (Michod *et al.*, 2006; Miller, 2010). First, they have diverged from their unicellular ancestor relatively recently, which makes it easier to identify which genetic changes can be attributed to multicellularity. Second, they are clonal, so all cells are related. Third, they currently exist in a variety of forms, ranging from a unicellular species (*Chlamydomonas reinhardtii*) to highly integrated species with complete germ-soma specialization (e.g., *Volvox carteri*), with many intermediate forms, including loosely organized groups of cells that exhibit no germ-soma specialization (e.g., *Gonium pectorale*). The presence of these species with varying degrees of complexity allows for a phylogenetic reconstruction of the morphological and developmental changes that likely occurred in the transition to multicellularity (Kirk, 2005; Herron and Michod, 2007).

Damuth and Heisler (1988) identify two, non-exclusive types of multilevel selection. *Multilevel selection 1* (MLS1) is concerned with the effect of group membership on individual fitness. MLS1 explains, for example, the evolution of altruism as a character trait that increases the fitnesses of individuals within a colony. MLS1 does not require the group to be a Darwinian population and, hence, the group does not necessarily possess fitness beyond the fitnesses of the individuals. For example, some slime moulds exist as collections of single-celled amoebae which coalesce into a collective for a time and then dissipate (Okasha, 2006). *Multilevel selection 2* (MLS2), on the other hand, is concerned with selection among groups. In order for MLS2 to take place, groups must reproduce in some way. For example, the geographic range of late-Cretaceous mollusc species increased due to selection at the species level because those species with greater geographic range, a heritable trait, produced more offspring species (Okasha, 2006).

The distinction between these two types of multilevel selection has implications for how group fitness should be measured. In the case of MLS1, defining group fitness as the average or total fitness of the individuals in the group is appropriate because natural selection is operating to maximize the expected number of offspring individuals. However, in the case of MLS2, it is the number of offspring groups that is being selected for and, as Damuth and Heisler (1988, p. 415) note, with MLS2 "group fitness need not (and often will not) be the same as mean individual fitness."

Michod (2005) describes the emergence of multicellularity as a transition from MLS1 to MLS2. The challenge is to determine how this transition took place. He and his collaborators have employed a number of different

approaches to analyze this problem. The most relevant one here is the optimization approach developed by Michod *et al.* (2006). They are primarily interested in understanding how germ-soma specialization and the emergence of a multicellular organism arise, which they investigate by employing a life-history analysis of the two components of fitness—viability and fecundity. They argue that it is the shape of the constraint set describing the feasible trade-offs between viability and fecundity that accounts for these phenomena. Moreover, the nature of the trade-offs at the group level (i.e., the curvature of the function describing the group-level trade-offs) is initially determined by the trade-offs at the cell level, but then the group-level trade-offs diverge from the cell-level trade-offs as the transition progresses.[4] In this way, an explanation for the transition from MLS1 to MLS2 is obtained.

But an analysis of the constraint is only half the story. In order to know how group fitness is maximized given the constraint, one needs to know how fitness is measured. The group fitness index that is used cannot be the average or total fitness of the individual cells, otherwise it would not be possible to capture the gains to group fitness that arise from germ-soma specialization. It is for this reason that Michod *et al.* (2006) need to introduce a new index of group fitness. Furthermore, in order to show that the emergence of a new biological entity—the multicellular organism—is fitness enhancing, it is necessary to have a single group fitness index that can be used whatever the degree of interrelatedness among the individual cells.

Our concern is with the functional form of the group fitness index, not with the fitness optimization problem or its solution. That is, we are interested in how group fitness is related to the characteristics of the individuals that comprise the group.

While several factors are involved in shaping an evolutionary transition, increasing group size plays a prominent role (Michod and Nedelcu, 2003; Michod, 2005). Whether a larger group is advantageous depends on its benefits and costs, which in turn depend on the stage of the transition. For example, for a multicellular organism, a larger organism may more effectively benefit from germ-soma specialization and may be better able to protect itself from predators. However, a larger organism may also make it more difficult for resources to be transported to the cells from the organism's environment and it may make reproduction more difficult. Michod and his collaborators (e.g., Michod and Nedelcu, 2003; Michod, 2005) argue that the formation of cooperative interactions between individuals and the emergence of group-level traits that align the interests of the individuals and the group are fundamental for the development of the group as a Darwinian population. Group size plays an important role in these processes. Therefore, if an index of group fitness

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[4] Formally, they argue that the function showing how maximum group viability is related to group fecundity is concave for unicellular organisms, but becomes increasingly convex as the transition to multicellularity progresses due to the increased cost of reproduction as group size increases.

is to be used to help explain the emergence of a new, higher-level Darwinian population, the index must allow for variable group size.

3 The MVSHN Index

For each positive integer n, we are interested in measuring the fitness of a biological group composed of n individuals. In Michod *et al.* (2006), the group is an organism and the individuals are the cells that comprise it. The organism is unicellular if $n = 1$ and it is multicellular otherwise. We let $\mathbb{N}$ denote the set of positive integers. Thus, $\mathbb{N}$ is the set of possible group sizes. While feasibility constraints may limit the size of groups in practice, here we are not concerned with feasibility, and so do not put any bound on group size. None of the points we make depend on this assumption.[5] We do not distinguish between distinct collections of individuals that exhibit the same physical characteristics. Thus, we can index the individuals in a group of size n by the integers 1 through n. With this convention, individual i is part of the group if and only if the group has at least i members.

We consider the following sets and vectors in Euclidean spaces. The real line is $\mathbb{R}$, the nonnegative real line is $\mathbb{R}_+$, the n-dimensional Euclidean space is $\mathbb{R}^n$, and the nonnegative orthants of $\mathbb{R}^n$ and $\mathbb{R}^{2n}$ are $\mathbb{R}^n_+$ and $\mathbb{R}^{2n}_+$, respectively.

