An extensive social choice characterization of the Michod measure of group fitness

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April 13, 2012

1 Introduction

According to the theory of evolution, if there is variation among a population of organisms, some variants produce more offspring than others, and offspring tend to resemble their parents, then natural selection will take place. These three properties are the principles of phenotypic variation, differential fitness, and heritability. Entities possessing these properties undergo natural selection. These entities, from individual cells to entire species, form a nested biological hierarchy. The modern theory of multi-level selection deals with natural selection that takes place at more than one level in the biological hierarchy. The multi-level selection framework has also been applied to study evolutionary transitions, the processes by which these hierarchies arose. A crucial question for these studies is: what is the relationship between the fitnesses of entities at different levels in the biological hierarchy?

Formally, the process of natural selection can be thought of as an optimization problem, where fitness is the quantity to be maximized, subject to a variety of constraints. The majority of research on natural selection addresses questions from the constraint side, focusing on the traits that affect fitness. The focus of this paper is on the objective function itself, in particular, the concept of fitness for individual entities and the collectivities they comprise.

There is a natural analogy between fitness and utility. Social choice theory deals with the relationship between individual and group utility. The parallels suggest that insights to the multilevel fitness problem might be found by applying frameworks from social choice theory.

A recent article by Samir Okasha, a philosopher of science, attempts this application problem (Okasha, 2009). The standard view in the selection theorist community treats group fitness as the sum or average of the individual fitnesses in the group. According to Okasha, this approach faces several problems. Okasha's paper focuses on an alternative measure—the Michod measure—proposed by Michod et al. (2006), which attempts to capture fitness information during evolutionary transitions, when individual organisms capable of living alone come together to form a single higher-level organism (Michod et al., 2006). When this transition takes place, the individuals specialize in different tasks and are no longer capable of surviving and reproducing on their own, so the fitnesses of the individuals converge to zero. Clearly, the fitness of the organism, which is non-zero, is not merely the sum of the individual fitnesses. The Michod measure of fitness attempts to model this transition. Okasha uses this as the motivation behind formalizing the fitness problem using the social choice framework.

This paper provides a characterization of the Michod measure using axioms from extensive social choice theory. Extensive social choice supposes that different social planners may have different opinions about the utilities of individuals for a given social alternative (Roberts, 1980; Ooghe and Lauwers, 2005). The planners each observe a different profile of individual utility functions, which are aggregated into a social ranking of the set of alternatives. We use this structure to capture the additional dimensions of the components of fitness. The formal axiomatization gives us the ability to analyze each property of the Michod measure, their implications about fitness, and how appropriate these implications are in the evolutionary setting.

2 Background

The entities that evolutionary biologists study are nested in a complex hierarchy of genes, chromosomes, organelles, cells, organs, organisms, colonies, species, and ecosystems. Multi-level selection is natural selection that occurs simultaneously at more than one level in the biological hierarchy, and it can take on many forms. Multi-level selection theory uses the terms "individuals" and "groups" relatively to refer to entities at two different levels in the hierarchy. What is considered an "individual" in one context may be a "group" in another.

Damuth and Heisler (1988) defines two types of multi-level selection. They are not mutually exclusive, and both types of selection are aspects of any multi-level selection process. Type 1 (MLS1) deals with the effect of group membership on individual fitnesses and is usually concerned with the social behavior of individuals. MLS1 explains, for example, the evolution of altruism as a character trait that increases the fitness of every individual within a colony. MLS1 does not require collective reproduction in the usual sense; that is, groups do not necessarily possess fitness beyond the fitnesses of the individuals. For example, some slime moulds exist as particles of different ancestry which coalesce into a collective for a time and then dissipate (Okasha, 2006). In this setting, defining group fitness as mean individual fitness makes sense. In other words, the collective fitness of the group can be defined simply in terms of the number of *individual* offspring. Okasha (2006) calls this definition of group fitness "collective fitness$_1$."

Multi-level selection type 2 (MLS2), on the other hand, deals with selection among groups. In other words, group fitness in this setting is defined in terms of the number of offspring *groups*. Okasha refers to this definition of group fitness as "collective fitness$_2$." In order for MLS2 to take place, then, groups must reproduce in some way. For example, the geographic range of mollusc species increased from selection at the species level, because those species with greater geographic range possessed greater collective fitness$_2$; that is, the species with greater geographic range, a heritable trait, produced more offspring species (Okasha, 2009). In this case, having information about the fitnesses of the individuals in the species does not necessarily give us any information about group fitness. In particular, Damuth and Heisler note that the notion of group fitness in MLS2 "need not (and often will not) be the same as mean individual fitness." Yet this is the definition of group fitness that is most frequently employed in selection theory, according to Okasha (2009).

A biological hierarchy did not always exist, however, since the earliest forms of life were presumably the simplest. The evolution of a biological hierarchy itself occurs during "evolutionary transitions," the process by which complex life is formed. Entities capable of surviving and reproducing independently before the transition can only do so as part of a larger group afterward (Maynard Smith and Szathmary, 1998). What happens during this transition? Okasha (2006) claims that the early stages of evolutionary transitions involve MLS1 processes while the later ones involve MLS2. In the early stages, individuals evolve social behaviors such as cooperation because it increases their individual fitnesses. As the transition takes place, group level traits emerge that are correlated with group level fitness. Michod et al. (2006) call this process the "decoupling" of group fitness from the fitnesses of the individuals, and claims it is completed when the fitnesses of individuals cease to contribute directly to group fitness. In other words, at the end of the evolutionary transition, average particle fitness converges to zero, and there is complete reproductive division of labor.

Why does this transition take place? Michod et al. (2006) attempt to explain why some volvocine algae colonies transition to multicellularity but not others. Since volvocine colonies are clonal, group-level selection must be key to the transition.

