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An Axiomatic Characterization of the MVSHN Group Fitness Ordering

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Abstract: In order to analyze a unicellular-multicellular evolutionary transition, a multicellular organism is identified with the vector of viabilities and fecundities of its constituent cells. The Michod–Viossat–Solari–Hurand–Nedelcu index of group fitness for a multicellular organism is a function of these cell viabilities and fecundities. The MVSHN index has been used to analyze the germ-soma specialization and the fitness decoupling between the cell and organism levels that takes place during the transition to multicellularity. In this article, social choice theory is used to provide an axiomatic characterization of the group fitness ordering of vectors of cell viabilities and fecundities underlying the MVSHN index.

Keywords: group fitness index; evolutionary transitions; germ-soma specialization; fitness decoupling; social choice

1. Introduction

Any biological entity that exhibits phenotypic variation, differential fitness, and heritability is subject to natural selection (Lewontin, 1970). Following Godfrey-Smith (2009), such an entity is called a *Darwinian population*. Darwinian populations form a nested hierarchy. Understanding how major *evolutionary transitions in individuality* in which a new level in this hierarchy arises has been a major focus of recent research (Maynard Smith and Szathmáry, 1995; Michod, 1999; Michod and Nedelcu, 2003; Michod, 2005, 2011). The theory of *multilevel selection*, which is concerned with natural selection that takes place at more than one level in this hierarchy, has contributed to this understanding (Okasha, 2006). During an evolutionary transition, there is often *fitness decoupling* as a group of Darwinian populations that interact with each other in a fitness-affecting way gradually lose their ability to survive and reproduce on their own as they combine to form a new higher-level Darwinian population (Michod and Nedelcu, 2003; Michod, 2005, 2011), with the consequence that the lower-level populations lose their individuality and a new higher-level entity emerges. A familiar example is a unicellular-multicellular transition in which a group of independent cells form a new multicellular organism. During this transition, cells differentiate and specialize in either reproductive (germ cells) or survival-enhancing (soma cells) functions. In this way, the fitnesses of the individual cells are sacrificed in order to enhance that of the new multicellular organism.

In the case of cells and multicellular organisms, fitness can be understood to have two components: *viability* and *fecundity* (Michod, Viossat, Solari, Hurand, and Nedelcu, 2006). Viability and fecundity are measures of vegetative ability and reproductive capacity, respectively. Natural selection operates so as to increase the fitness of a Darwinian population subject to the constraints imposed on it by its environment (Michod, Viossat, Solari, Hurand, and Nedelcu, 2006; Grafen, 2007). Michod, Viossat, Solari, Hurand, and Nedelcu (2006) have formally modeled this process so as to explain the emergence of germ-soma specialization and the fitness decoupling that takes place in a unicellular-multicellular transition. In particular, they have introduced an index of group fitness, henceforth referred to as the *MVSHN index*, that measures the fitness of the multicellular organism as a function of the viabilities and fecundities of its constituent cells and have used their index to investigate the circumstances in which group fitness is increased by germ-soma specialization taking into account the trade-offs that are feasible between the two fitness components.

The MVSHN index is the product of indices of group viability and group fecundity. In the MVSHN index, group viability and fecundity are respectively equal to the sum of the viabilities and fecundities of the individual cells that constitute the multicellular organism (the group). Germ-soma specialization typically increases group viability and fecundity. The MVSHN index captures the benefits of this functional specialization. The MVSHN index is a numerical representation of a *group fitness ordering* that ranks vectors of individual cell viabilities and fecundities in terms of the fitness of the corresponding group. An *axiomatic characterization* of a group fitness ordering factors the ordering into its constitutive properties. In this article, an axiomatic characterization of the MVSHN group fitness ordering is provided.

The functional form of the MVSHN index was developed to help understand the unicellular-multicellular transition for volvocine green algae. These algae diverged from their unicellular ancestor relatively recently, develop from a single cell, and exist in a variety of forms that differ in their degree of integration, which makes the *Volvox* clade a good model system for investigating the origins of multicellularity (Michod, Viossat, Solari, Hurand, and Nedelcu, 2006; Miller, 2010; Michod, 2011). However, the basic features of an evolutionary transition exhibit considerable variation across multicellular lineages (Rokas, 2008; Simpson, 2011). As a consequence, no single index of group fitness can be expected to apply across the range of all transitions to multicellularity, let alone to all evolutionary transitions. An axiomatic characterization of a particular group fitness ordering can be used to help determine the suitability of using this ordering for analyzing a specific evolutionary transition by evaluating whether the axioms in the characterization are appropriate for the model system under consideration. The axiomatization of the MVSHN group fitness ordering can be regarded as being a necessary first step in such an analysis.

Damuth and Heisler (1988) distinguish between two kinds of multilevel selection. *Multilevel selection 1* refers to selection that operates at the individual level when the group is not itself a Darwinian population. On the other hand, with *multilevel selection 2*, the group is itself a Darwinian population and the focus is on selection at the group level. In the early stages of an evolutionary transition, the group is not well integrated and is best described in terms of multiselection 1, but as fitness decoupling starts to take place, the process is best thought of in terms of multiselection 2 (Michod and Nedelcu, 2003; Michod, 2005; Okasha, 2006, 2009). When multiselection 1 applies, the fitness of the group can be measured by the sum or average of the individual fitnesses.[1] However, as Okasha (2009, p. 567) notes, neither of these measures can capture the fitness benefits of germ-soma specialization because each cell, and hence the group organism, has zero fitness if there is complete germ-soma specialization even though this functional specialization has enhanced the group's fitness.[2] Therefore, the sum and the average of the individual fitnesses are inappropriate ways of measuring group fitness in a well-integrated organism or during the final stages of a transition to multicellularity.

The kind of explanation for a unicellular-multicellular transition offered by Michod et al. (2006) focuses on the benefits that can be achieved by the formation of a multicellular organism. Calcott (2011) identifies two other kinds of explanations for the origins of multicellularity. The first focuses on the emergence of *conflict mediation* mechanisms that suppress conflict at the cell level so as to enhance the fitness of the group. This kind of explanation figures prominently in Maynard Smith and Szathmáry (1995) and Michod (1999). Alternatively, a *lineage explanation* describes the evolutionary pathway that connects a unicellular ancestor to a multicellular organism through a series of molec-

[1]For a fixed number of cells, these two measures rank organisms in terms of their fitness in the same way. With variable group size, the sum measures overall group fitness, whereas the average measures group fitness on a per-cell basis.

