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THE MULTIPLE REALIZABILITY OF BIOLOGICAL INDIVIDUALS*

Biological theory demands a clear organism[1] concept, but at present biologists cannot agree on one. They know that counting particular units, and not counting others, allows them to generate explanatory and predictive descriptions of evolutionary processes. Yet they lack a unified theory telling them which units to count. In this paper, I offer a novel account of biological individuality that reconciles conflicting definitions of "organism" by interpreting them as describing alternative realizers of a common functional role, and then defines individual organisms as essentially possessing some mechanisms that play this role.

In the first section, I argue that there is a real problem of biological individuality and a need to arbitrate over the solutions to it. In section II, I identify two critical functional roles, *policing* and *demarcation*, as well as some definitions that name their realizers. In section III, I argue that we should make the possession of mechanisms that play these roles—to greater or lesser effect—definitional of biological individuals.

I. THE PROBLEM OF BIOLOGICAL INDIVIDUALITY

The problem of biological individuality is a central conceptual issue in evolutionary biology, concerning our ability to delineate the biological units to which fitness can be properly attributed and which participate in the evolutionary process. The organism is the entity that emerges during an evolutionary transition,[2] and it is the unit that a population

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[1] I use the terms "biological individual" and "organism" interchangeably.

[2] Leo W. Buss, *The Evolution of Individuality* (Princeton: University Press, 1987); John Maynard Smith and Eörs Szathmáry, *The Major Transitions in Evolution* (New York:

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biologist counts. While there are some domains in which identifying an organism is relatively unproblematic, there are many more in which substantial "individuation puzzles" arise. These cases generate serious epistemological and metaphysical problems. In the first place, biologists are sometimes unsure which units they ought to count when they carry out fitness surveys. For example, there is a long-standing debate amongst plant scientists about whether vegetatively produced plants (that is, plants that are produced by mitotic cell division, in the absence of sexual fertilization) ought to add to the parent plant's fitness or not.[3] They need some generalized guidelines that tell them what to look for when deciding if some unit should be counted. This immediate empirical significance sets the problem of biological individuality apart from the more abstract debates concerning the units or levels of selection.[4]

More subtly, biologists implicitly import concepts of the individual into their models and discussions without general consensus about which concept should be used. In the absence of such consensus, theoretical debates about fitness, adaptation, sociality, the evolution of sex, and more are hampered because biologists are unaware that they are talking about slightly different things. For example, the truth value of a claim such as "selection always acts at the level of the individual" might vary according to whether "individual" picks out only common-sense creatures such as mammalian individuals, or whether it is meant to include so-called superorganisms, such as social insect societies, too.[5] There is an urgent need for the concept of the organism to be cleaned up so that such cross-talk is avoided.

Various suggestions have been made about the most appropriate way to define the biological individual.[6] The literature exhibits at

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Freeman, 1995), pp. 1–12; Richard E. Michod, *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality* (Princeton: University Press, 1999), pp. 81–107; Samir Okasha, *Evolution and the Levels of Selection* (New York: Oxford, 2006), pp. 218–41.

[3] Ellen Clarke, "Plant Individuality: A Solution to the Demographer's Dilemma," *Biology and Philosophy*, XXVII, 3 (May 2012): 321–61, at p. 332.

[4] Elisabeth Lloyd, "Units and Levels of Selection," *The Stanford Encyclopedia of Philosophy* (Winter 2012 Edition), Edward N. Zalta, ed., URL: <http://plato.stanford.edu/archives/win2012/entries/selection-units/>; H. Kern Reeve and Laurent Keller, "Levels of Selection: Burying the Units-of-Selection Debate and Unearthing the Crucial New Issues," in Keller, ed., *Levels of Selection in Evolution* (Princeton: University Press, 1999), pp. 3–14.

[5] David Sloan Wilson, "Altruism and Organism: Disentangling the Themes of Multilevel Selection Theory," *The American Naturalist*, CL, S1 (July 1997): S122–34.

[6] The problem I treat here is one of finding necessary and sufficient conditions for membership of the class, rather than of finding identity conditions for particular

least fifteen different candidate definitions, invoking reproduction, life-cycles, genetics, sex, developmental bottlenecks, germ-soma separation, policing mechanisms, spatial boundaries or contiguity, immune response, fitness maximization, cooperation and/or conflict, codispersal, adaptations, metabolic autonomy, and functional integration.[7] Most of these candidates can ultimately be reconciled, but in this paper I pay particular attention to definitions in terms of the following six properties: sex, bottlenecks, germ-soma separation, policing mechanisms, spatial boundaries, and immune response. Before I proceed to that analysis I must persuade the reader that these candidates are not merely different ways of picking out the same set. They generate non-coextensive classes of biological individuals. This means that a scientist using one definition can generate different predictions about the likely increase or decrease in the frequency of a particular trait over time, from a scientist using a different definition. To demonstrate this, let us consider the sexual view versus the bottleneck view.