2.1 The Michod model

Michod et al. (2006) propose a simple mathematical model for aggregating fitness. The fitness of any given individual cell i has two basic components: viability v_i, a measure of its ability to survive to reproductive age, and fecundity b_i, a measure of reproductive capacity. The fitness of cell i is simply the product of the two measures, $v_i b_i$. For a group of n cells, the average fitness C of the group is then

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

Michod et al. (2006) propose an alternative way to aggregate individual fitnesses that is more appropriate for evolutionary transitions. They suggest aggregating viability and fecundity separately to get measures of average group viability (V) and average group fecundity (B). The group fitness G is then the simple product of V and B. In other words,

$$G = VB = \frac{1}{n}\sum_{i=1}^{n} v_i \frac{1}{n}\sum_{i=1}^{n} b_i$$

or $G = C - Cov(v_i, b_i)$.

Selection theorists place formal constraints on the components of fitness to capture the natural relationship between them. Because there is a natural trade-off between investing in viability and investing in fecundity, the covariance between v_i and b_i should be non-positive. So we have that $G \geq C$. In essence, G rewards a group for the specialization of its individual cells, and this effect is greater when the trade-off between v and b is more convex. Michod's measure of group fitness gives a way to formalize the evolutionary advantage of division-of-labor for some groups of cells.

2.2 Okasha's approach

In his paper, Okasha follows the approach to the social choice problem formulated by Sen (1970). He considers a group S of n individuals, and A, a set of at least three alternatives. Okasha assumes A is finite, though this is not necessary in general. In the fitness framework, each alternative can be thought of as a particular state of the world, for example, a particular allocation of resources to the individuals within the group. In social choice theory, each individual i has a utility function U_i, so Okasha assigns each individual i a fitness function $U_i : A \to \mathbb{R}$.

A social welfare functional maps a permissible profile of utility functions to a single ordering of the alternatives that reflects the social utility of each alternative. Analogously, Okasha's defines a "group fitness functional" (GFFL), F, which maps a profile $U = (U_1, U_2, ..., U_n)$ to an ordering of the alternatives in terms of group fitness. Similarly, Okasha defines three well-known axioms from social choice theory for F, the group fitness functional.

Unrestricted Domain: The domain of the GFFL is the set of all possible profiles.

This axiom states that F should be defined for all possible fitness profiles, so there are no *a priori* restrictions on the permissible fitness profiles.

Binary Independence of Irrelevant Alternatives: For any alternatives $x, y \in A$, and for any two profiles U, V, if $U(x) = V(x)$ and $U(y) = V(y)$, then $(x, y) \in F(U)$ if and only if $(x, y) \in F(V)$.

This axiom requires that the social ranking of x and y do not depend on the fitnesses associated with other alternatives, so if U and V coincide over x and y, then the output of F for U and V must rank x and y in the same order.

Pareto Indifference: For all $x, y \in A$, and for any profile U, if $U(x) = U(y)$, then $(x, y) \in F(U)$ and $(y, x) \in F(U)$.

In other words, if all individuals have the same fitness in one alternative versus another, then the group fitnesses are the same in both cases.

In social choice, these axioms are known as the "welfarism axioms," because they are the necessary and sufficient conditions for a social welfare functional to be "welfarist." That is, the social welfare functional ranks the alternatives only based on the individual utilities associated with the alternatives. When welfarism is satisfied, the social welfare functional can be captured by a single ordering of the vectors of individual utilities.

Okasha then applies his framework to the Michod measure, and argues that it is inconsistent with Pareto Indifference. That is, according to the Michod measure, given two alternatives in which each individual cell has the same fitness level, it is not necessarily true that the group fitness of the two alternatives is also the same. This is due to the collective fitness advantage gained from cell specialization. More precisely, welfarism dictates that the only relevant information for ranking two alternatives should be the utility (fitness) of the individual cells. Michod's measure is not welfarist precisely because it relies on distinguishing between the components of fitness. Okasha argues this Pareto-violation is an indicator of "fitness decoupling," the process by which the fitness of the group becomes independent of the fitnesses of the individual cells during biological transitions.

3 An alternative approach

Okasha's conceptualization of the Michod measure violates welfarism because it fails to capture information differences at the level of the components of individual fitness. By using an alternative approach borrowed from extensive social choice, the individual viability and fecundity functions can be encoded separately. As a result, the Michod measure can be formulated without violating welfarism.

In the classical social choice problem, profiles of individual utility functions are aggregated into a social ordering. It is often unclear, however, what utilities individuals truly have for any given alternative. Extensive social choice (Roberts, 1980) deals with this issue by allowing different "social planners" to have different opinions about each individual's utility function. That is, each combination of planner and individual may have a different measure of utility on the same alternative. We refer to each of these combinations as a planner-individual pair. To capture the additional dimensions, an extensive social welfare functional aggregates the utilities for all planner-individual pairs into a single ordering. If we have just one social planner, then we reduce the problem to the classical approach from Sen (1970). In the fitness context, the extensive problem is equivalent to finding a group-level fitness ordering by aggregating the individual viability functions (v_i's) and fecundity functions (b_i's), instead of fitness functions (f_i's).

We now appeal to extensive social choice to formally axiomatize the Michod measure. The characterization uses the welfarism axioms as well as standard information invariance assumptions. It relies heavily on the extensive social choice axiomatizations of well-established rules from Ooghe and Lauwers (2005), whose notation we mostly use here. We also interpret the formal framework using the terminology of social choice theory. It is reinterpreted in terms of fitness in Section 8.

