The Problem of Biological Individuality

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Abstract

Darwin described forces of selection acting upon individuals, but there remains a great deal of controversy about the exact status and definition of a biological individual. Recently some authors have argued that the individual is dispensable—that an inability to pin it down is not problematic because little rests on it anyway. The aim of this article is to show that there is a real problem of biological individuality, and an urgent need to arbitrate among the current plethora of solutions to it.

If selection is a process of differential perpetuation of the units of selection, and if organisms are the primary focus of selection, then we had better know which entities we are to count.

—David L. Hull (2001: 17)

Darwin's classic *Origin of Species* (1859) described forces of selection acting upon individuals, but there remains a great deal of controversy about the exact status and definition of a biological individual. Recently some authors have argued that the individual (or its conceptually close cousin, the organism) is dispensable—that an inability to pin it down is not problematic because little rests on it anyway. J. Wilson (2000: 301) claims that "biology lacks a central concept that unambiguously marks the distinction between organism and non-organism because the most important questions about organisms do not depend on this concept." Others (Ruiz-Mirazo et al. 2000; Pepper and Herron 2008) argue to the contrary that the absence of a clear organism concept is such a serious problem for evolutionary theory that it must be remedied via revision of that theory (Gould 1980). The aim of this article is to show that there is a real problem of biological individuality, and an urgent need to arbitrate among the current plethora of solutions to it. First I will defend the claim that biological individuality is an essential concept that we cannot do without, and which we are therefore well motivated to clarify. Then I offer a brief survey of existing solutions to the problem to show that there is a genuine multiplicity and a pressing need for arbitration over it.

Why Do We Need the Notion of Biological Individuality?

A first answer to the question, "Why do we need a notion of biological individuality?" is simply that that is what we are. Human beings are sometimes happy to think of themselves as parts of social wholes but usually not to the degree that their personal autonomy and freedoms are subjugated. We also largely resist the idea that we may be viewed as mere collections of organs or cells. The human individual is idiosyncratically worthy of respect and moral treatment, more so even than the family unit or the ancestral lineage, because human individuals have separate minds—separate thoughts, feelings, and desires. Our separate minds coincide with physically separate bodies in a way that normally makes us easy to recognize and delineate from one another. Other organisms are physically delineated in similar ways to humans, and we automatically treat them as individuals too. We chastise only the dog that chewed the shoe, rather than its fellow pets too. If one cow is sick, we treat only that cow, not the whole herd (at least sometimes).

Biological individuals fall within the domain of the biological sciences. A distinction is sometimes drawn between evolutionary and non-evolutionary biology (Pradeu 2010), where the latter comprises disciplines such as medicine, developmental biology, immunology, ecology, and the reductionist sciences such as molecular or cell biology. In these domains the individual as a theoretical entity is sometimes left in the background, although it remains ubiquitous. Biological individuals are the entities that develop in ontogeny, whose parts have to be orchestrated to develop in synchrony with one another. They are the units that are described as occupying various roles in ecology, and whose daily interactions comprise ecosystems. They are the units that get sick, and whose immune systems mount responses to infections. Even in reductionist biology the organism is usually presupposed as the higher-level system, of which some type of object is a part, in order that we can make sense of the idea of objects such as molecules having functions (Cummins 1975).

Yet it is in an evolutionary context that the notion of the individual really does a lot of work. It is hard to overemphasize the importance of individuals within the Modern Synthesis. They are central to the inner logic of evolution by natural selection, according to which evolution occurs because of the differential survival and reproduction of individuals. Even in its most abstract minimal formulations, the action of a selection process requires that there be a multiplicity of objects that are sufficiently separate from one another that they can be differentially deleted or copied.

The received view of natural selection takes the organism to be the basic "unit of selection." This familiar skin-bound entity was taken by Darwin to be what natural selection "sees" when it acts on a population. The biological individual is the entity that population biologists count. It is everyday deaths and births of such individuals that sum over large numbers to constitute the evolutionary process itself. If fatal childhood illnesses afflict the smaller individuals in the population disproportionately with the larger individuals, and size is heritable, then we can expect the average size of members of that population to increase over time.

The notion of the biological individual is inextricably bound up with the notion of fitness. Fitness is used for describing evolutionary change—the relative change in gene frequencies, or frequencies of types, across generations. It is used for predicting the outcome of an evolutionary process, as well as for explaining such outcomes. It is used to explain the prevalence of traits, as well as the fit between phenotype and environment. Note that all these concepts—generation, trait, and phenotype—only have meaning in relation to the more primitive concept "individual." Biologists implicitly invoke a particular characterization of the individual any time they use these notions, and their choice of one concept over another will have consequences, acknowledged or otherwise, for their theories and explanations.

Measuring fitness requires that biologists count biological individuals. This fact is to some extent obscured by the

fact that fitness is a slippery notion that is interpreted in numerous ways and which can be attributed to various units. Some biologists are happy to count offspring, while others insist on counting grand-offspring so that unhealthy offspring aren't credited. Some people prefer to think about fitness as signifying potential, rather than actual offspring, but it will be assumed that the actual count will converge on the same figure when you average over enough organisms of the same type. Often the absolute figure will be converted to a relative one by comparing the number of offspring with the numbers produced by conspecifics. Either way, the person doing the counting needs to keep track of the rate at which organisms reproduce to leave individuals of the same type as themselves in the next generation.

We usually say that individuals bear fitness, but we can also talk about the fitness of a gene, or of a trait. The fitness measure tells us about which type of organism, or which trait, or which allele, we should expect to become more or less common in the future. However, measuring the fitness of a type, whether that is a type of organism, a trait, or an allele, *always* requires the population biologist to count individuals. Suppose we take fitness to be a property of a gene. The key quantity of interest is the rate at which new copies of that gene appear in subsequent generations—does a mutant increase or decrease in frequency from one generation to the next? In order to measure this, we'd need to do genetic analysis on a sample of individuals, making sure we know which individuals belong to which generation, so that we sample each individual only once. The same is true if we are interested in the fitness of a trait, although usually detection of a trait will be done on the basis of some phenotypically observable property, which makes it much easier and cheaper than doing genetic analysis. Furthermore, short-term numerical dominance (the "Malthusian parameter," or intrinsic rate of increase of an allele) is usually considered only to be an evidence of an allele's fitness, understood as some sort of characteristic or dispositional property, on the assumption that substituting that gene with a different allele would make a difference to the fitness, as in expected number of offspring, of the organism. In sexual populations this assumption is further complicated by the fact that the effect of any allele on the fitness of an organism will depend on the other alleles in the genome, but this complication is conceptually swept aside by assuming that such effects disappear once you average over a large enough set of possible genomes (Stearns 1992).