According to a *sexual view*, the organism is everything that develops by mitosis[8] from a sexually fertilized zygote.[9] In this view all reproduction involves the combining of genes from two parents into a single genotype. All forms of so-called asexual reproduction (vegetative propagation by cuttings or runners, parthenogenesis, apomixis, fragmentation, and fission) are actually just expansion or division of a single individual organism. In the *bottleneck view*, on the other hand, the organism is everything that develops by mitosis from a bottleneck

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organisms. In other words, my concern is not whether my definition will serve to re-identify one biological individual over space and/or time. For a treatment of this sort, see Thomas Pradeu, "What Is an Organism? An Immunological Answer," *History and Philosophy of the Life Sciences*, XXXII, 2–3 (2010): 247–68; Charles T. Wolfe, "Do Organisms Have an Ontological Status?," *History and Philosophy of the Life Sciences*, XXXII, 2–3 (2010): 195–232.

[7] A detailed investigation of the different concepts that biologists use goes beyond the scope of this paper, so I will do just enough here to show that there is a genuine multiplicity of candidate solutions on the table, and that there is no simple way of conjoining or otherwise assimilating them. See Clarke, "The Problem of Biological Individuality," *Biological Theory*, V, 4 (2010): 312–25, for a full list and references.

[8] Mitosis occurs when a cell divides to produce two identical copies.

[9] Thomas H. Huxley, "Upon Animal Individuality," *Proceedings of the Royal Institution of Great Britain*, XI (1852): 184–89; Alexander Braun, "The Vegetable Individual, in Its Relation to Species," trans. C. F. Stone, *Annals and Magazine of Natural History*, published in three parts: XVI (1855): 233–56, XVI (1855) 333–54, and XVIII (1857): 363–86; Daniel H. Janzen, "What Are Dandelions and Aphids?," *The American Naturalist*, CXI, 979 (May–June 1977): 586–89; Robert E. Cook, "Asexual Reproduction: A Further Consideration," *The American Naturalist*, CXIII, 5 (May 1979): 769–72.

stage in the life-cycle.[10] Reproduction in this view is any event during which the phenotype is funneled down to the size of a single cell (or a few cells) before fanning out again to the size of the adult.

Let us take an example to show how these candidate views affect counting decisions. Aphids are sap-sucking insects that undergo what is called "cyclical parthenogenesis." This means that the females spend all summer reproducing asexually, before reproducing sexually just once at the end of the season. By the sexual definition of the organism, only the sexual event constitutes genuine reproduction, and the entire cloud of cloned aphid insects are just parts of a single individual. Daniel Janzen argued that we can better explain the traits of aphids if we treat the whole summer generation as a large subdivided individual.[11] In this view there is no significant difference between asexually "reproducing" to make two aphids and growing to make one aphid twice as large as another.

The bottleneck view delivers a different verdict. Since the cloned aphid insects develop from single unfertilized cells, the bottleneck view accepts them as countable individuals.[12] If a scientist applies the sexual view, she will count each aphid clone, comprising numerous cloned insects, only once. If, on the other hand, she follows the bottleneck view, she will count the separate insects as individuals. If she asks "How many biological individuals are there?" her answer depends on which view she takes.

But what of this? Suppose the following. One of the insects acquires a mutation during the cloning process. This mutation increases the insect's fitness, and is passed on to its asexual progeny. Insects carrying this mutation therefore produce more clonal offspring than the others. In other words, natural selection is taking place. The mutant trait will increase in frequency within the clone. The trouble is that the scientist who measures aphid fitness only at the whole-clone level, by counting clones, will overlook this selection. By calling the clones individuals, she effectively assumes that there is no variation

[10] John Bonner, *On Development* (Cambridge: Harvard, 1974); Richard Dawkins, *The Extended Phenotype: The Long Reach of the Gene* (New York: Oxford, 1982), pp. 254–65; Maynard Smith and Szathmáry, *op. cit.*, p. 244; Peter Godfrey-Smith, *Darwinian Populations and Natural Selection* (New York: Oxford, 2009), pp. 91–108.

[11] Janzen, *op. cit.*, p. 588.