4 Notation

We define a set of alternatives $X \geq 3$, a set of individuals $I = \{1, 2, \ldots, m\}$ and planners $J = \{1, 2, \ldots, n\}$, with $m \geq 2$ and $n \geq 2$. $I \times J$ (denoted IJ) is the set of individual-planner couples. Each planner $j \in J$ has a vector valued utility function $U^j \colon X \to \mathbb{R}_+^{m*}$, where $\mathbb{R}_+^{m*} = \mathbb{R}_+^m \setminus \{0_m\}$.[1] $\mathcal{U}_+$ is the set of all such vector valued utility funtions. The ith component of U^j, U_i^j, is the utility function planner j attributes to individual i. A profile $U = (U_1^1, U_2^1, \ldots, U_m^n)$ is an l-tuple of utility functions, where $l = m \times n$ is the size of IJ. Let $\mathcal{R}$ be the set of orderings on X. An extensive social welfare functional F (or "rule," for short) is a map $F \colon \mathcal{D}_0 \to \mathcal{R}$ such that $U = (U_1^1, U_2^1, \ldots, U_m^n) \mapsto F(U)$, where $\mathcal{D}_0 \subseteq \mathcal{U}_+^n$ is the nonempty domain of the functional.

5 Welfarism

The welfarism theorem states that when certain axioms are satisfied, the ranking of two alternatives depends only on the utilities they generate, and all non-utility information can be discarded. In other words, if it is "welfarist," the extensive social welfare functional $F \colon \mathcal{D}_0 \to \mathcal{R}$ can be fully described

[1]Not including the origin as a possible vector of utilities allows us to simplify the discussion. In our biological application, this restriction is quite natural.

by an ordering on $(\mathbb{R}_+^{m*})^n$. We extend the welfarism theorem to extensive social welfare functionals by defining the extensive versions of the welfarism axioms. Because each component of fitness is separately captured in this extended space, a welfarist version of the Michod measure can be formulated. Let $F\colon \mathcal{D}_0 \to \mathcal{R}$ be an extensive social welfare functional.

Nonnegative Unrestricted Domain ($\mathbf{U}_+$): $\mathcal{D}_0 = (\mathbb{R}_+^{m*})^n$.

This axiom is useful if we want to formulate extensive social welfare functional before knowing which profiles of utility functions will be used. We are concerned only with $(\mathbb{R}_+^{m*})^n$ because we can only have nonnegative values of components of fitness, and it makes little sense to consider a group composed of individuals that all have zero viability or all have zero fecundity.

Independence of Irrelevant Alternatives (IIA): $\forall U, V \in \mathcal{D}_0$, $\forall x, y \in X$, if $U(x) = V(x)$ and $U(y) = V(y)$, then $(x, y) \in F(U)$ if and only if $(x, y) \in F(V)$.

This axiom states that if two profiles coincide over any two alternatives x and y, then the orderings produced by the extensive welfare functional for each of the profiles must rank the two alternatives in the same way.

Pareto Indifference (PI): $\forall U \in \mathcal{D}_0, \forall x, y \in X$, if $U(x) = U(y)$, then $(x, y) \in F(U)$ and $(y, x) \in F(U)$.

Pareto Indifference states that if the utility of all planner-individual pairs is the same between two alternatives, the resulting ordering must be indifferent between the alternatives. In the fitness setting, this axiom requires indifference between alternatives if each individual has the same viability and the same fecundity between the two alternatives.

We now prove the extensive version of the welfarism theorem.

Theorem 1 (Welfarism Theorem)**.** *If F is an extensive social welfare functional that satisfies U_+, then F satisfies IIA and PI if and only if there exists a unique social welfare ordering R on $(\mathbb{R}_+^{m*})^n$ such that $\forall U \in \mathcal{D}_0$ and $\forall x, y \in X$,*

$$(x, y) \in F(U) \iff (U(x), U(y)) \in R$$

The proof is straightforward, following Bossert and Weymark (2004).

Strong Neutrality: $\forall w, x, y, z \in X$, $\forall U, V \in \mathcal{D}_0$, if $U(x) = V(z)$ and $U(y) = V(w)$, then $(x, y) \in F(U)$ if and only if $(z, w) \in F(V)$.

Claim. *If an extensive social welfare functional F satisfies U_+, then F satisfies IIA and PI if and only if F satisfies Strong Neutrality.*

Proof. ($\Longleftarrow$) Suppose F satisfies Strong Neutrality. Let $x = z$ and $y = w$. If $U(x) = V(x)$ and $U(y) = V(y)$, then $(x, y) \in F(U)$ iff $(x, y) \in F(V)$. Hence, F satisfies IIA.

Now let $U = V$ and $y = z = w$. Then we have: If $U(x) = U(y)$, then $(x, y) \in F(U)$ iff $(y, y) \in F(U)$. By reflexivity of the ordering, $(x, y) \in F(U)$ and $(y, x) \in F(U)$. Therefore, PI is satisfied.

($\Longrightarrow$) Suppose F satisfies U_+, PI, and IIA. We want to show that F satisfies Strong Neutrality. Suppose, in addition, that $U(x) = V(z) = u$ and $U(y) = V(w) = \bar{u}$. By U_+, there exists an alternative $a \in X$ and profiles $U', U'', U''' \in (\mathbb{R}_+^{m*})^n$ such that

1. $U'(x) = U'(a) = u$ and $U'(y) = \bar{u}$.
2. $U''(z) = U''(a) = u$ and $U''(w) = \bar{u}$.
3. $U'''(a) = u$ and $U'''(y) = U'''(w) = \bar{u}$.