Someone might protest that biologists can do away with worrying about generations, and even individuals, if they just do genetic analysis on random samples of biomass, and then do another round of sampling later. However, in order to generalize from these samples you would need to know how representative your sample is of the genotype of the stuff sampled. Furthermore, in order to know how much time to leave between rounds you need to know something about the generation times of the life form involved. If your subject species is a type of tree that has a lifetime lasting hundreds of years, then separating your sampling rounds by only tens of years might fail to pick up any evolutionary change, even though across longer time frames there is a big change in gene frequencies. On the other hand, if your subject species is some sort of insect that has a very short lifetime, then by taking such a long view you are likely to miss many ups and downs in the frequency of the gene in question. Applying the notion of fitness to the right unit is essential, because it fixes the grain of description. Choosing the right unit allows you to describe the selection dynamics accurately and informatively so that you can correctly predict whether a particular gene (or trait, if you prefer) is going to increase in frequency over time or not.

These points still apply if you reject the Malthusian parameter in favor of viewing the fitter type as the one which endures the longest, that is, has the longest expected time to extinction (Cooper 1984; Stearns 1992). Although you might dispense with having to actually count anything, measuring time to extinction is also going to be much more successful if you have an idea of how often, and over what sort of time frame, you need to keep checking whether a given type is still around.

In sum, there are multiple competing ways to define fitness, to measure it, and to describe its role within the larger theory, but being fit is *always* about contributing to or being represented in future generations[1] of individuals.

Biological individuality is also indispensable to evolutionary biology more generally. Comparative biology is made possible by the assumption that we can compare like with like—that we are not comparing an *organism* in one lineage with a *colony* of organisms in another. For example, the float of a Portuguese man o'war (*Physalia physalis*) is thought to be an analogous rather than homologous structure to the float in cnidarians, because the latter are individuals, while a Portuguese man o'war is a colony. In the life history theory the goal is to see if conclusions can be drawn about the ways in which general life traits, such as age of sexual maturity or size at maturity, are modulated across species in ways that we could predict using information about the idiosyncratic environmental challenges faced by particular lineages. Interspecies comparison is illuminating only to the extent that we can be sure we are "comparing apples with apples" (Pepper and Herron 2008).

Adaptive hypotheses, one of the most widespread and successful of biological methodologies, depend upon being able to make judgments about the bearers of adaptations, that is, the unit for which a speculated trait or behavior would be useful. In studies of sociality, it is critical to decide what is an organism and what is a group of organisms because the answer to whether or not some environmental variable is correlated

with sociality may change depending on our answer (Pepper and Herron 2008). The concept of the individual is also essential for the possibility of nonsubjective trait decomposition (Wagner and Laubichler 2000).[2] Biological individuals express phenotypes and form lineages. All of these notions are inter-defined because individuals are the bearers of adaptations; these adaptations make them fit, which means that they successfully produce lots of offspring. Some authors might protest that populations, not individuals, are the real units of interest in evolutionary theory (Mayr 1994; Godfrey-Smith 2009), but it is clear at least that populations are a special sort of ensemble of individuals so that the notions of population and individual will be mutually inter-defined.

Another area of study in which biological individuality plays a critical role is that of major transitions in evolution (Maynard Smith and Szathmáry 1995; Michod and Roze 1997; Okasha 2006). Research into this area necessitates directly confronting questions about what is or is not an individual, because transitions just *are* events during which new kinds of individuals appear, at new levels of organization or "rungs on the ladder of life" (Queller 1997). Usually the new individual is formed by some sort of aggregation of former individuals. The history of past transitions is partially illustrated in the compositionally complex life forms that we see today. There are simple, unaggregated organisms such as bacteria, as well as more complex eukaryotic cells, and then the lumbering compounds such as ourselves, which are composed of millions of cells. The biological hierarchy did not spring into existence fully formed. It is itself the outcome of a long process of evolution. Even if it were the case that natural selection currently occurs exclusively at the level of multicellular organisms, such as mice, this cannot always have been the case because there have not always been multicellular organisms! This diachronic view (Okasha 2003) of levels of selection implies a new way of conceptualizing individuality as something derived rather than as primitive. The multicellular organism is not an ontological primitive in biology after all, but something whose appearance on the evolutionary scene must be explained.

Biological individuality is important to us for a number of different reasons. Critically, these go beyond the semantic. There are many important cases in which adopting one definition of the individual rather than another gives us a different answer to a biological question. We will make a different prediction about the outcome of an evolutionary process (Pedersen and Tuomi 1995) or the likelihood that a transplant will be rejected (Medawar 1957). So the problem is not purely conceptual—it makes an actual difference. Even genic reductionists like Richard Dawkins accept that the concept of biological individual cannot be eliminated. Dawkins says, "There is something pretty impressive about organisms. If we could actually wear spectacles that made bodies transparent and displayed only DNA, the distribution of DNA that we would see in the world would be overwhelmingly non-random" (1982: 251).

Putting Some Candidates on the Table

One might accept that we cannot do without a concept of the biological individual without also accepting that it is problematic. All I want to claim in this article is that there are a multiplicity of definitions available, and that because they are non-equivalent—they define non-overlapping classes—there is a choice to be made about which definition, or how many definitions, to accept. There is a problem of individuality at least in so far as this choice does not have an obvious answer.

Here I present a list of properties that have been suggested as definitive of biological individuals. I have included names to indicate that this plurality of candidates has not been gerrymandered—real people have suggested these positions, have argued for them, and have had good reasons for doing so. I will offer a brief motivation for each of the 13 candidates but it goes beyond the scope of this article to begin any actual evaluation. I will simply introduce some concrete examples to show that the candidates cannot be straightforwardly assimilated or conjoined because they generate different verdicts on the individuality of real life cases.

