Biological Individuality and Scientific Practice

Karen Kovaka*

I consider the relationship between scientific practice and the philosophical debate surrounding biological individuality. I argue for the sensitivity account, on which biologists do not require a resolution to the individuality debate. This view puts me in disagreement with much of the literature on biological individuality, where it has become common to claim that there is a relationship of dependence between biologists' conceptions of individuality and the quality of their empirical work.

1. Introduction. Do biologists need to know which objects are biological individuals in order to carry out good empirical work? Should we be concerned that scientists disagree about whether social insect colonies, the human holobiont, and coral reefs are biological individuals?

In this paper I answer "no" to both questions. I consider the relationship between scientific practice and the philosophical debate surrounding biological individuality, and I argue that although the question of biological individuality is relevant to the study of biological processes, biologists do not need a resolution to the individuality debate. This view puts me in disagreement with much of the literature on biological individuality, where it has become common to claim that there is a relationship of dependence between biologists' conceptions of individuality and the quality of their empirical work. In section 2, I provide an overview of the individuality debate. In section 3, I contrast the dominant view of the relationship between the individuality debate and scientific practice (the dependence account) with my own alternative view, the sensitivity account. Then, in section 4, I consider and reject three defenses of the dependence account. The failure of these defenses points to a flaw in the dependence account and gives reason to reject it in favor of the sensitivity account.

*To contact the author, please write to: University of Pennsylvania, Department of Philosophy, 433 Cohen Hall, Philadelphia, PA 19104; e-mail: kkovaka@sas.upenn.edu.

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2. The Individuality Debate. The individuality debate centers on two questions. First, what objects are biological individuals? Second, what criteria pick them out? Most scientists and philosophers agree that certain objects like single ants and human babies are biological individuals, but they do not agree about the status of many other objects, such as ant colonies (Wilson and Sober 1989) or the human holobiont (Zilber-Rosenberg and Rosenberg 2008). Can an ant colony be an individual, no less than the single ants that compose the colony? Is a human a set of cells with the same DNA, or are our obligate bacterial symbionts also part of the human individual?

These disagreements about which objects are individuals arise because of underlying disagreements about individuation criteria. If we use a criterion of genetic sameness to pick out individuals, then the human holobiont is not a biological individual. If, however, we use a criterion of functional integration, then both holobionts and social insect colonies are promising candidates. It is disagreement about individuation criteria that makes the problem of biological individuality a difficult one. Proposed individuation criteria are generally too broad or too narrow, and the dozen or so criteria defended in the literature all face a variety of objections (Clarke 2010). For example, according to the criterion of cooperation, an ant colony is an individual (Wilson and Sober 1989). This is a welcome result, since colonies are popular candidates for individuality. Unfortunately, the cooperation criterion also suggests that we should accept mutualisms, such as the strong symbiotic association between certain ant and acacia tree species, as individuals. For many scientists, a criterion that allows the ant–acacia mutualism is far too permissive, because ants and acacias are different species that reproduce separately and have independent evolutionary trajectories.

One strategy of response to individuation puzzles is to claim that there cannot be any unitary notion of biological individuality. Instead, there are various conceptions of individuality, and different ones are appropriate in different contexts (Santelices 1999; Dupre and O'Malley 2009). For instance, biologists might want to employ different individuation criteria depending on what biological process they are studying (Griesemer 2014). The criterion for being a metabolic individual might be different from the criterion for being a reproductive individual, which could be distinct from the criterion for being an evolutionary individual. This approach, though useful, does not resolve the individuality debate. Even if we give up on a unitary conception of biological individuality, there is still room for disagreement about the adequacy of narrower individuation criteria. We may trade disputes about biological individuation criteria for disputes about evolutionary and reproductive individuation criteria, but the basic structure of the puzzle remains.

The debate surrounding biological individuality is as lively today as it has ever been. Scientifically engaged philosophers are especially interested, because they see an empirical payoff to resolving the individuality question.

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They appeal to this empirical payoff to justify their attention to individuation puzzles and suggest that a resolution to the individuality debate is a precursor to breakthroughs in research.

In the next section, I examine the idea of an empirical payoff for resolving the individuality debate. I present the dominant defense of this idea, which I call the dependence account. Then I develop my own alternative view: the sensitivity account. On my alternative, biologists can get along perfectly well without settling theoretical individuation puzzles.

3. The Dependence and Sensitivity Accounts. Most of the literature on biological individuality implicitly accepts a view that casts the relationship between biological individuality and scientific practice in terms of dependence. The essential claim of the account is this:

> **Quality dependence:** the quality of empirical work in biology depends in part on the resolution of the debate about biological individuality.