[2]Godfrey-Smith (2011, p. 78) notes that germ cells exhibit some viability and soma cells do reproduce, so their fitnesses are not zero. Nevertheless, even in this case, using the sum or average of the individual fitnesses fails to capture the benefits of germ-soma specialization.

ular and developmental changes. Examples of this kind of explanation are provided by Kirk (2005), Herron and Michod (2007), and Rokas (2008). The focus here is on the benefit explanation for the emergence of multicellularity and germ-soma specialization.

The methodology of social choice theory is employed in order to obtain an axiomatization of the MVSHN group fitness ordering. In social choice theory, a *social welfare ordering* is an ordering of vectors of individual utilities (Bossert and Weymark, 2004). A group fitness ordering is a biological analogue of a social welfare ordering in which vectors of utilities are instead interpreted as being vectors of viabilities and fecundities. Variable group size is accommodated by drawing on the branch of social choice theory that uses social welfare orderings to address issues in population ethics (Blackorby and Donaldson, 1984; Blackorby, Bossert, and Donaldson, 2002, 2005). It is shown that the MVSHN group fitness ordering is characterized by biological counterparts of axioms that have been applied to social welfare orderings.

In the present analysis, a group fitness ordering is a primitive concept. Bossert, Qi, and Weymark (2012) show how a group fitness ordering can itself be derived from more fundamental considerations. This is done by reinterpreting the *extensive social welfare functional* framework introduced by Roberts (1995) and further developed by Ooghe and Lauwers (2005) in biological terms so as to model the group fitness measurement problem. In *extensive social choice*, different evaluators make judgements about how much utility each individual in society obtains from each of the alternatives being considered, with these judgements then being used to form a social ranking of the alternatives. Bossert, Qi, and Weymark (2012) employ a two-evaluator version of this framework with cells playing the role of the individuals and the two fitness criteria—viability and fecundity—playing the role of the two evaluators.

Okasha (2009) was the first to use social choice theory to analyze group fitness. He used an alternative way of modeling group fitness based on the *social welfare functional* framework of Sen (1970). Sen's framework can be thought of as being a one-evaluator special case of the one used in extensive social choice. In Okasha's approach, group fitness only depends on the fitnesses of the individual cells, rather than on their viabilities and fecundities. As a consequence, unlike the approach proposed by Bossert, Qi, and Weymark (2012), Okasha's methodology cannot capture the fitness gains from functional specialization that are observed in a unicellular-multicellular transition.

Section 2 provides a formal introduction to group fitness orderings and defines the MVSHN group fitness ordering and the corresponding index of group fitness. A number of properties for a group fitness ordering are considered in Section 3 and it is shown in Section 4 that they axiomatically characterize the MVSHN group fitness ordering. Some concluding remarks are offered in Section 5. Proofs of all results may be found in the Appendix.

2. Group Fitness Orderings

Natural selection can be viewed as a constrained optimization problem in which a Darwinian population behaves as if it is seeking to increase or to maximize fitness subject

to the constraints imposed by physical laws and by its environment (Michod et al., 2006; Grafen, 2007). In a constrained optimization problem, there is a sharp conceptual distinction between the objective function and the constraints. Thus, when formally analyzing natural selection, the measurement of fitness is independent of the identification of what is feasible. This article is concerned with the properties of the objective function in the fitness optimization problem, not with what is feasible or optimal. Specifically, the focus is on measuring the fitness of a multicellular organism, henceforth called a *group*. More precisely, the ranking of groups in terms of their overall fitness is considered. Given this group fitness ranking, it is then possible to determine which group is the fittest among those that are feasible and to identify the properties of this optimal group, as in Michod, Viossat, Solari, Hurand, and Nedelcu (2006). While what is feasible depends on various physiological constraints and on the environment that the group operates in, the ranking of groups in terms of their fitness does not depend on whether the groups being compared are in fact feasible in the circumstances under consideration. As a consequence, for each possible feasible set of groups, the same group fitness ranking is used to determine what is optimal given the constraints imposed by feasibility. The group fitness ranking is the objective function in this constrained optimization problem, and it is the focus of the present analysis.

Some notation is required in order to provide a precise formulation of the problem. The set of positive integers is $\mathbb{N}$. Let $N^n = \{1, \ldots, n\}$ for all $n \in \mathbb{N}$. For each $n \in \mathbb{N}$, $\mathbb{R}^n_+$ is the nonnegative orthant in the Euclidean n-space $\mathbb{R}^n$ and $\Omega^n = \mathbb{R}^n_+ \setminus \{\mathbf{0}^n\}$ is this orthant with its origin $\mathbf{0}^n = (0, \ldots, 0)$ deleted. The vector $\mathbf{1}^n = (1, \ldots, 1)$ is the n-dimensional vector composed of n ones and, for $i \in N^n$, $\mathbf{1}^n_i$ is the n-dimensional vector for which the ith coordinate is equal to one and all other coordinates are equal to zero. For $\mathbf{x}, \mathbf{x}' \in \mathbb{R}^n$, $\mathbf{x} > \mathbf{x}'$ denotes that $x_i \geq x'_i$ for all $i \in N^n$ and $x_i > x'_i$ for some $i \in N^n$.

In principle, the number of cells in a group—the *group size*—can be any integer $n \in \mathbb{N}$. If $n = 1$, then the group is a single-celled organism. As in Michod, Viossat, Solari, Hurand, and Nedelcu (2006), cells are only distinguished by their viabilities and fecundities. Therefore, without loss of generality, it is assumed that for a group of size n, its constituent cells are indexed by the set N^n. Associated with each cell $i \in N^n$ is a viability level v_i and a fecundity level b_i. As in Michod (2005), v_i and b_i measure the contribution of the ith cell to the multicellular organism's viability and fecundity, respectively. It is possible that a cell has no viability or fecundity, in which case it is called a *null cell*. The *viability profile* $\mathbf{v} = (v_1, \ldots, v_n)$ and the *fecundity profile* $\mathbf{b} = (b_1, \ldots, b_n)$ are elements of Ω^n and, hence, the *viability-fecundity profile* $(\mathbf{v}, \mathbf{b})$ is an element of the Cartesian product Ω^{2n}. A group (i.e., a multicellular organism) is identified with its viability-fecundity profile. Hence, there is no distinction between two groups that have the same viability-fecundity profile.