1. *Reproduction* (Gould and Lloyd 1999; Griesemer 2000; Godfrey-Smith 2009) or *persistence* (Van Valen 1989; Bouchard 2008).
2. *Life cycle* (T. H. Huxley 1852; Bonner 1979; Dawkins 1982; Donoghue 1985; Hull 2001; R. Wilson 2007).
3. *Genetics* (Harper 1977, 1985; Janzen 1977; Dawkins 1982; Smith et al. 1992; Maynard Smith and Szathmáry 1995; Santelices 1999).
4. *Sex* (T. H. Huxley 1852; Braun and Stone 1853; Janzen 1977; Cook 1979).
5. *Bottleneck life cycle* (Dawkins 1982; Maynard Smith and Szathmáry 1995; Godfrey-Smith 2009).
6. *Germ–soma separation* (Weismann 1885; Buss 1983, 1987; Fagerström 1992; Michod and Nedelcu 2003; Michod and Herron 2006; Godfrey-Smith 2009; Folse and Roughgarden 2010).
7. *Policing mechanisms* (Boyd and Richerson 1992; Frank 1995, 2003; Maynard Smith and Szathmáry 1995; Michod 1999; Okasha 2006) or *anti-subversion devices* (Godfrey-Smith 2009) or *conflict modifiers* (Michod and Roze 2001).
8. *Spatial boundaries/contiguity* (J. S. Huxley 1912; Hull 1978, 1980; Buss 1987; Gould 1991; Brasier 1992; Sterelny and Griffiths 1999; Leigh 2010).
9. *Histocompatibility* (Metchnikoff 1907; Loeb 1921, 1937; Medawar 1957; Burnet 1969; Tauber 2009; Pradeu 2010).
10. *Fitness maximization* (Grafen 2006, 2008; Gardner 2009; Gardner and Grafen 2009; West and Kiers 2009; Leigh 2010).

11. *Cooperation and conflict* (Wilson and Sober 1989; Queller and Strassmann 2009; West and Kiers 2009; Strassmann and Queller 2010).

12. *Codispersal* (Margulis 1970; Frank 1997; Folse and Roughgarden 2010; Leigh 2010).

13. *Adaptations* (Fisher 1930; Williams 1966; Vrba 1984; D. S. Wilson 2003; Folse and Roughgarden 2010; Strassmann and Queller 2010).

Before I go on to describe the items on this list in more detail, I need to talk about some possibilities that have been excluded. I have already ruled out phenomenal, vernacular, or commonsense definitions of the individual. Dupré (2010: 21) is certainly not wrong to insist that "to the average mushroom collector a single mushroom is an organism," but this pragmatic commonsense concept too often falls silent and is not the one we want to delineate for scientific purposes.

Another swathe of candidates are eliminated by distinguishing between definitions of "life" and definitions of "*a* life." In defining life, the goal is to distinguish living from dead organisms and inanimate matter and it is a notoriously thorny task (Cleland and Chyba 2002; see also the forthcoming special issue of *Synthese* on "Life"). However, a living individual is an individual that lives. The problem of biological individuality can be distinguished from the problem of defining living systems by focusing on what properties separate living individuals from living *parts* and from living *groups*, while taking the property of life itself for granted.

A more serious omission from the list is functional integration. This is a very popular criterion that defines the organism roughly as "any biological entity whose parts have evolved to function in a harmonious and coordinated fashion" (Wilson and Sober 1994: 606). It underpins a large class of individuality concepts that define the individual in terms of the nature of its parts, or the kind or amount of interaction that takes place amongst them. For example, the parts are said to be heterogeneous (J. S. Huxley 1912), semi-autonomous (Laubichler and Wagner 2000), or differentiated (McShea 2000). Their interaction is spelt out in terms of organization (Darwin 1859), a division of labor (Michod and Nedelcu 2003), or cohesion—behaving as a whole with respect to some (usually evolutionary) process (Hull 1980). Sometimes their interaction must be fitness-affecting (Sober 2010) while elsewhere it is more loosely defined in terms of cooperation (Queller and Strassmann 2009) or common purpose (West and Kiers 2009), or convergent design (Gardner and Grafen 2009). Sometimes the underlying idea is spelled out in terms of irreducibility—the fitness of the whole is more than the sum of its parts (Michod 1999; Okasha 2006) or emergent order (Goodwin 1994).

The trouble is that pretty much everything is organized, in some sense. The efficacy of these candidates in settling actual individuation problems—i.e., distinguishing clearly between parts, individuals, and groups—depends very much on the precise way in which organization is spelled out, and whether a measure of it can be generated. Many versions are going to be overly permissive because there are many respects and degrees to which functional integration is evident in systems we clearly don't want to describe as biological individuals. A cell within a metazoan regulates its internal environment and is extremely complex and integrated. The members of a pit crew can show a very high degree of coordination for a common purpose (Sterelny and Griffiths 1999).

At the same time, these candidates are in danger of excluding things that are obviously individuals. For example, if it is reasonable to describe distinct organs in a body as evolving somewhat independently of one another (Brandon 1999), then evolutionary cohesion seems to fail. Physiological interaction is often very local (Pradeu 2010) so that two sub-systems of an organism are relatively independent of one another (the organism is "functionally modular") (Schlosser and Wagner 2004). Furthermore, some organisms are not very well organized throughout their entire life cycle. During metamorphosis the parts of an organism de-differentiate, completely losing their internal organization.

Therefore insofar as this view is left vague it is not helpful. What we need to do is spell out the notion of interaction in some more objective and measurable way, with some theoretical justification for including some kind of interaction but not others. Pradeu (2010) does this in terms of biochemical interactions, while Gardner and Grafen (2009) try to spell out the idea of unity in purely selective terms. Another possibility is to understand integration more strictly as reproductive or germ–soma division of labor. I omit functional views in their most general form, and prefer to give a separate evaluation of the distinct ways of cashing them out.