Associated with each individual i is a *viability* level v_i and a *fecundity* level b_i. Viability is a measure of an organism's ability to perform vegetative functions, whereas fecundity measures its reproductive capacity. Naturally, v_i and b_i are nonnegative. We assume that, in principle, v_i and b_i can take on any nonnegative value. It is possible to place upper bounds on the values of the individual viabilities and fecundities without affecting our analysis, but, for simplicity, we suppose that these values are unbounded. If individual viability is interpreted as being the probability of surviving to some stage in the group's development (e.g., until the individual is able to reproduce if it has this capability), then v_i would be bounded above by one.

For a group of size n, the *viability profile* $\mathbf{v} = (v_1, \ldots, v_n)$ and the *fecundity profile* $\mathbf{b} = (b_1, \ldots, b_n)$ are both vectors in $\mathbb{R}^n_+$. Thus, the *viability-fecundity profile* $(\mathbf{v}, \mathbf{b})$ for a group with n individuals is a vector in $\mathbb{R}^{2n}_+$. Because the group size n can be any positive integer, the set of all possible viability-fecundity profiles is $\Omega = \cup_{n \in \mathbb{N}} \mathbb{R}^{2n}_+$.

The *fitness* of individual i is

$$f_i = v_i b_i,$$

the product of its viability and fecundity. Therefore, the *total group fitness* of a group of size n is

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[5] It is straightforward to modify our analysis to take account of a finite upper limit on the size of a group.

$$C = \sum_{i=1}^{n} v_i b_i.$$

Average group fitness is C/n. While C and C/n are the standard ways of measuring group fitness, as we have noted, they cannot capture the fitness advantages that are obtained by germ-soma specialization in a multicellular organism. When there is a complete separation of vegetative and reproductive functions, soma cells have zero fecundity and germ cells have zero viability. Hence, the values of C and C/n are zero even though the group may exhibit considerable fitness.

The MVSHN index of group fitness captures the benefits to the group from the vegetative-reproductive division of labor. Michod *et al.* (2006) measure *group viability v* and *group fecundity b* by taking the sum of the individual values. For a group of size n,

$$v = \sum_{i=1}^{n} v_i$$

is the group's viability and

$$b = \sum_{i=1}^{n} b_i$$

is its fecundity. The *MVSHN index of group fitness M* is the product of group viability and group fecundity. That is,

$$M = vb = \left(\sum_{i=1}^{n} v_i\right)\left(\sum_{i=1}^{n} b_i\right).$$

With this measure of group fitness, germ-soma specialization can contribute to the group's viability and fecundity and, hence, to its overall fitness. Even if an individual does not use the resources available to it to invest in, say, vegetative functions, it can nevertheless make a substantial contribution to group fitness by using them instead for reproductive purposes. This is simply not possible if average or total group fitness is used to measure group fitness.[6]

In addition to taking account of any group benefits that accrue from the vegetative-reproductive division of labor, the MVSHN index does not require that individuals exhibit fitness in order for the group to do so. Indeed, if there is complete germ-cell specialization, no individual has any fitness. Thus, the MVSHN index captures what Michod and Nedelcu (2003) and Michod (2005) argue is an important feature of the kind of evolutionary transition exemplified by a unicellular-multicellular transition—at the end of the transition,

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[6] Michod *et al.* (2006) normalize the value of their index by dividing by n^2 when comparing it with average group fitness. This amounts to replacing v and b with their individual averages. For a fixed number of individuals, it is of no consequence whether group fitness is measured using the indices C and M or their normalized versions. Okasha (2009) uses the normalized indices.

the individuals are no longer Darwinian populations themselves. Rather, the transference of fitness from the individuals to the group is complete.[7]

Defining group viability and fecundity as additive functions of the individual viabilities and fecundities is a simplifying assumption, but one that Michod *et al.* (2006) regard as being reasonable for organisms like the volvocine green algae that they use as a model system. They do, however, raise some reservations about treating the individual contributions to group viability additively. Volvocine green algae have flagella that are used to move cells in an aqueous environment towards light so that photosynthesis can take place (Miller, 2010). If flagellar motility is used as a proxy for viability, an additive relationship between the overall motility of the group and the motilities of the individuals is unlikely to hold in large, well-integrated groups.[8]

Michod *et al.* (2006) believe that defining group fitness as the product of group viability and group fecundity is appropriate for groups with discrete generations, such as the volvocine green algae. In addition, they note that their qualitative results concerning the benefits of individual specialization of function are valid more generally for any group fitness index that attains its lowest value of zero when either v or b is zero and that is increasing in either argument when they are both positive.

A *group fitness ordering* is an ordering R of the viability-fecundity profiles in Ω.[9] The statement that $(\mathbf{v}, \mathbf{b}) R (\mathbf{v}', \mathbf{b}')$ is interpreted as meaning that the group exhibits at least as much fitness with the viability-fecundity profile $(\mathbf{v}, \mathbf{b})$ as it does with $(\mathbf{v}', \mathbf{b}')$. These two profiles may or may not have the same number of individuals. The asymmetric ("is more fit than") and symmetric ("is equally fit as") factors of R are P and I, respectively.[10] In order to determine the implications of group fitness maximization, the group fitness ordering of the viability-fecundity profiles is needed, but not the group fitness index that is used to numerically represent this ordering.

The MVSHN index of group fitness defines the *MVSHN group fitness ordering* R^M obtained by setting, for all $n, n' \in \mathbb{N}$, $(\mathbf{v}, \mathbf{b}) \in \mathbb{R}^{2n}_+$, and $(\mathbf{v}', \mathbf{b}') \in \mathbb{R}^{2n'}_+$,

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[7] Okasha (2006, p. 238) regards this view as being overly restrictive and offers examples in which the individuals remain Darwinian populations at the end of an evolutionary transition.