The set Ω^{2n} is the set of all conceivable viability-fecundity profiles for a group of size n. Thus, $\Omega = \cup_{n \in \mathbb{N}} \Omega^{2n}$ is the set of all possible viability-fecundity profiles when group size is not a priori specified. A *group fitness ordering* is an ordering R on Ω. An *ordering* is a binary relation that is reflexive, complete, and transitive.[3] The symmetric

[3]A binary relation R on a set X is (i) *reflexive* if for all $x \in X$, xRx, (ii) *complete* if for all distinct

and asymmetric factors of R are denoted by I and P, respectively.[4] For any $n, n' \in \mathbb{N}$, any $(\mathbf{v}, \mathbf{b}) \in \mathbb{R}_+^{2n}$, and any $(\mathbf{v}', \mathbf{b}') \in \mathbb{R}_+^{2n'}$, the statement $(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}')$ is interpreted as saying that the viability-fecundity pair $(\mathbf{v}, \mathbf{b})$ exhibits at least as much group fitness as the viability-fecundity pair $(\mathbf{v}', \mathbf{b}')$. If I (resp. P) is substituted for R, then "the same" (resp. "strictly more") replaces "at least as much" in the preceding statement.

By defining R on Ω, it is implicitly assumed that there are no a priori upper bounds on a cell's viability or fecundity. The validity of this assumption depends on how viability and fecundity are measured. If, for example, a cell's viability is the probability that it will survive long enough to reproduce, then it is not possible for viability to exceed one. The characterization theorem presented here also holds if there are upper bounds on the individual viabilities and fecundities but, for simplicity, such bounds are ignored. In some applications (see below), individual viabilities or fecundities may only take on integer values. In such cases, the assumption that non-integer values are possible is a convenient approximation. Michod, Viossat, Solari, Hurand, and Nedelcu (2006) allow the individual viabilities and fecundities to have arbitrary nonnegative values, which permits them to use the methods of differential calculus to identify an optimal solution to the fitness maximization problem.

Excluding the possibility that a group is composed of cells none of which is viable or none of which is fecund allows for a simpler statement of the characterization theorem than would be possible without this assumption. An organism with no viable cells or no fecund cells is of no biological interest, so this restriction is quite natural. If there is complete germ-soma specialization, a cell has zero viability if and only if it has positive fecundity.

Michod, Viossat, Solari, Hurand, and Nedelcu (2006) make group fitness comparisons using a *group fitness index* that assigns a fitness value to each viability-fecundity profile. Their index is constructed in two steps by first computing measures of group viability and fecundity and then taking the product of these two values. Formally, for a group of size n, *group viability* is

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

and *group fecundity* is

$$b = \sum_{i=1}^{n} b_i. \tag{2}$$

The *MVSHN index of group fitness* is the function $M\colon \Omega \to \mathbb{R}$ that measures fitness by taking the product of group viability and group fecundity.[5] That is, for all $n \in \mathbb{N}$ and all

$x, y \in X$, xRy or yRx, and (iii) *transitive* if for all $x, y, z \in X$, $[xRy$ and $yRz] \Rightarrow xRz$.

[4]For a binary relation R on a set X, the *symmetric factor* I and *asymmetric factor* P are defined as follows: for all $x, y \in X$, $xIy \Leftrightarrow [xRy$ and $yRx]$ and $xPy \Leftrightarrow [xRy$ and not $(yRx)]$.

[5]Strictly speaking, Michod, Viossat, Solari, Hurand, and Nedelcu (2006) define their index for a fixed number of cells, but it is straightforward to extend their definition to groups of different sizes, as is done here. Such an extension is important because the number of cells in a group is a major determinant of the emergence and degree of germ-soma specialization (Michod and Nedelcu, 2003; Michod, 2005).

$(\mathbf{v}, \mathbf{b}) \in \Omega^n$, the value of the MVSHN index is

$$M(\mathbf{v}, \mathbf{b}) = vb = \left(\sum_{i=1}^{n} v_i \right) \left(\sum_{i=1}^{n} b_i \right). \tag{3}$$

Michod, Viossat, Solari, Hurand, and Nedelcu (2006) use the MVSHN index to help explain the functional specialization of cells into vegetative and reproductive activities during a unicellular-multicellular transition. They use volvocine green algae as a model system to analyze this transition and argue that the functional-form assumptions in (1), (2), and (3) are appropriate for the *Volvox* clade. For this clade, cell viability is measured by flagellar motility, which to a first approximation composes additively across the cells in a group. By assuming that a cell's fecundity is one if it can reproduce and zero otherwise, group viability is then simply the number of reproductive cells in the group. For any group with discrete generations, like the volvocine green algae, it is natural to measure overall fitness by taking the product of the group's viability and fecundity.

The MVSHN index in (3) can capture the fitness advantages of germ-soma specialization. Such specialization contributes to both group viability v and group fecundity b and, hence, to group fitness. This is not the case if group fitness is measured by the sum or average of the individual cell fitnesses. The fitness of cell i is

$$f_i = v_i b_i. \tag{4}$$

The *sum group fitness index* is the function $S\colon \Omega \to \mathbb{R}$ defined by taking the sum of the individual fitnesses in (4), whereas the *average group fitness index* the function $A\colon \Omega \to \mathbb{R}$ defined by taking their average. Formally, S and A are defined by setting, for all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}) \in \Omega^n$,

$$S(\mathbf{v}, \mathbf{b}) = \sum_{i=1}^{n} f_i = \sum_{i=1}^{n} v_i b_i \tag{5}$$

and

$$A(\mathbf{v}, \mathbf{b}) = \frac{1}{n} \sum_{i=1}^{n} f_i = \frac{1}{n} \sum_{i=1}^{n} v_i b_i. \tag{6}$$

With complete germ-soma specialization, the sum in (5) and the average in (6) are both zero even though this functional specialization is, in general, fitness enhancing.

The *MVSHN group fitness ordering* R^M of Ω is defined by letting

$$(\mathbf{v}, \mathbf{b}) R^M (\mathbf{v}', \mathbf{b}') \;\Leftrightarrow\; M(\mathbf{v}, \mathbf{b}) \geq M(\mathbf{v}', \mathbf{b}') \tag{7}$$

for all $n, n' \in \mathbb{N}$, all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$, and all $(\mathbf{v}', \mathbf{b}') \in \Omega^{2n'}$. That is, the viability-fecundity profile $(\mathbf{v}, \mathbf{b})$ exhibits 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. In order to determine the characteristics of a group that maximizes fitness given the constraints that it faces, only the ordering induced by the group fitness index is relevant, not the numerical values assigned by the index to each viability-fecundity profile. For this reason, the MVSHN group fitness ordering R^M rather than the MVSHN group fitness index M is axiomatized here.