The final notable omission is autonomy. "In our view, autonomy is the main feature of life, the key notion for any attempt to define it" (Boden 2008: 310). These candidates define individuality in terms of self-sufficiency (Spencer 1864) or independence (Steenstrup 1845; Owen 1849; Jeuken 1952; Santelices 1999; R. Wilson 2007). Biological individuals are defined by "the ability to do what one does independently, without being forced so to do by some outside power" (Boden 2008: 305). To some extent, autonomy can be seen as complementary to functional integration. Where integration binds the parts of an individual together, and so distinguishes groups from individuals, autonomy separates the individual from other entities, and so distinguishes parts from individuals.

Although many people think autonomy is important, there is little consensus on what it is, how to measure it, or how much of it is necessary. Once again, the usefulness of the notion depends on exactly how it is fleshed out. Sometimes the notion is spelled out in intentional terms, with the individual taking

on the role of an agent (R. Wilson 2007; Gardner and Grafen 2009). Individuals are end-directed (Ruse 1989), they "use the external world for their purposes" (Santelices 1999: 152). These notions can trace their historical roots to Aristotle's entelechy or Bergson's (1907) élan vital—an inherent force that motivates and guides the organism toward self-realization. Sometimes reproductive autonomy is made the focus of attention so that individuals are not somatically differentiated (Fagerström 1992). Alternatively, policing mechanisms may function to deprive the parts of an individual of their autonomy so that "entities that were capable of independent replication before (an evolutionary) transition can replicate only as part of a larger whole after it" (Maynard Smith and Szathmáry 1995: 4). As with integration before, I'll evaluate individual constituents, or interpretations, of autonomy rather than grappling with the notion in its most general form.

This leaves us with 13 remaining candidates, which are serious contenders for the task of differentiating individuals from parts and groups. Some of these are reasonably self-explanatory while others require a substantial amount of explanation.

Reproduction

Is reproduction essential to biological individuality, or can there be biological individuals who persist, without multiplying themselves? Some authors argue that natural selection could very well occur even if no entities ever reproduced. While most biologists view fitness as having two components—viability and fecundity—these biologists and philosophers argue against the mainstream that the former is sufficient. Instead of understanding fitness as rate of increase of some type, these authors use the definition in terms of expected time to extinction (Cooper 1984) and argue that reproduction is merely a special case of survival. They say that all that is necessary for selection to occur is that there are multiple entities that possess a differential capacity to persist. Reproducing another entity of the same kind as yourself is simply one (among many) ways of being good at persisting.

Van Valen (1989) argues that in general it is not useful to attempt to count organisms at all, but rather that the expansion of their biomass should be measured.[3] Bouchard (2007, 2008) argues independently that natural selection depends upon differential persistence, and not on differential reproduction. Some entities go extinct and others do not. For Bouchard (2007, 2008), reproduction—understood as the multiplication of entities at *any* level—is redundant. Evolution by natural selection could occur very well in its absence.

Life Cycle

These candidates define the biological individual as a cyclically repeating segment of a lineage—"an intergenerationally replicable series of events or stages through which a living

agent passes" (R. Wilson 2007). In somewhat more poetic words, an organism is "one beat of the pendulum of life" (T. H. Huxley 1852: 1849).

There is a sense in which reproduction already implies life cycles, insofar as it implies new lives. However, a new life does not have to imply a new beginning, starting from scratch. A new life could just as well start from where the parent left off, rather than repeating some process all over again. Dawkins (1982) argues that new starts are necessary for the evolution of complex adaptations. De Sousa (2005: 22) argues that lives must have not only new beginnings but definite end points too—"biological individuals in the full sense . . . have been so constructed by evolution as to be necessarily subject to death, by the very logic of the process" (see also Hull 2001).

Genetics

These candidates delineate a biological individual by genotype, either insisting that it must have a unique genotype—to render it different from other individuals of the same species; or a homogeneous genotype—so that all of its parts are maximally related; or both (Santelices 1999). For example, Smith et al. (1992) claimed on genetic grounds that they had found the world's largest and oldest organism in Michigan. Spanning 15 hectares and 1,500 years, and weighing 10,000 kg, *Armillaria bulbosa* is indeed a humongous fungus (Gould 1992). However, not everyone agreed that their (genetic) methods were appropriate for delineating a single individual. Brasier (1992) responded that because the giant *Armillaria* clone is functionally fragmented and lacking a defined boundary, it is better conceived as the "infection centre" of a fungal population.

Sex

These candidates equate the individual with the entire mitotic product of a sexually fertilized zygote (T. H. Huxley 1852, 1878; Janzen 1977; Cook 1979). 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 the expansion or division of a single biological individual. According to T. H. Huxley (1852: 150), "The individual animal is the sum of the phenomena presented by a single life: In other words, it is all those animal forms which proceed from a single egg taken together."

Bottleneck

The bottleneck view identifies the entire mitotic product of the bottleneck stage in the life cycle as the individual (J. S. Huxley 1912; Dawkins 1982; Maynard Smith and Szathmáry 1995; Godfrey-Smith 2009). Reproduction is any event during which the phenotype shrinks down to the size of a single cell (or a few cells) before ballooning up again to the size of the adult.

This view encompasses the sexual view because sex always involves a single-celled stage, but it is more permissive as it also counts certain asexual forms of propagation as genuine reproduction. For example, it includes cases of parthenogenesis in which a single-celled egg is produced but develops without fertilization. It includes cases of self-fertilization, and also apomixis, in which a single-celled seed is produced without fertilization. The bottleneck view also allows identical twins to be separate individuals as long as the embryo splits into sufficiently small pieces (J. S. Huxley 1912).

Germ–Soma Separation

A germ–soma view claims that an important or essential property of a biological individual is that there is a reproductive division of labor so that some parts are sterile and carry out only somatic functions, i.e., behaviors necessary for survival and growth, but not reproduction (Buss 1983, 1987; Michod 1999, 2007; Michod and Nedelcu 2003; Godfrey-Smith 2009).

The earliest version of the germ–soma view was probably the one given by Weismann (1885, 1893) although he was wrong in many details. Buss (1987) did more to emphasize that not all organisms show germ–soma separation, and even in those that do, the time of onset of sequestration during ontogeny is very variable. Buss (1987) further claims that maternally controlled germ sequestration is an adaptation that has evolved in some lineages to prevent different cell lineages from competing for representation in the immortal germ line. He argues that before germ separation was evolved, true individuality at the multicellular level was not possible.