[8] In an appendix to their article, Michod *et al.* (2006) show that germ-soma specialization can still be optimal if the individual contributions to group viability are not additive. However, they do not explicitly construct an index of group fitness with nonadditive viabilities.

[9] A binary relation R on a set S is an *ordering* if it is *reflexive* (for all $s \in S$, sRs), *complete* (for all distinct $s, t \in S$, sRt or tRs), and *transitive* (for all $r, s, t \in S$, $[rRs$ and $sRt] \Rightarrow rRt$).

[10] For a binary relation R on a set S, the asymmetric factor P and symmetric factor I are defined as follows: for all $s, t \in S$, $sPt \Leftrightarrow [sRt$ and $\neg(tRs)]$ and $sIt \Leftrightarrow [sRt$ and $tRs]$.

$$(\mathbf{v}, \mathbf{b}) R^M(\mathbf{v}', \mathbf{b}') \iff \left(\sum_{i=1}^{n} v_i \right) \left(\sum_{i=1}^{n} b_i \right) \geq \left(\sum_{i=1}^{n'} v_i' \right) \left(\sum_{i=1}^{n'} b_i' \right).$$

In other words, the viability-fecundity profile $(\mathbf{v}, \mathbf{b})$ is said to exhibit at least as much group fitness as $(\mathbf{v}', \mathbf{b}')$ if and only if the former has at least as large a value of the MVSHN index as the latter.

4 Group Fitness Functionals

Okasha (2009) takes a more foundational approach to measuring group fitness by investigating how group fitness depends on the characteristics of the group and its constituent individuals, and on the environment that they operate in. The formal framework used by Okasha presupposes that group size is fixed. In this section, we follow Okasha in making this assumption. However, because increases in the number of group members play an important role in evolutionary transitions, we shall consider variable group size in a later section. Individual and group fitness coincide when $n = 1$, so we suppose that group size n is at least two. Let $N = \{1, \ldots, n\}$ denote the set of individuals in the group.

An alternative describes all aspects of the state of the world that are relevant for the group. These would include descriptions of the nutrients available to the individuals, their physical relationships with one another, how tasks are allocated between them, what predators threaten them, and so on. Let A be the set of these alternatives. Okasha assumes that A is finite, but this is not necessary. We only require that A contains at least three alternatives. The objective is to order these alternatives according to how fit the group is with them. The set of possible orderings of A is $\mathcal{R}$.

The fitness of each individual in the group depends on the alternative in A that describes the situation it is in. Formally, for each individual $i \in N$, this relationship is described by a *fitness function* $F_i \colon A \to \mathbb{R}_+$ that specifies, for each alternative $a \in A$, the fitness $F_i(a)$ of individual i with alternative a. For an individual that has completely specialized in vegetative or reproductive functions, this value is zero. A *fitness function profile* is a list $F = (F_1, \ldots, F_n)$ that specifies the fitness function of each individual in the group. Thus, $F(a) = (F_1(a), \ldots, F_n(a))$ is an n-vector of numbers describing the fitness levels of every individual with the alternative a. Let $\mathcal{F}$ denote the set of all conceivable fitness function profiles. It may not be necessary to consider all profiles in $\mathcal{F}$. Let $\mathcal{D}^f \subseteq \mathcal{F}$ denote the profiles that are considered.[11]

Okasha introduced the concept of a *group fitness functional* to describe the dependence of the ordering of A in terms of group fitness on the profile of fitness functions.

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[11] We use the superscript f when the individual characteristics being considered are fitnesses and the superscript vb when they are viabilities and fecundities.

Group Fitness Functional. A group fitness functional is a mapping G^f : $\mathcal{D}^f \to \mathcal{R}$.

It is convenient to let R_F^f denote the ordering $G^f(F)$ of A obtained from the profile F.

A group fitness functional is a biological reinterpretation of the concept of a social welfare functional introduced by Sen (1970). In Sen's formulation, N is a set of people, A is a set of alternatives that are to be socially ordered, and F_i is the utility function of the ith individual. A *social welfare functional* specifies a social ordering of the alternatives for each profile of utility functions in some domain $\mathcal{D}^f$.

We focus on three of the axioms that Okasha considered for a group fitness functional. In their social welfare functional interpretations, they are known as the *welfarism axioms*.

Unrestricted Domain^f. The domain $\mathcal{D}^f$ of the group fitness functional G^f is all of $\mathcal{F}$.

This axiom requires that it be possible to determine an ordering of the alternatives in A no matter how the individual fitnesses depend on the alternatives. When considering the reasonableness of this axiom, it should be borne in mind that we are only focusing on the objective function in the group fitness optimization problem. Some individual fitness functions may not be feasible because they violate physical constraints, but that is not relevant when constructing a measure of group fitness.

Pareto Indifference^f. For any pair of alternatives $a, a' \in A$ and any profile of fitness functions $F \in \mathcal{D}^f$, if $F(a) = F(a')$, then $aI_F^f a'$.

Informally, for a given fitness function profile, this axiom says that if the fitness obtained with alternative a is the same as that obtained with a' for each individual, then the group exhibits the same overall fitness with either of these alternatives.[12]

Binary Independence of Irrelevant Alternatives^f. For any pair of alternatives $a, a' \in A$ and any pair of profiles of fitness functions $F, F' \in \mathcal{D}^f$, if $F(a) = F'(a)$ and $F(a') = F'(a')$, then $aR_F^f a'$ if and only if $aR_{F'}^f a'$.

This axiom implies that the ranking of any two alternatives in terms of group fitness does not depend on the individual fitnesses obtained with any of the other alternatives. An alternative is a complete description of the state of the world relevant for the group's fitness, so different possible states are irrelevant for group fitness in the states that are being considered. Moreover, if the individual fitnesses obtained with a are the same with both the profiles F

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[12] This axiom is named after the Italian economist-sociologist Vilfredo Pareto, who introduced a related criterion for ranking vectors of utilities.