Then, we have

$$\begin{aligned}
(x, y) \in F(U) &\iff (x, y) \in F(U') && \text{(by IIA)} \\
(x, y) \in F(U') &\iff (a, y) \in F(U') && \text{(by PI and transitivity)} \\
(a, y) \in F(U') &\iff (a, y) \in F(U''') && \text{(by IIA)} \\
(a, y) \in F(U''') &\iff (a, w) \in F(U''') && \text{(by PI and transtivity)} \\
(a, w) \in F(U''') &\iff (a, w) \in F(U'') && \text{(by IIA)} \\
(a, w) \in F(U'') &\iff (z, w) \in F(U'') && \text{(by PI and transitivity)} \\
(z, w) \in F(U'') &\iff (z, w) \in F(V) && \text{(by IIA)}
\end{aligned}$$

Therefore, $(x, y) \in F(U) \iff (z, w) \in F(V)$, and F satisfies Strong Neutrality. □

Proof of Theorem. Suppose that F satisfies U_+, IIA, and PI. From the claim, we know that F satisfies Strong Neutrality. Let $u, u' \in (\mathbb{R}_+^{m*})^n$ be given. By

U_+, $\exists U \in (\mathbb{R}_+^{m*})^n$ and $\exists x, y \in X$ such that $U(x) = u$ and $U(y) = u'$. We define an ordering R on $(\mathbb{R}_+^{m*})^n$:

$$uRu' \iff (x, y) \in F(U)$$

and

$$u'Ru \iff (y, x) \in F(U)$$

for any $u, u' \in (\mathbb{R}_+^{m*})^n$. R is well-defined because $F(U)$ does not depend on the profile U or the alternatives x, y, by Strong Neutrality. R inherits reflexivity from F and completeness because F satisfies U_+. To show that R is transitive, suppose that $u, v, w \in (\mathbb{R}_+^{m*})^n$ are given such that uRv and vRw. By U_+, $\exists U \in (\mathbb{R}_+^{m*})^n$ such that $U(x) = u$, $U(y) = v$, and $U(z) = w$. The construction of R implies $(x, y) \in F(U)$ and $(y, z) \in F(U)$. By the transitivity of $F(U)$, $(x, z) \in F(U) \implies uRw$. □

6 Information Invariance

In social choice theory, assumptions about the measurability and comparability of utility are formalized using invariance transforms of utility functions. These invariance transforms specify the degree to which measures of utility are meaningful and what kind of comparisons can be made across individuals. Naturally, we can formalize assumptions about the measurability and comparability of fitness in the same way.

We partition the set of admissible utility profiles into "information sets" using the equivalence relation $\sim$. All profiles within the same information set are assigned the same ordering by the extensive social welfare functional.

An invariance transform is a vector of strictly increasing transformations $\phi = (\phi_1^1, \phi_2^1, \ldots, \phi_m^n)$ such that for each profile U in $\mathcal{D}_0$, $U \sim \phi \circ U$, where $\phi \circ U = (\phi_1^1 \circ U_1^1, \phi_2^1 \circ U_2^1, \ldots, \phi_m^n \circ U_m^n)$, and $U \sim V \iff F(U) = F(V)$, $\forall U, V \in \mathcal{D}_0$.

We specify a set of admissible invariance transforms of utility profiles that lead to informationally equivalent profiles.

Information Invariance with Respect to Φ: $\forall u, v, u', v' \in (\mathbb{R}_+^{m*})^n$, if $\exists \phi \in \Phi$ such that $u' = \phi(u)$ and $v' = \phi(v)$, then $uRv \iff u'Rv'$.

Information Invariance with Respect to Φ_{rf}^{rn} ($\mathbf{I}_{rf}^{rn}$): $\phi \in \Phi$ iff $\exists \beta^1, \ldots, \beta^n \in \mathbb{R}_{++}$ such that $\phi_i^j(t) = \beta^j t$, $\forall ij \in IJ$.

With Φ^{rn}_{rf}, utility is measured on a ratio-scale that is common across individuals for a given planner, but these scales can be chosen independently across planners. Ratios or percentage changes of utilities are comparable across individual-planner pairs. Utility levels and differences are comparable across individuals for a given planner, but not across planners. With Φ^{rn}_{rf}, it is meaningful to make statements such as: "According to this planner, individual 1 has twice as much utility in alternative x as individual 2 has in alternative y."

7 Characterizing the Michod Measure

We now formally define the Michod measure using extensive social choice theory. Recall that Michod's model aggregates fitness by averaging the components of fitness across individuals and then multiplying across the two components. In the extensive social choice framework, this is equivalent to summing across individuals in I and multiplying across the social planners in J.

Michod Measure: R is the Michod Measure if and only if $\forall u, v, \in (\mathbb{R}^{m*}_{+})^n$,

$$uRv \iff \prod_{j \in J} \sum_{i \in I} u^j_i \geq \prod_{j \in J} \sum_{i \in I} v^j_i$$

We begin the formal characterization of the Michod measure by defining the axioms we will use.

Intraplanner Weak Pareto (WP$_I$): $\forall u, v \in (\mathbb{R}^{m*}_{+})^n$, if $\exists k \in J$ such that $u^k_i > v^k_i, \forall i \in I$ and $u^j_i = v^j_i$, $\forall ij \in IJ$ where $j \neq k$, then uPv.

Intraplanner Weak Pareto is an extensive variation of Weak Pareto, which states that a strict increase in the utility of all individuals for every planner is a social improvement. The intraplanner version is weaker and only requires that a strict increase in the utility of all individuals for a given planner, while the utility of individuals for all other planners remain the same.

Now we consider two interplanner anonymity axioms that prevent the identities of the planners from being important in determining the social ordering. The first axiom is an extensive social choice version of an axiom introduced by Suppes (1966). For every permutation σ on J and any $u \in (\mathbb{R}^{m*}_{+})^n$, let $\sigma(u) = (u^{\sigma(1)}, \ldots, u^{\sigma(n)})$.

Interplanner Suppes Indifference ($\mathbf{SI}^J$): $\forall u \in (\mathbb{R}_+^{m*})^n$, $uI\sigma(u)$.

Interplanner Suppes Indifference implies Interplanner Anonymity.

Interplanner Anonymity ($\mathbf{A}^J$): $\forall u, v \in (\mathbb{R}_+^{m*})^n$ and for every permutation σ on J, uRv iff $\sigma(u)R\sigma(v)$.