According to Michod's (1999) account, when a collection of parts is completely germ–soma separated, all parts have strictly zero fitness, for neither germ nor soma cells are individually able to carry out all the functions necessary for evolutionary success. During evolutionary transitions in individuality, when individuals become mere parts in new higher-level wholes, it is via germ–soma separation that fitness gets exported up to the new higher level (Michod and Roze 1997). This idea is adopted by Folse and Roughgarden (2010: 448) who talk about components being "interdependent on one another for reproduction." Fagerström (1992) has a sort of negative germ–soma view, as he makes totipotency a sufficient condition for individuality.

Policing Mechanisms

Candidates of this type define the biological individual as something that necessarily possesses "policing mechanisms" (Buss 1983; Boyd and Richerson 1992; Frank 1995, 2003; Michod and Nedelcu 2003; Okasha 2006), "anti-subversion devices" (Godfrey-Smith 2009), or "conflict modifiers" (Michod and Roze 2001).

Such mechanisms function to solve the problem of the commons—the fact that cooperation among a group of interactors can be undermined because they are tempted to "cheat" or "free ride"—reap the benefits of cooperation of others without contributing to costs. This temptation can be reduced if the group is policed so that defection is prevented or punished.

There are many hypothetical (Travisano and Velicer 2004) and actual examples of policing mechanisms. Leigh (1971) champions Mendelian segregation as the ultimate example of policing mechanism, designed to impose fairness in meiosis. Frank (2003) suggests that uniparental inheritance of mitochondria probably also emerged as a conflict reduction mechanism. Another oft-cited example is the behavior of workers in social insect societies, whereby they remove and eat eggs laid by other workers (Visscher 1996).

Conflict can be reduced by rewarding cooperative behavior, as well as by punishing cheaters. Frank (2003) understands relatedness as a kind of policing mechanism because it encourages self-restraint by incentivizing the members of a group with the possibility of large gains in inclusive fitness. "Repression of competition within groups joins kin selection as the second major force in the history of life shaping the evolution of cooperation" (p. 693).

Spatial Boundaries/Contiguity

These candidates emphasize that a biological individual should be physiologically discrete (Buss 1987; De Sousa 2005), spatially bounded (Brasier 1992; Sterelny and Griffiths 1999; Leigh 2010), and/or spatially localized (Brasier 1992; Hull 1980).

These candidates expect biological individuals to be visible and readily apprehensible phenomena, with edges and continuous existence in between. Their parts should be physically attached to each other and to nothing else. Brasier (1992) appealed to these considerations in the debate about the humongous fungus, claiming that true individuals don't have spatially scattered parts. Hull (1980), on the other hand, defends spatiotemporal criteria in virtue of the extent to which they impact upon functionality.

Histocompatibility

In this view, parents are distinguished from offspring (and from other organisms) in terms of immune response or allorecognition. Early versions of this view were suggested by Metchnikoff in the 1870s, Loeb in 1937, and Medawar in 1957. Burnet (1969) defined the "immune self" as characterized by a lack of immune response to its own parts, as opposed to the reaction elicited by all foreign items of living matter. Burnet argued that the criterion of immunogenicity for the immune self (i.e., the basis on which the immune system decides to either accept some entity, or to reject it—in which case it is targeted for destruction by lytic activity) is genetic.

Pradeu (2010) offers a recent refinement of the immunological view (Pradeu and Carosella 2006a, 2006b) that gives a new criterion of immunogenicity. Pradeu argues there is an ongoing biochemical interaction between immune receptors and the antigenic patterns on living cells, and that an immune response is triggered by a discontinuity in these interactions, rather than by the nature of the antigenic patterns themselves. Pradeu (Pradeu and Carosella 2006b) argues that the individual should be understood as the entire unit delineated by sameness of immunogenic patterning amongst cells, and that his criterion of continuity of molecular patterns better accommodates the empirical facts about immunity than does the "immune self" theory. For example, some objects that share a genotype with the rest of the organism (e.g., cancerous cells) will be rejected, while many objects that are genetically different (symbiotic microbes, fetuses) will be accepted.

Fitness Maximization

Gardner (2009) understands the organism as a unit whose parts are all under selection to maximize the unit's inclusive fitness. The view is developed out of Grafen's (2007) work on formal Darwinism, in which he shows that there is a mathematical isomorphism between the dynamics of gene frequency change under the action of natural selection and the optimization view of organisms as fitness-maximizing agents. Building on William Paley's insight that the parts of an organism appear as if designed for a common purpose, and Darwin's discovery that the common purpose in question is just the maximization of reproductive success, Gardner (2009) argues that Grafen's work shows how the action of natural selection can result in optimization.

The key claim is that the only way in which we can *explain* how it is that organisms come to seem, like a complex pocket watch, as if some agent has designed them with some purpose in mind, is by postulating that selection has acted as a proxy designer, and has caused the phenotype to be gradually molded according to a unified design objective. Every part of the organism has its properties just because they gave some ancestral organism an inclusive fitness advantage over its conspecifics, and not for any other reason. Specifically, those parts or traits have not been selected for the advantage they give to any other higher or lower level unit, for then the parts could have conflicting purposes, and we would not be looking at an organism—we would not see the unity of design that is an organism's hallmark. So the organism must not possess genes such as transposons, whose properties advance the gene's own fitness against the fitness of the organism as whole. "The action of natural selection only corresponds to the design principle of group-fitness maximization if within-group selection is absent" (Gardner and Grafen 2009: 863).

Cooperation/Conflict

Queller and Strassmann define "organismality" as an evolved trait that is constituted by cooperation and absence of conflict between groups of simpler units (Queller and Strassmann 2009; Strassmann and Queller 2010). Biological individuals, for them, are just cooperators which "have become so intimate as to blur their boundaries." They want to de-emphasize the physical indivisibility of the individual so as to include things like social insect colonies. In common with the fitness maximizer view (Gardner and Grafen 2009), they think that one of the idiosyncratic properties of organisms is their shared purpose, specifically viewing it in terms of cooperation. The organism is the largest unit of near-unanimous design (they say "near" because they acknowledge that some conflict, e.g., meiotic drive, always persists). Unlike Gardner and Grafen (2009), they focus on actual rather than potential conflict. This means that something like a clone of aphids does not count as an individual by their lights because despite their high relatedness making cooperation potentially very fruitful they do not actually cooperate.