3. Properties of Group Fitness Orderings

The objective of this article is to provide an axiomatic characterization of the MVSHN group fitness ordering. This section provides formal statements of the axioms used in this characterization and biological interpretations of them.

The axioms can be divided into three categories. Those in the first two categories concern group fitness comparisons involving the same number of cells. These axioms can be categorized according to their scope in the following sense. There are two components to fitness—viability and fecundity. If an axiom applies to comparisons in which both of these components may differ, then it is an *intercomponent* axiom. If, on the other hand, only one of the components differs, then it is an *intracomponent* axiom. The third category consists of a single *variable group size* axiom that is concerned with comparisons across group sizes.

The first three properties for a group fitness ordering are intercomponent axioms.

Intercomponent Separability. For all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$,

$$[((\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}) \Leftrightarrow (\mathbf{v}, \mathbf{b}')R(\mathbf{v}', \mathbf{b}')] \quad \text{and} \quad [(\mathbf{v}, \mathbf{b})R(\mathbf{v}, \mathbf{b}') \Leftrightarrow (\mathbf{v}', \mathbf{b})R(\mathbf{v}', \mathbf{b}')].$$

Consider comparing viability-fecundity profiles for two groups with n cells each. For any fixed fecundity profile $\mathbf{b}^0 \in \Omega^n$, the group fitness ordering R defines a conditional ordering R_n^v of the viability profiles in Ω^n by letting

$$\mathbf{v}R_n^v\mathbf{v}' \Leftrightarrow (\mathbf{v}, \mathbf{b}^0)R(\mathbf{v}', \mathbf{b}^0) \tag{8}$$

for all $\mathbf{v}, \mathbf{v}' \in \Omega^n$. The first equivalence statement in the definition of Intercomponent Separability says that this conditional ordering does not depend on the fecundity profile that is used to generate it. Similarly, the second equivalence statement says that for any fixed viability profile $\mathbf{v}^0 \in \Omega^n$, the conditional ordering R_n^b of the fecundity profiles in Ω^n defined by letting

$$\mathbf{b}R_n^b\mathbf{b}' \Leftrightarrow (\mathbf{v}^0, \mathbf{b})R(\mathbf{v}^0, \mathbf{b}') \tag{9}$$

for all $\mathbf{v}, \mathbf{v}' \in \Omega^n$ does not depend on the conditioning values for the individual viabilities. Thus, with Intercomponent Separability, group viability and fecundity comparisons can be performed independently of each other. Separability axioms are commonly used in economic problems when making multidimensional comparisons. See Blackorby, Primont, and Russell (1978) for a detailed discussion of separability axioms in general and Ooghe and Lauwers (2005) for an extensive social choice version of the separability axiom used here.

Intercomponent Ratio-Scale Measurability. For all $n \in \mathbb{N}$, all $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$, and all $\gamma^v, \gamma^b > 0$,

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') \Leftrightarrow (\gamma^v\mathbf{v}, \gamma^b\mathbf{b})R(\gamma^v\mathbf{v}', \gamma^b\mathbf{b}').$$

Intercomponent Ratio-Scale Measurability says that when comparing two viability-fecundity profiles for the same number of cells, the group fitness ordering of the two

profiles is unaffected if all of the individual viabilities (resp. fecundities) in the two groups being compared are multiplied by the same positive scaling factor. The scaling factor applied to the viabilities need not equal the scaling factor applied to the fecundities. Whenever the ranking of objects according to some trait is invariant to a proportionate change in the measurement scale, it is being measured on a *ratio scale*. Familiar examples of ratio-scale measurable quantities are length and weight. When combined with Intercomponent Separability, Intercomponent Ratio-Scale Measurability implies that only the relative, and not the absolute, values of indices of group viability and fecundity are of any significance.[6] Intercomponent Ratio-Scale Measurability corresponds to the social choice theory axiom that requires a social welfare ordering to be invariant to independent proportional rescalings of the individual utilities (Bossert and Weymark, 2004; Ooghe and Lauwers, 2005).

Intercomponent Symmetry. For all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$,

$$(\mathbf{v}, \mathbf{b}) I (\mathbf{b}, \mathbf{v}).$$

Intercomponent Symmetry requires the two fitness components—viability and fecundity—to play interchangeable roles when performing group fitness comparisons. For a group of n cells, viability and fecundity profiles are lists of n numbers. This axiom says that when measuring overall group fitness, it does not matter which is the viability profile and which is the fecundity profile; they make symmetric contributions to the overall group fitness comparison. Intercomponent Symmetry is a biological analogue of the Suppes Indifference for Planners axiom used in extensive social choice (Ooghe and Lauwers, 2005). Recall that in that context, different evaluators (planners) form judgements about what the utilities of the individuals in society are. Suppes Indifference for Planners requires that the social welfare ordering of the vectors that describe what utility each evaluator assigns to each individual be invariant to any permutation of the identities of the evaluators. A group fitness ordering is a biological counterpart of a two-evaluator version of this social welfare ordering, with viability and fecundity playing the roles of the two evaluators.[7]

Next, two intracomponent axioms are considered.

Intracomponent Minimal Increasingness. For all $n \in \mathbb{N}$, all $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$, and all $\alpha, \beta > 0$ such that $\alpha > \beta$,

$$(\alpha \mathbf{1}^n, \mathbf{b}) P (\beta \mathbf{1}^n, \mathbf{b}) \quad \text{and} \quad (\mathbf{v}, \alpha \mathbf{1}^n) P (\mathbf{v}, \beta \mathbf{1}^n).$$

Intracomponent Minimal Increasingness is a weak monotonicity property. It requires group fitness to increase as a consequence of increasing the viabilities (resp. fecundities) of all of the cells, holding the values of the other fitness component fixed provided that all

[6] Grafen (2007, p. 1248) describes an individual's fitness as being a measure of the individual's contribution to the gene pool of the species to which it belongs, which implies that doubling fitness also doubles this contribution. He interprets this statement as saying that individual fitness should be measured on a ratio scale.

[7] The terminology for this social choice axiom is based on a related property for a social welfare ordering for a single evaluator due to Suppes (1966). See Sen (1970) for a detailed discussion of Suppes' principle.

of the cells have the same viability (resp. fecundity) both before and after the change. It is only in these very limited kinds of comparisons that this axiom places any restriction on the group fitness ordering. The analogue of this axiom in social choice theory requires a common increase in each person's utility to be welfare improving if everybody has the same utility to begin with (Blackorby, Bossert, and Donaldson, 2005).