Table 1. Fitness consequentialism

	a	a'	a''	a'''
F	$(2,3)$	$(4,1)$		
F'			$(2,3)$	$(4,1)$
F''	$(2,3)$	$(4,1)$	$(2,3)$	$(4,1)$

and F' and the same is true with a', then the ranking of these two alternatives in terms of group fitness must be the same with both profiles.

   An implication of these three axioms is that the only information needed to know how to rank alternatives in terms of group fitness is the individual fitnesses obtained with them.

Theorem 1. *For a group of size $n \geq 2$, if a group fitness functional $G^f : \mathcal{D}^f \to \mathcal{R}$ satisfies Unrestricted Domain^f, then it satisfies Pareto Indifference^f and Binary Independence of Irrelevant Alternatives^f if and only if there exists an ordering R^f of $\mathbb{R}^n_+$ such that for every fitness function profile $F \in \mathcal{D}^f$ and every pair of alternatives $a, a' \in A$,*

$$a R^f_F a' \iff F(a) R^f F(a').$$

   Theorem 1 is simply a restatement in biological terms of the *welfarism theorem* for social welfare functionals (see Bossert and Weymark, 2004, Theorem 2.2). *Welfarism* is the principle that requires the social ranking of alternatives to only depend on the utilities achieved with them.

   The group fitness functional G^f determines an ordering of the alternatives for each profile of fitness functions in its domain. With Unrestricted Domain^f, there are an infinite number of such profiles and, hence, an infinite number of orderings. What Theorem 1 shows is that all of these orderings are coded in a single ordering R^f of the nonnegative orthant in Euclidean n-space if it is additionally assumed that Pareto Indifference^f and Binary Independence of Irrelevant Alternatives^f are satisfied. This ordering ranks vectors of achieved individual fitnesses. For example, for the profile F, the alternatives a and a' are ranked the same way that R^f ranks the individual fitness levels $F(a)$ obtained with a and the individual fitness levels $F(a')$ obtained with a'. In other words, the ordering of the alternatives in terms of group fitness is determined solely on the basis of the individual fitnesses obtained with them. This is a form of consequentialism. We call it *fitness consequentialism* because it is only the fitness consequences of an alternative that matter.

   We illustrate why the assumptions of Theorem 1 entail fitness consequentialism using the example in Table 1. In this example, there are two individuals

in the group, each row is a profile of fitness functions, and each column is an alternative. In any row and column, the first entry is the fitness of individual 1 and the second is the fitness of individual 2. Blank entries are left unspecified, as are the fitnesses associated with any other alternative not listed in the column headings. For concreteness, suppose that when the profile is F that the group is fitter with a than with a'. With the profile F', the individual fitnesses are the same with a'' (resp. a''') as they are with a (resp. a') when the profile is F. If the procedure for determining group fitness is fitness consequentialist, then the group must be fitter with a'' than it is with a''' with the profile F'.

To see why this is the case, consider the profile F'' in the third row of the table. The existence of a profile with this pattern of individual fitnesses is guaranteed by Unrestricted Domain^f. The individual fitnesses for alternatives a and a' coincide for the profiles F and F''. Because the group is fitter with a than with a' when the profile is F, by Binary Independence of Irrelevant Alternatives^f, the same must be true with the profile F''. With the latter profile, Pareto Indifference^f implies that group fitness is the same with a and a'' and with a' and a'''. For the profile F'', because the group is fitter with a than with a', using the transitivity of the fitness relation twice then implies that it is also fitter with a'' than with a'''. Invoking Binary Independence of Irrelevant Alternatives^f once more, it then follows that the same is true with the profile F', as required by fitness consequentialism.[13]

Using the total group fitness index C to rank the alternatives in A is obviously fitness consequentialist. However, constructing this ranking using the MVSHN group fitness index M or its associated group fitness ordering R^M is not. With fitness consequentialism, only the fitnesses of the individuals are considered when ranking the alternatives in A in terms of group fitness. The ordering R^M is a ranking of viability-fecundity profiles. When R^M is used to determine a group fitness ranking of the alternatives, it takes account of both the viability and fecundities of the individuals so as to capture the group fitness advantage that emerges when the individuals begin to specialize in vegetative and reproductive functions. In other words, with the MVSHN index M or ordering R^M, it is not necessarily true that the group fitness obtained with a and a' are the same when the individual fitnesses are equal in these two alternatives.

The violation of fitness consequentialism with the MVSHN index is illustrated in Table 2, which modifies the first two lines of Table 3 in Okasha (2009) by using total rather than average values. The fitness of each individual is 6 with either a or a' and, hence, these alternatives are declared to exhibit the same group fitness using the index of total group fitness C. With alternative a, both individuals have the same viability and fecundity, so there is no functional specialization. With a', on the other hand, there is some specialization, with individual 2 investing relatively more in vegetative functions than in-

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[13] The example involves four distinct alternatives but the argument also applies if there are only three alternatives in A.

Table 2. Fitness consequentialism violated with the MVSHN index

alternative	(v_1, b_1)	(v_2, b_2)	C	M
a	$(2, 3)$	$(2, 3)$	12	24
a'	$(2, 3)$	$(3, 2)$	12	25

dividual 1 and vice versa for reproductive functions. The MVSHN index M captures the group fitness advantage of this division of labor, ranking a' above a.

Okasha (2009) argues that the MVSHN index violates both Pareto Indifference[f] and Binary Independence of Irrelevant Alternatives[f] when the group fitness functional framework is used to evaluate its merits. For example, in Table 2, the individual fitnesses are the same in both alternatives, but M does not assign them the same group fitness value, thereby violating Pareto Indifference[f]. However, the problem is more fundamental than that. The very *definition* of a group fitness functional rules out considering individual viabilities and fecundities when determining a group fitness ranking of the alternatives. However, as Michod *et al.* (2006) argue, these are essential components of group fitness. This suggests that we need a richer framework in order to model the contributions of the individual viabilities and fecundities to group fitness. In the next section, we propose that a more appropriate framework for this purpose is a biological reinterpretation of an extensive social welfare functional.