Codispersal

The term "codispersal" is Frank's (1997) alone but many others say that distinct entities can come to be parts of a single biological individual if their reproductive interests are brought into perfect alignment so that they share a common evolutionary fate. Margulis' (1970) endosymbiont theory argues that this is how mitochondria came to be domesticated parts of the eukaryotic cell. Although mitochondria do not literally reproduce at the same time as the cell does, their numbers are kept constant relative to cell numbers by autophagy, under the control of cell lysosomes. Leigh (1971) argued that the essential innovation of meiosis is that it eliminates competition between genes for preferential representation in the gametes by enforcing strict reproductive fairness, although meiotic driver genes have found a way to get round this. Folse and Roughgarden (2010: 448) talk about the alignment of fitness components.

The codispersal view is allied to the argument that parasite virulence decreases whenever parasite transmission is vertical, i.e., the parasite is carried from parent host to offspring host, rather than switching hosts. The reasoning is that when reproduction is coupled so that immortality for the parasite lineage depends upon the host reproducing, each parasite's success is therein tied to the success of the group. Parasites that killed their host or prevented it from breeding would soon go extinct. "A symbiont that harms its host harms itself" (Frank 1997: 84).

However, Frank shows that matters are not quite so simple because host–symbiont conflicts can emerge as a consequence of within-host competition amongst parasites (Frank 1997; Aanen and Hoekstra 2007). The degree of harm to the host

depends on how closely related its symbionts are to one another. For this reason, domestication of mitochondria required not just that mitochondria are unable to transfer between cells but are also inherited from only one parent. Uniparental inheritance of mitochondria reduces conflict among them by increasing the extent to which they are closely related (Hoekstra 2000). Therefore, vertical transmission is neither necessary nor sufficient for individuality. Instead the parts must meet the stricter requirement of codispersal—"a measure of the frequency at which two particular replicator molecules are transmitted together"—so that the reproductive interests of two loci (one in each partner) are bound together (Frank 1997: 90).

Many symbiotic alliances involve high levels of codispersal, though Frank (1997: 10) says that "few groups have mechanisms suppressing selection among their individuals as effective as fair meiosis and the lock-step simultaneity in reproduction of all chromosomal genes."

Adaptations

These candidates say that biological individuals are the entities who bear adaptations. The question of whether individuality is located at the level of a single unit or a group of such units can be answered, in this view, by finding out the level at which adaptations occur, because natural selection causes individuals to become well adapted to their environment (Fisher 1930; Williams 1966; Vrba 1984).[4] Folse and Roughgarden (2010: 449) say that "the organism must display adaptations at the level of the whole that are not present at the level of the components."

However, remaining questions have to be answered in order to clarify a candidate of this sort—what is an adaptation? How can we tell at which level an adaptation occurs? Some scientists appeal to the notion of emergence in order to define an adaptation. This notion itself is hard to unpack, but the idea is that an emergent trait is not straightforwardly equivalent to or reducible to a multitude of lower level traits. The height of a group of organisms, for example, is usually understood as the average height of its members—there is no new property at the group level. The intelligence of a monkey, on the other hand, seems genuinely emergent—it is not simply the average intelligence of all of a monkey's cells. Other examples are intermediate however. Some would argue that altruism is an emergent trait because it is not a property that isolated individuals can possess. However, others might say that the group benefit produced by altruism just depends on the proportion of altruists in the group.

Some people understand an adaptation at a level as any product of (or response to) selection at that level, whereas Gardner and Grafen (2009) reserve the term for products of exclusive selection at that level. In other words, they say that adaptations only come into existence once lower levels of selection are completely suppressed. These two views therefore

generate different verdicts about when some entity is a biological individual, even though they both define it according to the possession of adaptations.

The Multiplicity

The key point to take from this necessarily brief survey is that there is a surfeit of definitions on offer.[5] My next aim is to demonstrate that these candidates are operationally nonequivalent, i.e., they do not overlap in application. In this section I describe some living objects that we will take as real-life cases for the problem of biological individuality and assess each example according to the different criteria outlined above. This analysis will serve three purposes. Firstly, it will show exactly what the criteria are supposed to be doing—how they can be operationalized so as to generate verdicts about the individuality of a particular case. Secondly, it will demonstrate the sense in which the different candidates are nonequivalent by showing that they make different partitions of real-life cases.

The third purpose of this analysis is to reply to the critic who still insists that there is no real problem of individuality. He might argue that the very ubiquity of the notion in everyday life provides evidence that it is a concept that we know and understand well. Even children can count sheep. What is wrong with a phenomenal view of individuality, according to which individuals are things that we can easily see? Most of the creatures we encounter in everyday life come in well-delineated skin-bound parcels. We can see that a new individual has been born because the number of entities in front of us has multiplied. People, dogs, sheep, even insects and crustaceans, all yield rather well to this straightforward analysis. So why agonize over what is the essence of individuality when we all know an organism when we bump into one? When posed with respect to *some* organisms, these problems can look needlessly complicated—like typical philosopher's questions. Yet, as usual in biology, pick a change of example suitably and any apparently obvious matter can become obscure and mysterious. Our everyday notion of the biological individual functions well in many contexts but fails in others. It works better for some species than for others, but there are also cases when it fails for a species that is ordinarily unproblematic. The failures concern examples about which we either have no intuitions, or we have numerous intuitions that seem to pull in different directions.

I propose the following subjects:

- *A lobster's claw*. Lobsters (*Homarus gammarus*) have the remarkable talent of regenerating their claws. Just like a lizard's tail, the claw can be abandoned or "thrown" during life or death situations, and later a new claw appears and grows to normal size. The potential individual here is the claw alone, not the whole lobster.[6]

Table 1. Verdicts for candidate h.