The next axiom is separability, which prevents "unconcerned" planners from influencing the social ordering. $\forall u \in (\mathbb{R}_+^{m*})^n$ and $\forall H \subseteq J$, the restriction of u to H is $u|_H := (u_i^j)_{j \in H}$.

Interplanner Separability $\mathbf{SE}^J$: $\forall u, u', v, v' \in (\mathbb{R}_+^{m*})^n$ and $\forall H \subseteq J$, if $u|_H = v|_H, u'|_H = v'|_H$, $u|_{J \setminus H} = u'|_{J \setminus H}$, and $v|_{J \setminus H} = v'|_{J \setminus H}$, then uRv iff $u'Rv'$.

In this definition, the planners in H are "unconcerned" while the planners in $J \setminus H$ are "concerned".

Intraplanner Incremental Equity ($\mathbf{IE}_I$): $\forall u \in (\mathbb{R}_+^{m*})^n$, $\forall \delta \in \mathbb{R}$, $\forall i_1, i_2 \in I$ and $\forall j \in J$ such that $(u + \delta \mathbf{1}_{i_1 j}^l) \in (\mathbb{R}_+^{m*})^n$ and $(u + \delta \mathbf{1}_{i_2 j}^l) \in (\mathbb{R}_+^{m*})^n$, $(u + \delta \mathbf{1}_{i_1 j}^l)\ I\ (u + \delta \mathbf{1}_{i_2 j}^l)$, where $\mathbf{1}_{ij}^l$ is the vector $\mathbf{x} \in \mathbb{R}^l$ with $x_{ij} = 1$ and $x_{i'j'} = 0, \forall i'j' \neq ij$.

This axiom requires that we are indifferent between increasing by the same amount the utility of one individual versus another, provided they are paired with the same planner (Blackorby et al., 2002).

Before we state the characterization theorem for the Michod measure, we present two lemmas.

Lemma 1 (Ooghe and Lauwers (2005), Lemma 3)**.** *An ordering R on $(\mathbb{R}_+^{m*})^n$ that satisfies SE^J induces orderings R^j on $\mathbb{R}_+^{m*}$ such that $\forall u, v \in (\mathbb{R}_+^{m*})^n$,*

1. *If $(u_1^j, \ldots, u_m^j) R^j (v_1^j, \ldots, v_m^j)$ $\forall j \in J$, then uRv.*
2. *If in addition, $\exists j \in J$ s.t. $u^j P^j v^j$, then uPv.*

Lemma 2 (Multiplicative Principle, Ooghe and Lauwers (2005, A.4.a))**.** *$\forall u \in (\mathbb{R}_+^{m*})^n$, $\forall j, k \in J$, and $\forall \gamma \in \mathbb{R}_{++}$, we have $u\bar{I}u'$, where $u' = (u^1, \ldots, \gamma u^j, \ldots, \frac{1}{\gamma} u^k, \ldots, u^n)$.*

Proof.

$u\bar{R}v$

$$\begin{aligned}
&\iff (u^1,\ldots,\gamma u^j,\ldots,u^k,\ldots,u^n)\bar{R}(v^1,\ldots,\gamma v^j,\ldots,v^k,\ldots,v^n) \quad (\text{by } \mathrm{I}_{rf}^{rn})\\
&\iff (u^1,\ldots,\gamma u^j,\ldots,u^k,\ldots,u^n)\bar{R}(v^1,\ldots,v^k,\ldots,\gamma v^j,\ldots,v^n) \quad (\text{by } \mathrm{SI}^J)\\
&\iff (u^1,\ldots,\gamma u^j,\ldots,\frac{1}{\gamma}u^k,\ldots,u^n)\bar{R}(v^1,\ldots,v^k,\ldots,v^j,\ldots,v^n) \quad (\text{by } \mathrm{I}_{rf}^{rn})\\
&\iff (u^1,\ldots,\gamma u^j,\ldots,\frac{1}{\gamma}u^k,\ldots,u^n)\bar{R}(v^1,\ldots,v^j,\ldots,v^k,\ldots,v^n) \quad (\text{by } \mathrm{SI}^J).
\end{aligned}$$

Therefore, $u'\bar{R}v'$. Let $v = u$. It follows that $u'\bar{I}u$. □

We now state the characterization theorem for the Michod measure.

Theorem 2. *A social welfare ordering R on $(\mathbb{R}_+^{m*})^n$ is the* Michod measure *iff R satisfies Information Invariance with Respect to Φ_{rf}^{rn} (I_{rf}^{rn}), Intraplanner Weak Pareto (WP_I), Interplanner Suppes Indifference (SI^J), Interplanner Separability (SE^J), and Intraplanner Incremental Equity (IE_I).*

Proof. $\Longrightarrow$ It is easy to check that the Michod measure satisfies the axioms stated. Let $u, v \in (\mathbb{R}_+^{m*})^n$ be given such that uRv, where R is the Michod measure.

- WP_I: Let $u, v \in (\mathbb{R}_+^{m*})^n$ be given such that $u_i^j \geq v_i^j$, $\forall ij \in IJ$ and $u_i^k > v_i^k$ for some $k \in J$. Then,

$$\prod_{j\in J}\sum_{i\in I} u_i^j > \prod_{j\in J}\sum_{i\in I} v_i^i$$

  and hence uPv.

- SI^J: Clearly the order in which we multiply the intraplanner sums does not matter because multiplication is commutative.