Okasha (2009) suggests that the violation of Pareto Indifference[f] (or of a related Pareto condition) can help explain the decoupling of group fitnesses from the individual fitnesses in an evolutionary transition (Michod and Nedelcu, 2003; Michod, 2005; Okasha, 2006). For example, at the beginning of a unicellular-multicellular transition, there is no germ-soma specialization, and so group fitness is simply some function of the individual cell fitnesses. However, as the transition proceeds, group fitness cannot be determined from the cell fitnesses alone; there is what Okasha calls a "Pareto violation." When the transition is complete, the cells are no longer Darwinian populations and, therefore, do not have their own fitnesses. We believe that Okasha's focus on Pareto violations is misplaced. In order for social choice theory to aid in our understanding of fitness decoupling, the framework used must allow the components of fitness—viability and fecundity—to play a role in the analysis. It must also allow for the number of individuals in the group to vary.

5 Extensive Group Fitness Functionals

Okasha's conceptualization of the MVSHN index violates fitness consequentialism because it fails to capture individual differences at the level of the components of fitness. By using an alternative approach borrowed from extensive social choice theory, the contributions of the individual viability and fecundity functions to group fitness can be accounted for. The MVSHN index satisfies a different form of consequentialism, one that can be accommodated in our approach. In order to compare our approach with that of Okasha, we first restrict attention to situations in which the number of individuals is fixed. We deal with the more general case of variable group size in the next section.

As in the preceding section, N is the set of individuals in the group, A is the set of alternatives, and $\mathcal{R}$ is the set of orderings of A, where each element of $\mathcal{R}$ is interpreted as being an ordering of the alternatives in A in terms of group fitness. Now, two characteristics are used to describe the situations of the individuals, viability and fecundity. For each individual $i \in N$, the *viability function* $V_i \colon A \to \mathbb{R}_+$ specifies, for each alternative $a \in A$, the viability $V_i(a)$ of individual i with alternative a. Similarly, for each individual $i \in N$, the *fecundity function* $B_i \colon A \to \mathbb{R}_+$ specifies, for each alternative $a \in A$, the fecundity $B_i(a)$ of individual i with alternative a. A *viability function profile* is a list $V = (V_1, \ldots, V_n)$ of the individual viability functions. The corresponding list $B = (B_1, \ldots, B_n)$ of the fecundity functions is a *fecundity function profile*. The pair (V, B) is a *viability-fecundity function profile*.

Given $a \in A$, $V(a) = (V_1(a), \ldots, V_n(a))$ and $B(a) = (B_1(a), \ldots, B_n(a))$ are n-vectors of nonnegative numbers that respectively list the viabilities and fecundities of each individual with a. For a group of size n, let $\mathcal{V}^n$ and $\mathcal{B}^n$ respectively denote the set of all viability function profiles and the set of all fecundity function profiles for which the individual viabilities and fecundities are nonnegative for each alternative in A. Let $\mathcal{D}^{vb} \subseteq \mathcal{V}^n \times \mathcal{B}^n$ be the set of all viability-fecundity function profiles under consideration.

We use an *extensive group fitness functional* instead of Okasha's group fitness functional to model the dependence of group fitness on the characteristics of the individuals in the group.

Extensive Group Fitness Functional. An extensive group fitness functional is a mapping $G^{vb} \colon \mathcal{D}^{vb} \to \mathcal{R}$.

The functional G^{vb} assigns a group fitness ordering of the alternatives in A to each viability-fecundity function profile in $\mathcal{D}^{vb}$. Unlike a group fitness functional, an extensive group fitness functional takes account of the contributions of the individual viabilities and fecundities to group fitness, not just the individual fitnesses. Indeed, it is not necessary to attribute any fitness to the individuals in order to use an extensive group fitness functional. Hence, when analyzing a unicellular-multicellular transition, our framework can be used even when there is complete germ-soma specialization, whereas Okasha's framework cannot. Moreover, if, in fact, only individual fitnesses matter for

group fitness, as with multilevel selection 1 (Damuth and Heisler, 1988), this can be accommodated in our framework by aggregating the individual viabilities and fecundities into individual fitnesses.

An extensive group fitness functional is a biological analogue of an extensive social welfare functional. The concept of an extensive social welfare functional was introduced by Roberts (1995) as a generalization of a social welfare functional. With an extensive social welfare functional, there are outside evaluators in addition to the individuals whose well-beings are being considered. Each evaluator attributes a profile of utility functions to the individuals, but because they may make different intrapersonal and interpersonal comparisons of utility, different evaluators need not have the same profile. An extensive social welfare functional determines a social ordering of the alternatives as a function of these profiles. Roberts calls this the "double aggregation problem" because the aggregation involves both the utilities of the individuals and the opinions of the evaluators. Ooghe and Lauwers (2005) have provided a comprehensive analysis of the implications of different sets of axioms for the functional form of an extensive social welfare functional.

The characteristics used to describe the situations of the individuals in a biological group are the analogues of the outside evaluators. In our application, there are only two characteristics—viability and fecundity. The viability function profile corresponds to the profile of utility functions for one evaluator and the fecundity function profile corresponds to the profile of utility functions for a second evaluator. While we only use two characteristics to describe the contributions of individuals to group fitness, the framework is general enough to allow for more individual characteristics to be considered if they are relevant.

There are extensive group fitness functional counterparts to each of the three welfarism axioms considered in the preceding section. We use the same names for these axioms, but now indexed with the superscript vb. In these axioms, R_{VB}^{vb} denotes the ordering $G^{vb}(V,B)$ of A obtained when the profile is (V,B).