Candidate	Lobster claw	Aspen grove	Puppy	Bee colony	Man o'war	Bacterium
Intuition	No	No	Yes	No	Yes	Yes
Spatial bounds	Yes	u-d	Yes	No	Yes	Yes

- *A grove of aspen trees*. Aspen (*Populus tremula*) have a hidden secret. What looks like a normal forest of separate trees is actually a network of contiguous parts. The trees are connected underground by multicellular runners. Each tree sends out runners from its rootstock, and these fuse with other runners, and also grow upwards toward the light where they grow into new trees. The trees share nutrients and other resources among their common root structure.

- *A puppy, or immature Canis familiaris.* These are paradigmatic higher metazoans. They share with humans all of the features that have been historically taken to be reliable hallmarks of individuality. Any definition that excludes this example will be strongly counterintuitive. We'll assume it's a "normal" healthy puppy—it doesn't have any twins, transplanted organs, or tumors, although each of these suppositions would be interesting in their own right.

- *A honeybee (Apis mellifera) colony*. Like many bee species, this one is eusocial—the bees live in groups of thousands of insects, where most of the members are sterile and often physically differentiated workers. The vast majority of reproduction is carried out by only one or a few queens.

- *A Portuguese man o'war (Physalia physalis)*. This looks just like a jellyfish, but it has a completely different developmental process so that it is usually considered a group or colony rather than an individual. It is composed of different kinds of parts that are homologous to different life stages in a single jellyfish and each has its own nervous system.

- Finally, a *bacterium* (*Helicobacter pylori*), which is a single-celled prokaryote. These reproduce by binary fission but may also go in for lateral gene transfer with unrelated cells. In other words, bacterial cells don't have sex but they do swap DNA.

I am going to illustrate what happens when we apply the candidate definitions to these cases. First of all, we can ask what our common intuition is about these examples, though we may not agree. I would claim that the most commonsensical view would say that a lobster is an individual while its claw is a mere part, and an aspen grove is composed of many individuals (the trees). I think most people would agree that a young dog is an individual. I suspect intuitions would diverge regarding the bees, but anyone well isolated from science would take each insect to be an individual. It takes substantial investigation to cause doubts about the Portuguese man o'war's status—as far as appearance goes it is incontrovertibly a single organism. Finally, we might not be able to see bacteria at all, but I suppose we still think of them as tiny individuals.

Let us now evaluate the thesis that biological individuals have proper boundaries (see "Spatial Boundaries/Contiguity" above) just because it is quite easy to apply because we are supposed to be able to see clearly whether something is spatially bounded and continuous. We need to look at the problem cases, and decide if they are organism all-the-way-through rather than gappy, and look for edges or boundaries, such as skin or a cell wall.

A lobster claw is contiguous with the rest of the lobster, but actually here there has to be a boundary so that the claw can be easily "thrown." It is certainly a distinct part with visible edges and no internal "gaps"; on balance I would say a claw is a passable object. We cannot know whether an aspen grove is contiguous without doing a lot of digging. Sometimes the grove will be spatially continuous, with each tree connected to others by runners. More often, especially in older groves, animal activity and subsidence will have caused parts of the root structure to decay and fragment. The puppy easily passes this test after it has been born, though not before. The beehive definitely fails; it lacks both clear edges and spatial contiguity. Its parts are spatially dispersed. The Portuguese man o'war passes, and so does the bacterium. The results for the spatial bounds candidate are presented in Table 1.

We can do this for some other candidates too, as presented in Table 2. For now I have included some of the simpler, more readily operational candidates. In the tables, I use u-d to stand for "undetermined." I need to say a few words about how I arrived at each of these verdicts.

- *Sex*: Only the puppy has straightforward sexual origins. I said the verdict is undetermined for aspen because what we see as a grove might have sprung from a single fertilized or apomictic seed, from many seeds, or from

Table 2. Verdicts for six candidates.

Candidate	Lobster claw	Aspen grove	Puppy	Bee colony	Man o'war	Bacterium
Intuition	No	No	Yes	No	Yes	Yes
Sex	No	u-d	Yes	No	u-d	No
Bottleneck	No	u-d	Yes	Yes	Yes	Yes
Germ–soma	No	No	Yes	Yes	Yes	No
Spatial bounds	Yes	u-d	Yes	No	Yes	Yes
Histocompatibility	No	u-d	Yes	u-d	Yes	Yes
Adaptations	Yes	u-d	Yes	Yes	Yes	Yes

no seed at all but via runners from elsewhere. Bee colonies are not the mitotic products of a single sexually fertilized zygote. A Portuguese man o'war begins as a sexually produced zygote, but this splits into several discrete multicellular units, each of which then reproduces clonally; so I delivered an undetermined verdict here too. Bacteria do have sex, as they recombine their DNA, but this does not coincide with reproduction; bacteria always divide by mitotic fission.

- *Bottleneck*: Only the puppy and man o'war have clear bottleneck origins. The lobster claw definitely doesn't, while with the aspen we cannot know. If it was vegetatively propagated, then it fails because the runners are multicellular. The question is not well defined for either the bee colony or the bacterium. With bees I delivered a positive verdict because the bottleneck candidate could be interpreted as specifying that the propagule should be small relative to the mature colony size rather than single celled (in which case bees fail). With respect to bacteria, some would argue that they pass because they always have a single-celled form. Others would insist that this is no bottleneck—there is no reducing in size and then funneling out again, as with multicellulars.

- *Germ–soma*: The puppy, beehive, and man o'war all have some parts that are specialized for reproduction and others that are somatic. Aspen show somatic embryogenesis, which really just means the same thing as lacking germ–soma separation. The lobster claw is regenerated using specialized stem cells but these have to come from the lobster itself, not the lost part.

  I said no for the bacterium, although it could perhaps be argued that some genes or genetic pathways are devoted specifically to mitosis.

- *Histocompatibility*: Dogs are the only examples that possess an adaptive immune system, although bacteria pass this test too because they do have mechanisms for resisting invasion by foreign bodies—a kind of innate immunity. Lobster claws definitely do not exhibit an immune reaction to the rest of the lobster. The other

cases are unclear. Trees such as aspen do exhibit systemic immune responses, but because they are mediated by airborne chemicals, they do not delimit groups in any ordered way. The cue is simply passed to nearby plants, whether they are related, or are in the same species or not. Whether or not you say bee colonies possess histocompatibility depends on how you want to define it. They recognize members of their own colony and expel foreign matter from their hives—perhaps that is enough.