[12] The two views also diverge with respect to monozygotic twins. A sexual (and genetic) view treats them as two halves of a whole, while a bottleneck view can separate them, on the grounds that the zygote splits into two sufficiently small pieces. See Julian S. Huxley, *The Individual in the Animal Kingdom* (Cambridge, UK: University Press, 1912), p. 70.

or selection within the clone.[13] She will look for evolution across clone generations, not within clones.

Within-clone selection can reduce the heritability of traits measured at the clone level, because the sample of traits transmitted to descendant clones is altered by selection between insects within the ancestor clone. To see this, suppose at the beginning of the summer all of the clone members carry allele A_1. By the end of the summer, selection between insects means that only 20% of the clone carries A_1 while 80% carries a mutant, A_2, at the same locus. In the assumed absence of within-clone selection, the scientist who applies the sexual definition of an individual assumes that the clone-level heritability of A_1 matches the insect-level heritability of A_1, so that next summer's offspring clones are expected to mostly carry A_1. However, since the offspring clones are derived from parents in whose population only 20% of members carried allele A_1, the real heritability of A_1 at the clone level may be much lower. In other words, within-clone selection can cause informational decay, by altering the similarity between ancestor and descendant clones.[14]

The point is that different counts of the number of individuals in existence can lead to different measures of the fitness of their traits, and thereby lead the scientist to generate a different figure for total evolutionary change than she would have done if she had counted aphid insects, instead of aphid clones. This undermines our ability to understand how natural selection acts on wild populations, as well as our efforts to conserve and manage our natural environment. This is the sense in which the biological counting problem is real. There is a genuine multiplicity of concepts of the organism, and this multiplicity is potentially damaging to the discussion and application of evolutionary theory.

[13] We now know this assumption to be false in the aphid case. See Hugh Loxdale, "Was Dan Janzen (1977) Right about Aphid Clones Being a 'Super-organism', i.e. a Single 'Evolutionary Individual'?," *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, XVI (2008): 437–49.

[14] In the terms of Price's equation, between-insect selection will increase the amount of transmission bias at the clone level—assuming that the two levels of selection are antagonistic, that is, that the two components of the covariance term in the multilevel Price equation are opposite in sign. Without taking this into account, our clone-counting scientist will end up overestimating the amount of evolutionary change that is going to take place. See George R. Price, "Selection and Covariance," *Nature*, CCXXVII, 5257 (Aug. 1, 1970): 520–21; Okasha, *op. cit.*, p. 70. See Clarke, "Plant Individuality," p. 354, for additional ways in which organism counts can go wrong. For a recent explanation of the way in which selection at one level can bring about transmission bias or lowered heritability at a higher level see S. A. Frank, "Natural Selection. III. Selection versus Transmission and the Levels of Selection," *Journal of Evolutionary Biology*, XXV, 2 (February 2012): 227–43.

One might think that a genetic view would be of assistance here. This view delineates a biological individual by the uniqueness or homogeneity (or both) of its genotype. A living mass is genetically homogeneous if all its parts carry copies of the same genes. For example, a genetically homogeneous aphid insect would carry a copy of the A_1 allele in each and every one of its cells. A proponent of a "gene's eye view" might suggest that we do not need to worry about which of the bottleneck and sexual definitions of the individual yields the right measure of evolutionary change, because we can measure fitness at the gene level and so dispense with the need to count individuals altogether.

The problem with this solution is that we have no means of directly counting how many copies of an allele are present in a particular lump of living matter, and have to rely on the organism concept, and on associated assumptions about homogeneity or heritability, to generate a measure of it. If we had some magical glasses with which we could apprehend genetic heterogeneity directly, then we might be able to say some illuminating things about the way in which gene frequencies change over time. However, as I will argue in section III, this will still fall short of being sufficient to secure claims about evolution by natural selection. In the absence of such glasses, and in so far as we are seeking a definition that can assist biologists in actual counting decisions, the genetic view is not sufficient.

In the next section of this paper I present a way in which we can interpret different definitions of the individual so that, despite their referential divergence, they can be reconciled, and without moving too far away from their core motivations. The argument proceeds in two parts. First I show how several candidates focus on mechanisms that reduce the capacity of an object's parts to undergo selection. In the second, more novel part, I explain why this effect is not sufficient to capture the organism.

II. RECONCILIATION

II.1. From Bottlenecks to Policing Mechanisms. Why adopt a bottleneck view? Dawkins defends the bottleneck view because of the role bottlenecks play in making individuals genetically homogeneous.[15] When development proceeds from a single-celled stage, all of the millions of cells in the body of a multicellular organism are clonal copies of just one cell. Their DNA is replicated from a single template, and this increases the degree to which the multicellular

[15] Dawkins, *op. cit.*, p. 260.