Unrestricted Domain^{vb}. The domain $\mathcal{D}^{vb}$ of the extensive group fitness functional G^{vb} is all of $\mathcal{V}^n \times \mathcal{B}^n$.

Pareto Indifference^{vb}. For any pair of alternatives $a, a' \in A$ and any viability-fecundity function profile $(V,B) \in \mathcal{D}^{vb}$, if $(V(a), B(a)) = (V(a'), B(a'))$, then $aI_{VB}^{vb}a'$.

Binary Independence of Irrelevant Alternatives^{vb}. For any pair of alternatives $a, a' \in A$ and any pair of viability-fecundity function profiles (V,B), $(V',B') \in \mathcal{D}^{vb}$, if $(V(a), B(a)) = (V'(a), B'(a))$ and $(V(a'), B(a')) = (V'(a'), B'(a'))$, then $aR_{VB}^{vb}a'$ if and only if $aR_{V'B'}^{vb}a'$.

If Unrestricted Domain^{vb} is satisfied, then it is possible to determine a group fitness ordering of the alternatives in A no matter how the individual

viabilities and fecundities depend on them. With Pareto Indifference^{vb}, for a given viability-fecundity function profile, overall group fitness is the same in two alternatives if each individual has the same viability and fecundity in them. As with Binary Independence of Irrelevant Alternatives^{f}, Binary Independence of Irrelevant Alternatives^{vb} precludes the group fitness ranking of two alternatives from depending on the characteristics of the individuals with any other alternative. However, what are considered to be the relevant features of the alternatives being compared are the individual viabilities and fecundities, not the individual fitnesses.

Taken together, these three axioms imply that the ordering of the alternatives in terms of group fitness only depends on the individual viabilities and fecundities obtained with them, what we call *viability-fecundity consequentialism*.

Theorem 2. *For a group of size $n \geq 2$, if an extensive group fitness functional $G^{vb} \colon \mathcal{D}^{vb} \to \mathcal{R}$ satisfies Unrestricted Domain^{vb}, then it satisfies Pareto Indifference^{vb} and Binary Independence of Irrelevant Alternatives^{vb} if and only if there exists a group fitness ordering R^{vb} of $\mathbb{R}_{+}^{2n}$ such that for every viability-fecundity function profile $(V, B) \in \mathcal{D}^{vb}$ and every pair of alternatives $a, a' \in A$,*

$$aR_{VB}^{vb}a' \iff (V(a), B(a))R^{vb}(V(a'), B(a')).$$

Theorem 2, like Theorem 1, is a biological reinterpretation of the welfarism theorem described above. Now, each individual viability and fecundity function corresponds to the utility functions of two distinct individuals in the social welfare functional version of the theorem.[14]

The MVSHN group fitness ordering R^{M} only takes account of the individual viabilities and fecundities, and so it satisfies viability-fecundity consequentialism. Unlike with fitness consequentialism, the components of fitness matter when evaluating group fitness. Because the viability-fecundity profiles for the two alternatives considered in Table 2 are different, they need not be regarded as exhibiting the same group fitness. Indeed, they are not by the MVSHN index.

If characteristics of the individuals other than their viabilities and fecundities are relevant for measuring group fitness, the definition of a group fitness functional can be modified to take them into account by adding additional functions that measure the values of these characteristics to its list of inputs. For example, in a honey bee colony, some non-reproductive bees forage for food, while others defend the colony from predators. Hence, in addition to fecundity, success at foraging and at defence are relevant characteristics.[15]

Our approach to measuring group fitness implicitly assumes that group fitness only depends on the functional relationships between the relevant characteristics of the individuals and the various possible states of the world (here,

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[14] See Ooghe and Lauwers (2005, Proposition 1) for a statement of the extensive social choice version of the welfarism theorem.

[15] We are indebted to Samir Okasha for this example.

Table 3. Two-stage aggregation

individual	v_i	b_i	f_i
1	v_1	b_1	f_1
2	v_2	b_2	f_2
$\vdots$	$\vdots$	$\vdots$	$\vdots$
n	v_n	b_n	f_n
	v	b	

the viability and fecundity functions). This is a form of reductionism. Provided that this form of reductionism is valid, once all of the relevant characteristics have been considered, the corresponding Unrestricted Domain, Pareto Indifference, and Binary Independence of Irrelevant Alternatives axioms are all natural restrictions to impose on the extensive group fitness functional. In other words, group fitness should only depend on the characteristics of the individuals once all of the relevant characteristics have been identified.

The form of reductionism that we are appealing to does not preclude selection from taking place at both the individual and group levels. Rather, it simply requires that group fitness be explicable in terms of the characteristics of the individuals. Okasha (2006, p. 140) argues that "[a]n MLS2 explanation of a collective [i.e., group] character need assume nothing about how the character depends on underlying particle [i.e., individual] characters, so it is inherently non-reductionist." In contrast, MLS1 is reductionist in the sense that the characteristics of the group are explained by the characteristics of the individuals. While, in principle, the characteristics of a group subject to MLS2 need not be explicable in terms of the characteristics of the individuals, it may nevertheless be the case that they are. Our approach, and those of Michod *et al.* (2006) and Okasha (2009), presuppose that group fitness, but not necessarily any other group characteristic, is reductionist.