Intracomponent Incremental Symmetry. For all $n \in \mathbb{N}$, all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$, and all $i, j \in N^n$,

(i) for all $\delta \in \mathbb{R}$ such that $(\mathbf{v} + \delta \mathbf{1}_i^n), (\mathbf{v} + \delta \mathbf{1}_j^n) \in \Omega^n$,

$$(\mathbf{v} + \delta \mathbf{1}_i^n, \mathbf{b}) I (\mathbf{v} + \delta \mathbf{1}_j^n, \mathbf{b});$$

(ii) for all $\delta \in \mathbb{R}$ such that $(\mathbf{b} + \delta \mathbf{1}_i^n), (\mathbf{b} + \delta \mathbf{1}_j^n) \in \Omega^n$,

$$(\mathbf{v}, \mathbf{b} + \delta \mathbf{1}_i^n) I (\mathbf{v}, \mathbf{b} + \delta \mathbf{1}_j^n).$$

This axiom captures a way in which the contributions of the cells to group fitness are symmetric. Specifically, it requires that the change in group fitness as a result of either an increase or a decrease in a cell's viability or fecundity to be independent of which cell undergoes this change. In its social choice formulation, this axiom says that it is a matter of social indifference which individual experiences a given change in utility (Blackorby, Bossert, and Donaldson, 2002).

The final property is the only variable group size axiom.

Null Cell Invariance. For all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$,

$$(\mathbf{v}, \mathbf{b}) I ((\mathbf{v}, 0), (\mathbf{b}, 0)).$$

This axiom says that the addition of a null cell (i.e., a cell with no viability or fitness) to a group has no effect on group fitness. Recall that a group fitness ordering provides a ranking of all *conceivable* viability-fecundity profiles. Natural selection may well prevent null cells (or cells with little viability or fecundity) from forming or from existing for any length of time, but what is feasible or optimal is a separate issue. The corresponding social choice axiom is the *critical-level principle with a zero critical level* (Blackorby and Donaldson, 1984). A *critical level* is a level of utility such that the addition of an individual with this utility is a matter of social indifference. In variable-population social choice theory, the choice of a critical level is an important ethical value judgement and the choice of zero as the critical level has some unattractive implications (Blackorby and Donaldson, 1984; Blackorby, Bossert, and Donaldson, 2002, 2005).

4. An Axiomatic Characterization of the MVSHN Group Fitness Ordering

The main result of this article shows that the MVSHN group fitness ordering is characterized by the six axioms introduced in the preceding section. The proof of this theorem

proceeds by first showing that these axioms imply that the MVSHN group fitness ordering must be used to compare viability-fecundity profiles for groups with the same number of cells. This is done in a series of four lemmas. The proofs of these lemmas make use of proof strategies employed by Blackorby, Bossert, and Donaldson (2002) and Ooghe and Lauwers (2005). The proof of the theorem is completed by showing that the MVSHN group fitness ordering must also be used when the number of cells in the groups being compared differ.

Lemma 1 demonstrates that Intercomponent Separability by itself implies that group fitness comparisons can be decomposed into comparisons of group viability and group fecundity.

Lemma 1. *If the group fitness ordering R satisfies Intercomponent Separability, then for all $n \in \mathbb{N}$, there exist orderings R_n^v and R_n^b of Ω^n such that for all $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$,*

(i) $[\mathbf{v} R_n^v \mathbf{v}' \text{ and } \mathbf{b} R_n^b \mathbf{b}'] \Rightarrow (\mathbf{v}, \mathbf{b}) R (\mathbf{v}', \mathbf{b}')$;

(ii) $[\mathbf{v} P_n^v \mathbf{v}' \text{ and } \mathbf{b} R_n^b \mathbf{b}'] \Rightarrow (\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}')$;

(iii) $[\mathbf{v} R_n^v \mathbf{v}' \text{ and } \mathbf{b} P_n^b \mathbf{b}'] \Rightarrow (\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}')$.

The ordering R_n^v provides an ordering of viability profiles in terms of group viability. Similarly, the ordering R_n^b provides an ordering of fecundity profiles in terms of group fecundity. These orderings are the conditional orderings defined in (8) and (9). Furthermore, if one group exhibits at least as much group viability and group fecundity as a second, then the first group is at least as fit overall as the second. If, in addition, either the group viability or group fecundity ordering is strict, then so is the group fitness ordering.

With the addition of Intracomponent Minimal Increasingness and Intracomponent Incremental Symmetry to Intercomponent Separability, Lemma 2 shows that the group viability ordering R_n^v and the group fecundity ordering R_n^b can be represented by indices of group viability and group fecundity that take the additive forms in (1) and (2). That is, group viability (resp. fecundity) is the sum of the individual cell viabilities (resp. fecundities).

Lemma 2. *If the group fitness ordering R satisfies Intercomponent Separability, Intracomponent Minimal Increasingness, and Intracomponent Incremental Symmetry, then the orderings R_n^v and R_n^b established in Lemma 1 are such that*

(i) *for all $\mathbf{v}, \mathbf{v}' \in \Omega^n$,*

$$\mathbf{v} R_n^v \mathbf{v}' \Leftrightarrow \sum_{i=1}^{n} v_i \geq \sum_{i=1}^{n} v_i';$$

(ii) *for all $\mathbf{b}, \mathbf{b}' \in \Omega^n$,*

$$\mathbf{b} R_n^b \mathbf{b}' \Leftrightarrow \sum_{i=1}^{n} b_i \geq \sum_{i=1}^{n} b_i'.$$

It has now been established that for comparisons for a fixed number of cells, group fitness is a function of indices of group viability and group fecundity that have the additive functional form used in the MVSHN index. It remains to show that group fitness is obtained by multiplying the values of these group viability and group fecundity indices. A necessary condition for this to be the case is that group fitness is unchanged if all of the cell viabilities are multiplied by a positive constant γ and all of the cell fecundities are multiplied by its reciprocal $1/\gamma$. The corresponding property for a social welfare ordering is called the *multiplicative principle* (Ooghe and Lauwers, 2005). Lemma 3 shows that the group fitness ordering R satisfies the multiplicative principle if it satisfies Intercomponent Ratio-Scale Measurability and Intercomponent Symmetry.