- SE^J: If $u|_H = v|_H, u'|_H = v'|_H$, $u|_{J\setminus H} = u'|_{J\setminus H}$, and $v|_{J\setminus H} = v'|_{J\setminus H}$, then

$$\begin{aligned} uRv &\iff \prod_{j\in J}\sum_{i\in I} u_i^j \geq \prod_{j\in J}\sum_{i\in I} v_i^j \\ &\iff \prod_{j\in J\setminus H}\sum_{i\in I} u_i^j \geq \prod_{j\in J\setminus H}\sum_{i\in I} v_i^j \quad \text{(because } u \text{ and } v \text{ coincide on } j\in H) \\ &\iff \prod_{j\in J\setminus H}\sum_{i\in I} u_i'^j \geq \prod_{j\in J\setminus H}\sum_{i\in I} v_i'^j \\ &\iff \prod_{j\in J}\sum_{i\in I} u_i'^j \geq \prod_{j\in J}\sum_{i\in I} v_i'^j \quad \text{(because } u' \text{ and } v' \text{ coincide on } j\in H) \\ &\iff u'Rv'. \end{aligned}$$

- IE_I: Let $u_1 = (u + \delta\mathbf{1}^l_{i_1 j})$ and $u_2 = (u + \delta\mathbf{1}^l_{i_2 j})$ for some $j \in J$. Clearly,

$$\sum_{i\in I}(u_{1i}^j) = \left(\sum_{i\in I} u_i^j\right) + 1 = \sum_{i\in I}(u_{2i}^j).$$

  Therefore, $u_1 I u_2$.

- I^{rn}_{rf}: We need to show that a transform ϕ has the property that $uRv \iff \phi(u)R\phi(v)$ whenever $\phi_i^j(t) = \beta^j t, \forall ij \in IJ$ where $\beta^1, \beta^2, \ldots, \beta^n \in \mathbb{R}_{++}$. Suppose that ϕ is given, where $\phi_i^j\colon t \mapsto \beta^j t$. Then, for any $u, v \in (\mathbb{R}_+^{m*})^n$, we have

$$\begin{aligned} uRv &\iff \prod_{j\in J}\sum_{i\in I} u_i^j \geq \prod_{j\in J}\sum_{i\in I} v_i^j \\ &\iff \left(\prod_{j\in J}\beta^j\right)\prod_{j\in J}\sum_{i\in I} u_i^j \geq \left(\prod_{j\in J}\beta^j\right)\prod_{j\in J}\sum_{i\in I} v_i^j \end{aligned}$$

(because all the β^js are positive)

$$\begin{aligned} &\iff \prod_{j\in J}\left(\beta^j\sum_{i\in I} u_i^j\right) \geq \prod_{j\in J}\left(\beta^j\sum_{i\in I} v_i^j\right) \\ &\iff \prod_{j\in J}\sum_{i\in I} \beta^j u_i^j \geq \prod_{j\in J}\sum_{i\in I} \beta^j v_i^j \\ &\iff \phi(u)R\phi(v). \end{aligned}$$

$\Longleftarrow$ Let $\bar{R}$ be an ordering on $(\mathbb{R}_+^{m*})^n$ that satisfies the axioms. By Lemma 1, $\bar{R}$ induces orderings R^j on $\mathbb{R}_+^{m*}$. Because SI^J implies A^J, $\bar{R}^1 = \bar{R}^2 = \cdots = \bar{R}^n$. Call this ordering $\bar{R}^0$. We can redefine the WP and IE axioms for this smaller space. $\bar{R}^0$ satisfies these versions of WP and IE, inherited from $\bar{R}$.

Consider any planner $j \in J$. Without loss of generality, we can suppose that $u_1^j \geq u_2^j \geq \cdots \geq u_n^j$. Note that $\sum_{i=1}^k u_i^j - \frac{k}{n}\sum_{i=1}^n u_i^j \geq 0$ for all $k = 1, 2, \ldots, n-1$. By IE$_I$, we have

$$
\begin{aligned}
u^j \bar{I}^0 & \left(\frac{1}{n}\sum_{i=1}^n u_i, u_2, \ldots, u_n + u_1 - \frac{1}{n}\sum_{i=1}^n u_i \right) \\
\bar{I}^0 & \left(\frac{1}{n}\sum_{i=1}^n u_i, \frac{1}{n}\sum_{i=1}^n u_i, \ldots, u_n + u_1 + u_2 - \frac{2}{n}\sum_{i=1}^n u_i \right) \\
\vdots & \\
\bar{I}^0 & \left(\frac{1}{n}\sum_{i=1}^n u_i, \ldots, \sum_{i=1}^n u_i - \frac{n-1}{n}\sum_{i=1}^n u_i \right).
\end{aligned}
$$

Hence,

$$
u^j \bar{I}^0 \left(\frac{1}{n}\sum_{i=1}^n u_i, \ldots, \frac{1}{n}\sum_{i=1}^n u_i \right).
$$

Similarly, we have

$$
v^j \bar{I}^0 \left(\frac{1}{n}\sum_{i=1}^n v_i, \ldots, \frac{1}{n}\sum_{i=1}^n v_i \right).
$$

It then follows from WP$_I$ that

$$
u\bar{R}^0 v \iff \sum_{i=1}^n u_i \geq \sum_{i=1}^n v_i.
$$

Thus, $\bar{R}^0$ is the utilitarian rule.[2]

Now we want to show that if $u, v \in (\mathbb{R}_+^{m*})^n$ are such that

$$
\prod_{j \in J} \sum_{i \in I} u_i^j \geq \prod_{j \in J} \sum_{i \in I} v_i^j,
$$

[2]The preceding argument is adapted from the proof of Blackorby, Bossert, and Donaldson (2002, Theorem 10). Their proof is developed for an ordering on all of $\mathbb{R}^m$, and needs some modification to deal with our restricted domain.

then $u\bar{R}v$.

Suppose such $u, v \in (\mathbb{R}_+^{m*})^n$ are given. Apply the multiplicative principle in Lemma 2 (repeatedly, if necessary) to obtain u' such that $u'\bar{I}u$ and $\forall j \in J$, $\sum_{i\in I} u_i'^j \geq \sum_{i\in I} v_i^j$. Then we have $u'^j \bar{R}^j v^j$ for all planners $j \in J$ because $\bar{R}^j$ is the utilitarian rule. Because the rule is the same for all planners, we have $u'\bar{R}v$ by Lemma 1. Transitivity then implies $u\bar{R}v$.