- *Adaptations*: Here I used a loose understanding of adaptation in which the object in question seems well designed for what it needs to do. Lobster claws are well adapted for the ecological challenges they face, as are all the other examples. The only exception is the aspen grove because it is not immediately clear whether the grove possesses any properties that aren't straightforwardly reducible to properties of aspen trees, although nutrient transport in the root system might be an exception.

So, with this rough and ready analysis in hand what lessons emerge? One obvious fact to emerge from this quick survey is that the puppy passed every single test. Notice also that nothing has definitively ruled in the aspen grove, or ruled out the Portuguese man o'war. I think the case of the Portuguese man o'war is particularly interesting. Although it is an individual according to an intuitive view, in books and papers about the problem of biological individuality it is usually referred to as a colony of many zooids (J. Wilson 1999; De Sousa 2005; Godfrey-Smith 2009). E. O. Wilson ([1975] 2000) is a significant exception. However, it is rather difficult to find out why this is so. *Physalia* development is not very different from the other Cnidaria, true jellyfish, which they closely resemble. In siphonophores, the zygote undergoes multiple fissions to form a protozooid, which then starts budding—reproducing asexually to produce different zooids. This is referred to as "astogeny"—defined as the development of a colony—rather than "ontogeny" (Dunn 2005). What is not obvious is why we

say that the protozooid buds, rather than just describing it as an embryo that is undergoing normal cleavage. Sometimes people appeal to the fact that the zooids have their own nervous system (perhaps an appeal to some sort of autonomy criterion). E. O. Wilson (2000) claims that the only reasonable grounds for calling a siphonophore a colony rather than an individual are phylogenetic. Siphonophore zooids are genetically homologous (as well as structurally analogous) to solitary Cnidarians. Dunn (2009) says that we can define an individual by descent, by taking a look at two animals and asking which structures descend from a common ancestor. Just as bat wings are modified arms, siphonophore zooids are modified cnidarian individuals (Dunn 2009). Note, however, that if we were to make it a criterion of individuality that all individuals should be homologous with other individuals, then we would be forced to say that the cells in a multicellular organism are biological individuals. In fact, we would make transitions in individuality definitionally impossible—a troublesome conclusion, and a good illustration of the perils of gerrymandering a candidate.

It is an interesting fact in itself that some organisms pass more tests than others. Higher metazoans are in general relatively easy to individuate, most tests agree on their individuation, and give or take a few worries about parthenogenesis or regenerative abilities, there aren't real problems regarding these organisms. It is a separate but also interesting fact that some of the candidates offer convergent verdicts in particular areas (but not others!) and I would hope that a theory of biological individuality would be able to explain both of these sorts of fact in the end.

Nonetheless, even for a group of candidates that use criteria that usually coincide—the bottleneck and germ–soma and sexual views, for example—even here the living world is generous enough to furnish a wealth of examples, which exemplify some criteria in the absence of others. Parthenogenetically produced aphids have bottleneck life cycles and germ–soma separation but no sex. Slime mold slugs have germ–soma separation but do not develop mitotically from a bottleneck. Coral colonies may develop from a small fragment but lack somatic differentiation. So in order to preserve the organism definition's generality we will always need to make a choice of one candidate over another. To the extent that they are inconsistent (that they give different verdicts on the individuality of real-life cases), these candidates cannot all be right.

Conclusion

The reader may disagree with any of these judgments; there is plenty of room for argument about every single example that I have described, and this is only a tiny sample. There are plenty of other enigmatic creatures, which would give us pause—slime mold, starfish, eukaryotic cells, and lichen. I've also neglected to provide results for all of the 13 candidates.

Some of them are just too hard to operationalize—for example, I cannot judge in a thought experiment which of these cases are genetically homogeneous.

This analysis is only intended to show that the verdicts generated by different candidates do not overlap. This shows that there is a real plurality. For any two candidates we can find an example on which their verdicts will diverge. Scientists using different candidates are going to treat some organisms differently, and therefore make different evolutionary predictions, no two of which can turn out to be correct. This is important because it shows the unfeasibility of lumping the candidates together in any straightforward way. In order to assimilate candidates with one another we would need to appeal to some external standard for arbitrating over which candidate takes priority with respect to specific cases.

In summary, organisms are indispensable objects in biology. We know that counting particular lumps of living matter, and not others, allows us to describe and make predictions about evolutionary processes. Yet we lack a theory telling us which lumps to count. This problem has serious scientific as well as philosophical importance. Biologists rely heavily on the concept of the organism, but they import different concepts into their models and discussions without reaching a consensus about which concept should be used, and usually without even being aware that they are talking about different things. There is an urgent need for the concept to be cleaned up.

Acknowledgments

Notes

1. By a copy, which is of the same type, or—if you prefer to eliminate typological talk—by an entity with a certain degree of similarity, as argued by Godfrey-Smith (2009).

2. Laubichler and Wagner (2000)argue that an operational organism concept would help to overcome the structural deficiency of mathematical models in biology.

3. However, expansion or increase of biomass causes a change in gene frequencies only in so far as it involves an increase in the number of gene copies, by gene replication. Van Valen's (1989) view does not, therefore, dispense with the necessity of multiplication at *all* levels.

4. This should be distinguished from a different view about the unit that is the beneficiary of adaptations—the answer to which is usually given as either genes or lineages (Lloyd 1995).

5. Pepper and Herron (2008) offer a table detailing 12 separate individuality concepts that have resulted from this multiplicity of individuality definitions.

6. This might seem like a strange choice of subject case, on the grounds that nobody would seriously call this an individual anyway. However, in the 19th century Cuvier, Owen, and others argued that the regenerative capacity of organisms, such as lobsters and newts, constitutes evidence that they are compound individuals, with the property of life belonging to cells rather than to the organism as a whole (Elwick 2007). Even if such an idea strikes us

as silly, it is all the more important that all our candidates should be able to exclude this subject from the class of individuals.

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