Lemma 3. *If the group fitness ordering R satisfies Intercomponent Ratio-Scale Measurability and Intercomponent Symmetry, then for all $n \in \mathbb{N}$, all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$, and all $\gamma > 0$,*

$$(\mathbf{v}, \mathbf{b}) I (\gamma \mathbf{v}, (1/\gamma)\mathbf{b}).$$

The first three lemmas use various combinations of the five intracomponent and intercomponent axioms. Lemma 4 demonstrates that if all five of them are satisfied, then group fitness comparisons for a fixed number of cells must be made using the MVSHN index M in (3).

Lemma 4. *If the group fitness ordering R satisfies Intercomponent Separability, Intercomponent Ratio-Scale Measurability, Intercomponent Symmetry, Intracomponent Minimal Increasingness, and Intracomponent Incremental Symmetry, then for all $n \in \mathbb{N}$, the restriction of R to Ω^{2n} is equal to the restriction of the MVSHN group fitness ordering R^M to Ω^{2n}.*

Theorem 1, which is the main result of this article, provides an axiomatic characterization of the MVSHN group fitness ordering. It shows that the six axioms considered here are necessary and sufficient for the group fitness ordering R to be the MVSHN group fitness ordering R^M. The addition of the Null Cell Invariance axiom to the other five axioms implies that R^M must be used to make group fitness comparisons when the number of cells differ, not only when they are the same. A comparison of viability-fecundity profiles for two groups with different numbers of cells can be transformed into a comparison for the same number of cells by adding null cells to the smaller group until the number of cells in the two groups are equalized. A null cell has no viability or fecundity, so the addition of such a cell has no affect on the fitness of the initially smaller cell. It is because the addition of a null cell has no affect on group viability or group fecundity as measured in the MVSHN index and, hence, on their product, that the MVSHN index must be used for all group fitness comparisons, not just for comparing groups with the same number of cells. It is straightforward to verify that all six axioms are satisfied by R^M.

Theorem 1. *The group fitness ordering R satisfies Intercomponent Separability, Intercomponent Ratio-Scale Measurability, Intercomponent Symmetry, Intracomponent Minimal Increasingness, Intracomponent Incremental Symmetry, and Null Cell Invariance if and only if R is the MVSHN group fitness ordering R^M.*

The six axioms in Theorem 1 are independent. Hence, any five of them are satisfied by other group fitness orderings in addition to R^M. The ordering R^M also satisfies other properties that are not independent of those in the theorem statement. Two of them are described below.

Strict Monotonicity. For all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$,

$$(\mathbf{v}, \mathbf{b}) > (\mathbf{v}', \mathbf{b}') \;\Rightarrow\; (\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}').$$

Strict Monotonicity says that increasing either the viability or the fecundity of any cell increases group fitness provided that no cell has its viability or fecundity decreased. The ordering R^M satisfies this property because the MVSHN group fitness index M is strictly increasing in each of its arguments.

Continuity. For all $n \in \mathbb{N}$ and all $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$, the sets $\{(\mathbf{v}', \mathbf{b}') \in \Omega^{2n} \mid (\mathbf{v}', \mathbf{b}') R (\mathbf{v}, \mathbf{b})\}$ and $\{(\mathbf{v}', \mathbf{b}') \in \Omega^{2n} \mid (\mathbf{v}, \mathbf{b}) R (\mathbf{v}', \mathbf{b}')\}$ are both closed.

Informally, Continuity requires a small change in the viability-fecundity profile to have only a small effect on group fitness. The ordering R^M satisfies this property because the MVSHN group fitness index M is continuous in its arguments.

5. Concluding Remarks

The MVSHN group fitness index M and its associated group fitness ordering R^M were designed to show that, at least in some circumstances, germ-soma specialization is a property of the solution to a formal constrained group fitness optimization problem in which M is the objective function. But, as Michod, Viossat, Solari, Hurand, and Nedelcu (2006) note, this conclusion can also be obtained using other group fitness indices. Which is the most appropriate index to use to analyze a unicellular-multicellular transition depends on the multicellular lineage being considered. Knowing the properties that characterize different candidate group fitness orderings can help identify which one of them best describes how the evolution of group fitness is related to the characteristics of a lineage.

In spite of their advantages, M and R^M are not suitable for analyzing group fitness during all stages of a unicellular-multicellular transition. The problem is that the functional form of M is independent of group size. However, during the early stages of a transition, the group is not well integrated, so the evolutionary forces that it is being subjected to are best described by multiselection 1. But, in that case, the sum or average of the individual fitnesses, not the MVSHN index, measures group fitness. It is only in the later stages of the transition that it is more appropriate to measure group fitness with an index like the MVSHN index that separately accounts for the contributions to group fitness of the viabilities and fecundities of the individual cells.

This observation suggests that some of the axioms that characterize the MVSHN group fitness ordering should not be applied for all group sizes. If viability-fecundity profiles are compared using the sum group fitness index S, then all the axioms are satisfied except for Intercomponent Separability and Intracomponent Incremental Symmetry. When there

is little or no germ-soma specialization, the contribution that a cell's viability (resp. fecundity) makes to group fitness depends more on this cell's fecundity (resp. viability) than either of these axioms permit. When the average group fitness index A is used instead of S to make group fitness comparisons, Null Cell Invariance is violated in addition to Intercomponent Separability and Intracomponent Incremental Symmetry. A cell with no viability or fecundity has no fitness, so the addition of a such a cell reduces average cell fitness.

Here, the axiomatic method has been employed to factor the MVSHN group fitness index into its constitutive properties. This methodology can also be used to help construct a different group fitness index that is better suited for analyzing any particular evolutionary transition. This is done by first identifying the properties that the index should satisfy if it is to accurately describe the fitness of the lineage being considered and then determining which group fitness indices satisfy these properties.

The MVSHN index only depends on the individual cell viabilities and fecundities. Other cell properties might also be important determinants of group fitness, such as the ease with which cells adhere to or communicate with other cells (Rokas, 2008). If so, then a group fitness ordering should also depend on these properties. The social choice approach employed here to study group fitness can easily take factors such as these into account.

Appendix

Proof of Lemma 1. Suppose that R satisfies Intercomponent Separability. Consider any $n \in \mathbb{N}$ and any $(\mathbf{v}^0, \mathbf{b}^0) \in \Omega^{2n}$. Let R_n^v and R_n^b be the binary relations on Ω^n defined in (8) and (9), respectively. By Intercomponent Separability, R_n^v and R_n^b are independent of the choice of $\mathbf{v}^0$ and $\mathbf{b}^0$. Because R is an ordering, R_n^v and R_n^b are orderings as well.