Now suppose that $\prod_{j\in J}\sum_{i\in I} u_i^j > \prod_{j\in J}\sum_{i\in I} v_i^j$. We need to show that $u\bar{P}v$. Using the Lemma 2, we can construct a u' such that $u'\bar{I}u$ and $\sum_{i\in I} u_i'^j > \sum_{i\in I} v_i^j$, $\forall j \in J$. Because $\bar{R}^0$ is the utilitarian rule, we have $u'^j \bar{P}^j v^j$, $\forall j \in J$. By Lemma 1, $u'\bar{P}v$. Transitivity implies $u\bar{P}v$.

□

8 Biological Interpretation

To translate the social choice framework into the biological context, we need first to reinterpret the notation. The finite set of alternatives X can be thought of as states of the universe over which the fitnesses of members of the group might vary. Following Okasha, examples of alternatives in X might be a particular allocation of resources among members in the group, or some way of allocating tasks among members in the group. As before, we have a set of individuals or members in the group, $I = \{1, 2, \ldots, m\}$. Instead of "planners," we now have a set of components (of fitness) $J = \{v, b\}$, comprised of viability (v) and fecundity (b). (Note that the framework allows for any number of fitness components) Hence, the individual-component couple (ij) in this context represents a specific component of fitness for a member of the group. For each component of fitness $j \in J$, there is a vector valued function $U^j : X \to \mathbb{R}_+^{m*}$ that specifies the value of this component for each individual. A profile $U = (U_1^v, U_2^v, \ldots, U_m^v, U_1^b, U_2^b, \ldots, U_m^b)$ is a $2m$-tuple that specifies the viability and fecundity of each individual in the group. An extensive group fitness functional F (or "rule," for short) maps a profile of these functions to a group fitness ordering on X.

The welfarism theorem can be stated for extensive group fitness functionals. An extensive group fitness functional satisfies U_+, IIA, and PI if and only if the ranking of any pair of alternatives depends only on the individual fitness components in those alternatives, and any additional information is irrelevant. When welfarism is satisfied, we can work directly with profiles of v and b instead of fitness functions. As noted earlier, we exclude from consideration the possibility that all individuals have zero fecundity and the possibility that all individuals have zero viability.

Okasha claims that the Michod measure violates Pareto Indifference (as well as Independence of Irrelevant Alternatives). Because his framework does not distinguish between the components of fitness at the individual level, he uses the non-extensive version of Pareto Indifference, which states that if all individuals have the same *fitness* across two alternatives, then the social welfare functional must rank them as indifferent. In his paper, Okasha shows that when two groups of cells have exactly the same cell fitnesses, one group can nevertheless have higher group fitness. This is because the Michod measure "rewards" groups for specialization. This can occur when the individual cells have the same fitness, but they differ in viability and fecundity. When the individual cells also have the same viability and fecundity, the groups of cells have equal group fitness. Because the extensive version of the axiom requires the *components* of fitness for individuals to coincide across the alternatives, the Michod measure satisfies the axiom. Similarly, the Michod measure does not violate the extensive version of Independence of Irrelevant Alternatives, so it is welfarist, when viewed from the perspective of extensive social choice theory.

Unlike the definition of group fitness as the sum or average of individual fitnesses, the Michod measure does not actually require entities at the individual level to possess fitness in the conventional sense. According to the Michod measure, the concept of fitness makes sense at the group level even if it does not at the individual level. The aggregation index is well-defined, but it is unclear to what extent it is appropriate.

Now we apply the fitness interpretation to the axioms characterizing the Michod measure. The degree to which these axioms are reasonable in the evolutionary setting provides additional insight into the usefulness of the Michod measure.

- **Information Invariance with Respect to Φ^{rn}_{rf}:** Ratio-scale measurability and full comparability across components of fitness means relative measures of v and b are meaningful, not absolute ones. It implies that the components of fitness are measured in the same way we measure length, by units with a fixed ratio and a common origin between them, like inches and centimeters. Specifically, every individual's viability (fecundity) is measured on a common ratio scale, and it is possible to compare viability (fecundity) levels across individuals. Moreover, it is meaningful to make statements such as "individual 1 possesses twice as much viability in alternative x as individual 2 possesses in alternative y," because this type of ratio is preserved by the similarity transforms we allow. Okasha claims that ratio-scale measurability and full comparability is the most appropriate invariance assumption for fitness. He does not, however, distinguish between the components of fitness, so he does not need to place additional measurability and comparability assumptions between viability and fecundity.

According to I_{rf}^{rn}, the ratio-scale by which viability and fecundity can be measured is not common across the two components of fitness. In other words, it is not possible to make comparisons between the viability levels of one individual and the fecundity levels of another individual. Non-comparability across the two components of fitness agrees with our intuition that few meaningful comparisons can be made between v and b. It is, however, meaningful to compare percentage changes in viability and fecundity across individuals, because these ratios are preserved by independent similarity transforms. This comes from the fact that proportional changes exist independently of the unit used to measure the fitness components.

Grafen (2007) discusses the concept of fitness as part of an attempt to formalize the fitness optimization problem. Grafen maintains that fitness is the quantity to be maximized in the formal optimization problem. He argues that fitness, like the concepts of weight or length, should be measured on a ratio scale, because each individual's fitness represents "the extent of its contribution to the gene pool of the species." So one individual has "twice as much fitness" in one alternative as another individual has in a different alternative is a meaningful statement, because the former is making twice the contribution. This type of statement is only meaningful if the ratios $U_i^v(x)/U_j^v(y)$ and $U_i^b(x)/U_j^b(y)$ are preserved by the set of invariance transforms we allow. Furthermore, Grafen claims that the quantity that is maximized must be defined as fitness relative to the mean population fitness. We can reasonably extend these claims to the components of fitness, so I_{rf}^{rn} indeed seems to be the appropriate set of invariance transforms to use on the components of fitness.