A viability-fecundity profile can be thought of as being a matrix with n rows and two columns, as illustrated in Table 3. The entry in the first (resp. second) column of the ith row is individual i's viability (resp. fecundity). An index of group fitness assigns each of these matrices a number, which is then used to order the possible matrices according to the group fitness that they exhibit. With viability-fecundity consequentialism, the value of the group fitness index can be any function of the entries in this matrix. Fitness consequentialism requires that the index be computed using a two-stage procedure in which the fitness of each individual is first calculated from its viability and fecundity values and then the individual fitnesses are aggregated into an overall measure of group fitness. In other words, the two columns in Table 3 are replaced with

a single column whose entries are the individual fitnesses, which are then used to compute the value of the group fitness index. This a *row-first aggregation* procedure. With a *column-first aggregation* procedure, the entries in the first and second columns, respectively, are first aggregated into measures of group viability and group fecundity, which are then aggregated into an overall measure of group fitness. That is, the two columns are replaced by a single row whose entries are group viability and group fecundity, as shown in Table 3, and these two values are then used to determine the value of the group fitness index. The total group fitness index C uses row-first aggregation, whereas the MVSHN index M uses column-first aggregation.[16]

Both row-first and column-first aggregation place strong restrictions on the functional form of a group fitness index. Neither restriction is implied by viability-fecundity consequentialism. Any row-first aggregation procedure, not just the total group fitness index C, precludes taking account of the gains from the specialization of individuals into vegetative and reproductive functions. Column-first aggregation procedures do not.[17]

For a fixed group size n, the extensive group fitness functional $G^M : \mathcal{V}^n \times \mathcal{B}^n \to \mathcal{R}$ underlying the MVSHN group fitness ordering R^M is defined by setting

$$aR^M_{VB}a' \iff (V(a), B(a))R^M(V(a'), B(a'))$$

for all $(V, B) \in \mathcal{V}^n \times \mathcal{B}^n$ and all $a, a' \in A$. By construction, G^M satisfies Unrestricted Domain^{vb}, Pareto Indifference^{vb}, and Binary Independence of Irrelevant Alternatives^{vb}. This functional does not satisfy Pareto Indifference^f or Binary Independence of Irrelevant Alternatives^f, nor should it if the individual viabilities and fecundities matter for group fitness. The extensive group fitness functional G^M satisfies a Pareto condition and captures the benefits from functional specialization, so it cannot be a Pareto violation *per se* that accounts for the decoupling of individual and group fitness during an evolutionary transition.

6 Variable Group Size

The use of an extensive group fitness functional for a fixed group size allows us to take account of the two components of the individuals' fitnesses when determining group fitness, but it does not allow us to take account of group size. Group size is an important determinant of group fitness, particularly

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[16] We are grateful to Burak Can for suggesting that it would be useful to describe the indices C and M in terms of two-stage aggregation.

[17] Row-first and column-first aggregation procedures are commonly used in the measurement of multidimensional inequality (see Weymark, 2006). The analogue of the matrix in Table 3 has a row for each individual and a column for each of the components of well-being (e.g., income, health status, educational attainment, etc.) being considered.

during an evolutionary transition. We now consider how our analysis needs to be modified so as to allow for variable group size.

As above, the set of positive integers $\mathbb{N}$ is the set of possible group sizes, A is the set of alternatives, and $\mathcal{R}$ is the set of possible orderings of A, with each ordering $R \in \mathcal{R}$ interpreted as being an ordering of the alternatives in A according to how fit the group is with them. The description of an alternative now includes the size of the group. For each alternative $a \in A$, let $N(a)$ denote the set of individuals that constitute the group and let $n(a)$ denote the number of individuals in this group. Using the convention introduced earlier, $N(a)$ consists of individuals 1 through $n(a)$. For each positive integer i, let A_i denote the set of alternatives in A for which there are at least i individuals in the group. Thus, i is part of the group when the alternative is a if and only if $a \in A_i$. We assume that for any group size $n \geq 1$, there are at least three alternatives in A_n.

The viability and fecundity of each individual in the group depends on the alternative that describes the situation it is in. If the group size with alternative a is less than i, then either individual i does not exist or it is not part of the group. In the latter case, how viable and fecund it is is irrelevant for measuring the group's fitness. As a consequence, individual i's viability and fecundity functions only need to be defined for the alternatives in A_i. Formally, for each individual $i \in \mathbb{N}$, the functions that show the dependence of viability and fecundity on the relevant alternatives are the *viability function* $V_i \colon A_i \to \mathbb{R}_+$ and *fecundity function* $B_i \colon A_i \to \mathbb{R}_+$, respectively. Profiles of these functions now have a countably infinite number of components, one for each potential group member. That is, a *viability function profile* is the ordered list $V_1, V_2, \ldots$, which we write as $V = (V_i)_{i \in \mathbb{N}}$. Similarly, a *fecundity function profile* is the ordered list $B = (B_i)_{i \in \mathbb{N}}$. The sets of all such profiles are $\mathcal{V}$ and $\mathcal{B}$, respectively. As above, (V, B) is a *viability-fecundity function profile*. For each alternative $a \in A$, the viability and fecundity levels of the $n(a)$ individuals in the group are $V(a) = (V_1(a), \ldots, V_{n(a)}(a))$ and $B(a) = (B_1(a), \ldots, B_{n(a)}(a))$, respectively. An extensive group fitness functional is defined as in the preceding section, but now its domain $\mathcal{D}^{vb}$ is a subset of $\mathcal{V} \times \mathcal{B}$.[18]

The three welfarism axioms need to be reformulated to allow for variable group size.

Extended Unrestricted Domain^{vb}. The domain $\mathcal{D}^{vb}$ of the extensive group fitness functional G^{vb} is all of $\mathcal{V} \times \mathcal{B}$.

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[18] Sen's social welfare functionals have been generalized to allow for variable population size by Blackorby and Donaldson (1984). See Blackorby, Bossert, and Donaldson (2005) for a detailed investigation of population issues in ethics, social choice, and welfare economics using this framework. No variable population version of an extensive social welfare functional has been used up to now.

Extended Pareto Indifference^{vb}. For any pair of alternatives $a, a' \in A$ for which $n(a) = n(a')$ and any viability-fecundity function profile $(V, B) \in \mathcal{D}^{vb}$, if $(V(a), B(a)) = (V(a'), B(a'))$, then $a I_{VB}^{vb} a'$.