(i) Suppose that $\mathbf{v} R_n^v \mathbf{v}'$ and $\mathbf{b} R_n^b \mathbf{b}'$. By the definitions of R_n^v and R_n^b,

$$(\mathbf{v}, \mathbf{b}^0) R (\mathbf{v}', \mathbf{b}^0) \text{ and } (\mathbf{v}^0, \mathbf{b}) R (\mathbf{v}^0, \mathbf{b}').$$

By Intercomponent Separability,

$$(\mathbf{v}, \mathbf{b}) R (\mathbf{v}', \mathbf{b}) \text{ and } (\mathbf{v}', \mathbf{b}) R (\mathbf{v}', \mathbf{b}').$$

Because R is transitive, it follows that $(\mathbf{v}, \mathbf{b}) R (\mathbf{v}', \mathbf{b}')$.

(ii) Suppose that $\mathbf{v} P_n^v \mathbf{v}'$ and $\mathbf{b} R_n^b \mathbf{b}'$. By the definitions of R_n^v and R_n^b,

$$(\mathbf{v}, \mathbf{b}^0) P (\mathbf{v}', \mathbf{b}^0) \text{ and } (\mathbf{v}^0, \mathbf{b}) R (\mathbf{v}^0, \mathbf{b}').$$

By Intercomponent Separability,

$$(\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}) \text{ and } (\mathbf{v}', \mathbf{b}) R (\mathbf{v}', \mathbf{b}').$$

Because R is transitive, it follows that $(\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}')$.

(iii) The proof of (iii) parallels that of (ii) with the roles of viability and fecundity interchanged. □

Proof of Lemma 2. Lemma 1 ensures that the orderings R_n^v and R_n^b exist.

(i) Consider any $\mathbf{v} \in \Omega^n$. If $v_1 = \cdots = v_n$, it follows immediately that

$$v_j = \frac{1}{n}\sum_{i=1}^{n} v_i$$

for all $j \in N^n$ and, thus,

$$\mathbf{v} I_n^v \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^n \tag{A.1}$$

because R_n^v is reflexive. If not all of the coordinates of $\mathbf{v}$ are equal, suppose, without loss of generality, that $v_1 = \max\{v_1, \ldots, v_n\}$ and $v_n = \min\{v_1, \ldots, v_n\}$. Thus,

$$v_1 \;>\; \frac{1}{n}\sum_{i=1}^{n} v_i \;>\; v_n. \tag{A.2}$$

By (A.2), $(\mathbf{v} - \delta\mathbf{1}_1^n + \delta\mathbf{1}_j^n) \in \Omega^n$ for all $j \in \{2, \ldots, n\}$ and all δ in the open interval (v_n, v_1) because $\mathbf{v} \in \Omega^n$. Hence, for any such j and δ, Intracomponent Incremental Symmetry implies that

$$\mathbf{v} I_n^v (\mathbf{v} - \delta\mathbf{1}_1^n + \delta\mathbf{1}_j^n). \tag{A.3}$$

Using (A.3) and the transitivity of R_n^v (repeatedly if necessary) with

$$\delta = \frac{1}{n}\sum_{i=1}^{n} v_i - v_j$$

at each step $j \in \{2, \ldots, n\}$, it follows that

$$\begin{aligned}
&\mathbf{v} I_n^v \left(v_1 + v_2 - \frac{1}{n}\sum_{i=1}^{n} v_i, \frac{1}{n}\sum_{i=1}^{n} v_i, v_3, \ldots, v_n\right)\\
&\quad\vdots\\
&\mathbf{v} I_n^v \left(\sum_{i=1}^{n} v_i - \frac{n-1}{n}\sum_{i=1}^{n} v_i, \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^{n-1}\right).
\end{aligned}$$

Because

$$\left(\sum_{i=1}^{n} v_i - \frac{n-1}{n}\sum_{i=1}^{n} v_i, \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^{n-1}\right) = \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^n,$$

(A.1) holds for this case as well.

Now consider any $\mathbf{v}, \mathbf{v}' \in \Omega^n$. By applying (A.1) to $\mathbf{v}$ and to $\mathbf{v}'$, it follows that

$$\mathbf{v} I_n^v \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^n \quad \text{and} \quad \mathbf{v}' I_n^v \left(\frac{1}{n}\sum_{i=1}^{n} v_i'\right)\mathbf{1}^n.$$

Transitivity then implies that

$$\mathbf{v}R_n^v\mathbf{v}' \;\Leftrightarrow\; \left(\frac{1}{n}\sum_{i=1}^{n} v_i\right)\mathbf{1}^n R_n^v \left(\frac{1}{n}\sum_{i=1}^{n} v_i'\right)\mathbf{1}^n.$$

Hence, by Intracomponent Minimal Increasingness,

$$\mathbf{v}R_n^v\mathbf{v}' \;\Leftrightarrow\; \frac{1}{n}\sum_{i=1}^{n} v_i \geq \frac{1}{n}\sum_{i=1}^{n} v_i' \;\Leftrightarrow\; \sum_{i=1}^{n} v_i \geq \sum_{i=1}^{n} v_i',$$

which establishes the first part of the lemma.

(ii) The proof of the second part of the lemma is analogous to that of the first with viability replaced by fecundity. □

Proof of Lemma 3. Consider any $n \in \mathbb{N}$, any $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{v}') \in \Omega^{2n}$, and any $\gamma > 0$. By Intercomponent Ratio-Scale Measurability,

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') \;\Leftrightarrow\; (\gamma\mathbf{v}, \mathbf{b})R(\gamma\mathbf{v}', \mathbf{b}'). \tag{A.4}$$

By Intercomponent Symmetry,

$$(\gamma\mathbf{v}', \mathbf{b}')I(\mathbf{b}', \gamma\mathbf{v}'). \tag{A.5}$$

Transitivity, (A.4), and (A.5) imply that

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') \;\Leftrightarrow\; (\gamma\mathbf{v}, \mathbf{b})R(\mathbf{b}', \gamma\mathbf{v}'). \tag{A.6}$$

Similarly, Intercomponent Ratio-Scale Measurability implies that

$$(\gamma\mathbf{v}, \mathbf{b})R(\mathbf{b}', \gamma\mathbf{v}') \;\Leftrightarrow\; (\gamma\mathbf{v}, (1/\gamma)\mathbf{b})R(\mathbf{b}', \mathbf{v}') \tag{A.7}$$

and Intercomponent Symmetry implies that

$$(\mathbf{b}', \mathbf{v}')I(\mathbf{v}', \mathbf{b}'). \tag{A.8}$$

Transitivity, (A.7), and (A.8) imply that

$$(\gamma\mathbf{v}, \mathbf{b})R(\mathbf{b}', \gamma\mathbf{v}') \;\Leftrightarrow\; (\gamma\mathbf{v}, (1/\gamma)\mathbf{b})R(\mathbf{v}', \mathbf{b}'). \tag{A.9}$$