- **Intraplanner Weak Pareto**: For any two profiles of fitness components, if every individual has strictly higher viability (or fecundity) and every individual has equal fecundity (or viability) in the first profile, then the first profile is strictly preferred over the second. In other words, holding one component of fitness constant and strictly increasing the other component across all members in the group increases overall group fitness. Intuitively, this axiom seems reasonable for simple collectives of cells such as volvocine algae, the organisms modeled by Michod et al. (2006). Volvocine algae colonies reproduce by the division of the reproductive function cells. Since the colonies are clonal, reproduction in the collective sense depends directly on the fecundity of the individual cells. However, as is the case with many of the axioms below, this property is likely inappropriate for many cases of multi-level selection type 2 (MLS2). Recall in MLS2, group fitness is a measure of the reproductive success of the collective itself. Therefore, the appropriateness of any fitness aggregation procedure depends on the manner in which groups reproduce more groups. There are a variety of modes of group reproduction, and many of them are not summarized by the reproductive and survival functions of the individuals in the collective. For example, consider the case of species selection. If we think of individuals as members of the species, it is unclear that strictly increasing the survival functions of all members in the species increases the number of new species propagated by the first one.

- **Interplanner Suppes Indifference**: Permuting the components of fitness (reversing v and b) does not affect overall fitness. This implies that survival functions, v, and reproductive functions, b, contribute equally to the fitness of the group. This axiom is reasonable in the simple model where v might be the probability of surviving to reproductive age and b is the number of offspring produced at the reproductive age.

- **Interplanner Separability**: Since we have only two "planners" in the fitness problem, v and b, separability means that if one component of fitness is preserved across alternatives, then the overall ranking of alternatives should correspond with the conditional ranking based only on the other component. This axiom, too, seems intuitively reasonable in the simple volvocine algae case. However, in other cases of MLS2, we run into the same problems discussed above in reference to Intraplanner Weak Pareto. Namely, the relationship between survival or reproductive functions at the individual level and the same functions at the group level is not clear.

- **Intraplanner Incremental Equity**: Overall group fitness is indifferent between increasing one component of fitness by some amount for one individual and increasing the same component of fitness by the same amount for another individual in the group. This is a direct result of a simplifying assumption in the Michod model, wherein individual contributions to group viability and group fecundity are additive. For example, this assumption holds for simpler forms of volvocine algae in which cells stay together after cell division (Michod et al., 2006). Additivity makes sense initially when cells begin to form groups, when, for example, the group motility, the ability to move actively and spontaneously, is simply the sum of the individuals' motility. However, this assumption breaks down as individuals specialize and the group approaches complete reproductive division of labor. For example, increasing the fecundity of a reproductive cell might have a greater impact on overall group fitness than increasing the fecundity of a cell specialized in survival-enhancing vegetative functions. This property is problematic even for some species of volvocine algae, in particular those with higher degrees of specialization.

The Michod measure also satisfies the following continuity axiom

Continuity (C): $\forall u \in (\mathbb{R}_+^{m*})^n$, the sets $\{v \in (\mathbb{R}_+^{m*})^n \mid (v,u) \in R\}$ and $\{v \in (\mathbb{R}_+^{m*})^n \mid (u,v) \in R\}$ are closed with respect to Euclidean topology.

As a consequence, small changes in the fitness component profiles result in a small change in the value of the Michod measure. While the Michod measure satisfies this axiom, it is not needed in the characterization theorem.

Note that Intraplanner Weak Pareto is stronger than requiring Weak Pareto over the entire space $(\mathbb{R}_+^{m*})^n$. We cannot use the latter to generate a utilitarian rule over the smaller space $\mathbb{R}_+^{m*}$ because WP specifies how we rank two profiles only when all individual-planner pairs are strictly better off in one profile. It does not specify how two profiles are ranked when individual-planner pairs are strictly better off for one planner and equally well off for all other planners. WP_I is implied by Strong Pareto, but Strong Pareto is incompatible with I_{rf}^{rn} and C on $(\mathbb{R}_+^{m*})^n$ (Tsui and Weymark, 1997, Theorem 1).

9 Conclusion

This paper uses extensive social choice to axiomatize the Michod model for defining group fitness. We have followed Okasha's application of social choice theory to explicate the relationship between individual fitness and group fitness. Okasha's social choice version of the Michod measure violates Pareto Indifference, and he claimed that the Pareto-violation is connected to Michod's notion that group fitness becomes "decoupled" from individual fitness during evolutionary transitions. We have shown that the Pareto-violation is a result of the fact that the components of fitness are not encoded separately at the individual level. In the extensive social choice framework, the Michod measure does not violate Pareto Indifference and satisfies the welfarism axioms.

The axiomatization of the Michod measure allows us to parse out properties that define the model. In particular, the measurability and comparability axiom aligns with evolutionary theorists' notions of the fitness measure. Many of the other axioms seem intuitively reasonable, but they rely on the idea that viability and fecundity at the individual level can be aggregated to describe the reproductive and survival functions of the collective. This does not always hold, particularly in multi-level selection type 2 problems, when we are interested in how groups reproduce to form more groups. Finally, the Incremental Equity axiom reveals a weakness in the assumption that the viability and fecundity are additive across individuals. This axiom likely breaks down in the later stages of the evolutionary transition when there is a higher degree of reproductive division of labor.

Okasha chose to examine the Michod model in particular because it is one of the only explicit definitions of group fitness in the selection literature that is not simply a sum or average over the individuals. The parallels between utility theory and fitness theory suggest that the extensive social choice framework we have employed here might be used to analyze other fitness aggregation procedures similarly.

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