Extended Binary Independence of Irrelevant Alternatives^{vb}. For any pair of alternatives $a, a' \in A$ and any pair of viability-fecundity function profiles (V, B), $(V', B') \in \mathcal{D}^{vb}$, if $(V(a), B(a)) = (V'(a), B'(a))$ and $(V(a'), B(a')) = (V'(a'), B'(a'))$, then $a R_{VB}^{vb} a'$ if and only if $a R_{V'B'}^{vb} a'$.

The interpretation of these axioms is the same as in their fixed group size counterparts. Note that Extended Pareto Indifference^{vb} only places restrictions on the comparison of alternatives for which the same number of individuals are in the group, whereas with Extended Binary Independence of Irrelevant Alternatives^{vb}, group size may be different in the two alternatives being considered.

Recall that $\Omega = \cup_{n \in \mathbb{N}} \mathbb{R}_+^{2n}$. When Extended Unrestricted Domain^{vb} is satisfied, Ω is the set of all vectors of individual viabilities and fecundities that are achievable with some alternative in A. Viability-fecundity consequentialism requires that the ordering of alternatives in terms of group fitness is determined by a group fitness ordering R^{vb} of Ω. This form of consequentialism is implied by our three variable group size axioms.

Theorem 3. *If an extensive group fitness functional $G^{vb} \colon \mathcal{D}^{vb} \to \mathcal{R}$ satisfies Extended Unrestricted Domain^{vb}, then it satisfies Extended Pareto Indifference^{vb} and Extended Binary Independence of Irrelevant Alternatives^{vb} if and only if there exists a group fitness ordering R^{vb} of Ω such that for every viability-fecundity function profile $(V, B) \in \mathcal{D}^{vb}$ and every pair of alternatives $a, a' \in A$,*
$$a R_{VB}^{vb} a' \iff (V(a), B(a)) R^{vb} (V(a'), B(a')).$$

Theorem 3 follows immediately from the variable population welfarism theorem in Blackorby and Donaldson (1984, p. 31) by identifying each viability and fecundity function with a utility function. We thus see that the viability-fecundity consequentialism theorem for fixed group size, Theorem 2, straightforwardly extends to variable group size comparisons. In other words, the ordering of the alternatives in terms of group fitness only depends on the individual viabilities and fecundities obtained with them. In particular, it does not matter which viability-fecundity function profile generated these viabilities and fecundities. Group size now matters when determining group fitness because there are more individual viabilities and fecundities to take account of with a larger group.

Theorem 3 is illustrated with Table 4. First, consider the viability-fecundity function profile (V, B) and the alternatives a and a'. With alternative a, there are two individuals in the group. Their viabilities and fecundities are shown in the first line of the table. There is one more individual with the alternative a'. In this case, the individual viabilities and fecundities are shown in the second

Table 4. Viability-fecundity consequentialism

	(v_1, b_1)	(v_2, b_2)	(v_3, b_3)	M
$(V, B), a$	$(2, 3)$	$(3, 2)$		25
$(V, B), a'$	$(4, 1)$	$(2, 3)$	$(1,1)$	35
$(V', B'), a''$	$(2, 3)$	$(3, 2)$		25
$(V', B'), a'''$	$(4, 1)$	$(2, 3)$	$(1,1)$	35

line of the table. For concreteness, suppose that according to the group fitness ordering R^{vb}, a' exhibits more group fitness than a for the profile (V, B). Now, consider the viability-fecundity function profile (V', B') and the alternatives a'' and a'''. In this case, the individual viabilities and fecundities are shown in the last two lines of the table. The first two and the last two lines are the same and, hence, are ranked the same way by R^{vb}. Viability-fecundity consequentialism thus requires that a''' exhibits more group fitness than a'' for the profile (V', B'). Note that these are the rankings that would be obtained if the group fitness ordering R^{vb} is the MVSHN group fitness ordering R^M.

Michod and Nedelcu (2003), Michod (2005), and Okasha (2006, 2009) have all argued that the early stages of an evolutionary transition are best described as a multilevel selection 1 process, whereas once the group takes on its own individuality, then the transition is best described in terms of multilevel selection 2—there is fitness decoupling. The stages of an evolutionary transition are typically positively correlated with group size. This suggests that group fitness should be measured by the average or sum of the individual fitnesses for small groups, but that some other measure that captures the benefits of specialization into vegetative and reproductive functions should be used when the size increases beyond some threshold. If this is correct, then neither the index C nor the index M should be used to measure group fitness for all group sizes. Our approach to measuring group fitness using an extensive group fitness functional permits the way that the individual viabilities and fecundities are aggregated to depend on group size. For example, for small groups, group fitness might be measured by the index C, whereas for large groups it might be measured by M, with possibly one or more other aggregation procures used for intermediate sizes. There is therefore no need to appeal to Pareto violations to elucidate the nature of fitness decoupling, as is done in Okasha (2009).

7 Concluding Remarks

We have argued that extensive social choice theory is a more appropriate framework for modeling the measurement of group fitness in a biological hierarchy than the one used by Okasha (2009). By drawing on the welfarism theorems of social choice theory, we have identified the properties of an extensive group fitness functional that imply that viability-fecundity consequentialism is satisfied. Extensive social choice theory provides a good analytical framework for measuring group fitness. This framework is very flexible. For example, the method used to aggregate the individual viabilities and fecundities into a group fitness index can be made dependent on group size so as to allow for fitness decoupling. In addition, if group fitness in fact depends on more characteristics than the individual viabilities and fecundities, then the extensive group fitness functional can be modified to take them into account.

The approach proposed here also opens up new directions for future research. For example, rather than positing a functional form for a group fitness index from the outset, one can instead first identify the properties that it should satisfy and then determine which indices satisfy these properties. These properties may well depend on the particular kind of biological entity that is being considered (cell, organism, species, etc.), so one should not expect that a single index of group fitness is appropriate in all circumstances.

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