Using (A.6), (A.9), and transitivity, it now follows that

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') \;\Leftrightarrow\; (\gamma\mathbf{v}, (1/\gamma)\mathbf{b})R(\mathbf{v}', \mathbf{b}'). \tag{A.10}$$

By letting $(\mathbf{v}', \mathbf{b}') = (\mathbf{v}, \mathbf{b})$ in (A.10), it follows that

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}, \mathbf{b}) \;\Leftrightarrow\; (\gamma\mathbf{v}, (1/\gamma)\mathbf{b})R(\mathbf{v}, \mathbf{b}),$$

which, by the reflexivity of R, implies that

$$(\mathbf{v}, \mathbf{b})I(\gamma\mathbf{v}, (1/\gamma)\mathbf{b}),$$

as was to be shown. □

Proof of Lemma 4. Consider any $n \in \mathbb{N}$ and any $(\mathbf{v}, \mathbf{b}), (\mathbf{v}', \mathbf{b}') \in \Omega^{2n}$. It is sufficient to prove that

(i) $(\mathbf{v}, \mathbf{b}) I^M (\mathbf{v}', \mathbf{b}') \Rightarrow (\mathbf{v}, \mathbf{b}) I (\mathbf{v}', \mathbf{b}')$

and

(ii) $(\mathbf{v}, \mathbf{b}) P^M (\mathbf{v}', \mathbf{b}') \Rightarrow (\mathbf{v}, \mathbf{b}) P (\mathbf{v}', \mathbf{b}')$.

(i) Suppose that $(\mathbf{v}, \mathbf{b}) I^M (\mathbf{v}', \mathbf{b}')$. That is, by (3) and (7),

$$\left(\sum_{i=1}^{n} v_i \right) \left(\sum_{i=1}^{n} b_i \right) = \left(\sum_{i=1}^{n} v'_i \right) \left(\sum_{i=1}^{n} b'_i \right). \tag{A.11}$$

Let

$$\gamma = \frac{\sum_{i=1}^{n} v'_i}{\sum_{i=1}^{n} v_i} = \frac{\sum_{i=1}^{n} b_i}{\sum_{i=1}^{n} b'_i}. \tag{A.12}$$

Clearly, $\gamma > 0$ is well-defined because $\mathbf{v}$ and $\mathbf{b}'$ are both in $\Omega^n = \mathbb{R}^n_+ \setminus \{\mathbf{0}^n\}$ and, thus, the sums in the above denominators are non-zero. Rearranging these equalities, it follows that

$$\sum_{i=1}^{n} v'_i = \sum_{i=1}^{n} \gamma v_i \quad \text{and} \quad \sum_{i=1}^{n} b'_i = \sum_{i=1}^{n} \frac{1}{\gamma} b_i. \tag{A.13}$$

Thus, by Lemma 2,

$$\gamma \mathbf{v} I^v_n \mathbf{v}' \quad \text{and} \quad (1/\gamma) \mathbf{b} I^b_n \mathbf{b}'. \tag{A.14}$$

Hence, by Lemma 1,

$$(\gamma \mathbf{v}, (1/\gamma)\mathbf{b}) I (\mathbf{v}', \mathbf{b}'). \tag{A.15}$$

By Lemma 3,

$$(\mathbf{v}, \mathbf{b}) I (\gamma \mathbf{v}, (1/\gamma)\mathbf{b}). \tag{A.16}$$

Using (A.15), (A.16), and transitivity, it follows that

$$(\mathbf{v}, \mathbf{b}) I (\mathbf{v}', \mathbf{b}'), \tag{A.17}$$

which completes the proof of the first case.

(ii) Now, suppose that $(\mathbf{v}, \mathbf{b}) P^M (\mathbf{v}', \mathbf{b}')$. The proof is the same as the proof of case (i) with the following modifications. The equality in (A.11) is replaced by $>$ and the second equalities in (A.12) and (A.13) are replaced by $<$. In (A.14), I^b_n is replaced by P^b_n and in (A.15) and (A.17), I is replaced by P. □

Proof of Theorem 1. That R^M satisfies the requisite axioms is straightforward to verify. Lemma 4 has established that, given the axioms in the theorem statement, comparisons involving the same number of cells must be carried out with the ordering R^M. Thus, the proof is complete once it is established that the same is true for comparisons involving different numbers of cells.

Consider any $n, n' \in \mathbb{N}$ with $n \neq n'$, any $(\mathbf{v}, \mathbf{b}) \in \Omega^{2n}$, and any $(\mathbf{v}', \mathbf{b}') \in \Omega^{2n'}$. Without loss of generality, suppose that $n > n'$. By (repeated if necessary) application of Null Cell Invariance (and transitivity), it follows that

$$(\mathbf{v}', \mathbf{b}')I((\mathbf{v}', \mathbf{0}^{n-n'}), (\mathbf{b}', \mathbf{0}^{n-n'})).$$

Transitivity then implies that

$$(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') \;\Leftrightarrow\; (\mathbf{v}, \mathbf{b})R((\mathbf{v}', \mathbf{0}^{n-n'}), (\mathbf{b}', \mathbf{0}^{n-n'})). \tag{A.18}$$

The viability-fecundity profiles $(\mathbf{v}, \mathbf{b})$ and $((\mathbf{v}', \mathbf{0}^{n-n'}), (\mathbf{b}', \mathbf{0}^{n-n'}))$ are both for groups with n cells. It has been established in Lemma 4 that group fitness comparisons for groups with the same number of cells must be performed in accordance with the ordering R^M. Hence, it follows from (3), (7), and (A.18) that

$$\begin{aligned}(\mathbf{v}, \mathbf{b})R(\mathbf{v}', \mathbf{b}') &\Leftrightarrow (\mathbf{v}, \mathbf{b})R^M((\mathbf{v}', \mathbf{0}^{n-n'}), (\mathbf{b}', \mathbf{0}^{n-n'})) \\ &\Leftrightarrow \left(\sum_{i=1}^{n} v_i\right)\left(\sum_{i=1}^{n} b_i\right) \geq \left(\sum_{i=1}^{n'} v'_i\right)\left(\sum_{i=1}^{n'} b'_i\right),\end{aligned}$$

as was to be shown. □

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