Philosophers often use the quality dependence claim to motivate their own research. For example, various authors have claimed that some research questions "cannot be addressed effectively without confronting the question of what is, and is not, an organism" (Pepper and Herron 2008, 622), and that until we clarify the organism concept, "it is questionable whether there can be a science of the living" (Ruiz-Mirazo et al. 2000, 210). According to Clarke (2013, 414), the individuality debate has an "empirical significance" that other, more abstract debates in philosophy of biology lack.

These authors are persuaded that we will not see progress in many research areas until the disagreements I highlighted in section 2 resolve into a theory of biological individuality. More specifically, their worries are that biologists will study pseudo-individuals, ignore true individuals, operate under different conceptions of individuality without realizing it, or become invested in futile terminological disputes. If biologists can actually determine what is and is not a biological individual, then they will not investigate the wrong things or waste time arguing about what qualifies as an object of study. The only way biologists can make these determinations is to resolve the individuality debate by settling on the appropriate individuation criteria. Therefore, getting individuality right matters for the work that biologists do.

The sensitivity account shares with the dependence account a conviction that the individuality debate is relevant to biologists. It deviates from the dependence account by denying that settling the individuality debate has priority over empirical work. Instead, the link between the individuality debate and scientific practice is best described in terms of sensitivity. The central claim in the account is this:

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Content sensitivity: Biologists' understanding of biological processes is sensitive to the individuals they take to be participants in those processes.

Biologists do not need to know what a biological individual is in order to do good empirical work, but which objects they count as individuals does affect their thinking about biological processes. In this sense, philosophical discussions of individuality do impinge on biological research.

Biology aims to achieve a better understanding of biological processes such as reproduction, development, metabolism, and evolution. Biologists cannot, however, study these processes in the abstract. Instead, they learn about biological processes by investigating the objects that participate in the process—the biological individuals. For biologists who study social evolution, the focal individuals are often ants or honeybees, perhaps even whole social insect colonies. For biologists interested in asexual reproduction, the relevant individuals are a diverse collection of microbes, plants, insects, and fish.

Because biologists study processes by observing and manipulating individuals, their conclusions about these processes are affected by the individuals they choose to investigate. Many considerations, some practical and some theoretical, guide scientists as they select their objects of study, but the choice is always constrained by what they consider to be biological individuals. In other words, their understanding of and approach to biological processes is sensitive to the things they take to be biological individuals. This observation is at the heart of the relationship between the individuality debate and scientific practice.

Content sensitivity has two specific meanings in the context of empirical work. When biologists consider certain objects to be individuals with respect to a focal biological process, then (*a*) it is permissible to study those individuals in order to learn more about the focal process, and (*b*) what the biologists believe to be true about the focal process must accommodate facts about the individuals. If a social insect colony is an evolutionary individual, then biologists can study colonies as individuals in order to learn about evolution. Further, whatever biologists believe about the way evolution works must be responsive to facts about colonies, even if these facts challenge their existing understanding of the evolutionary process.

The sensitivity account is weaker than the dependence account. I take it that defenders of the dependence account will accept the content sensitivity claim but also assert the stronger view that doing the best empirical work requires a resolution to the individuality debate. The question is whether we have reason to go beyond the sensitivity account and accept this stronger view.

4. Against the Dependence Account. Advocates of the dependence account have yet to provide a convincing justification for their view. They

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argue that biologists need the individuality debate to be resolved, but the examples they offer of biological research suffering for lack of a resolution are not compelling. In this section I survey three defenses of the dependence claim and show that none of them succeed. Their failure suggests that the prospects for developing a successful defense are dim. We do not need to settle the individuality debate to do good science. Rather, good science may be our best hope for settling the individuality debate.

4.1. Inferring Dependence from Sensitivity. The first strategy is to infer the quality dependence claim from the content sensitivity claim. According to this line of reasoning, if the ways biologists study biological processes are sensitive to what they consider to be individuals, then being correct about which objects are individuals will make for better ways of studying biological processes. Likewise, being wrong about which objects are individuals will make for worse ways of studying biological processes. Resolving the individuality debate is the path to being correct about which objects are individuals. So, if the content sensitivity claim is true, then the quality dependence claim is true as well.

The problem with this strategy is its assumption that content sensitivity is one-directional. It takes the idea of empirical work being sensitive to conceptions of individuality and ignores the possibility that conceptions of individuality are equally sensitive to empirical work. Content sensitivity can run in both directions. Suppose that a biologist believes that social insect colonies are individuals with respect to reproduction. Her view is that colonies reproduce as individuals. This view will motivate the research questions the biologist asks, but if she is a good scientist, it is her observations of colonies that have made this conception of individuality plausible to her in the first place. Behind any instance of a particular conception of individuality influencing the empirical work that gets carried out is a further instance of empirical work influencing that conception of individuality. This two-directional content sensitivity means that the quality dependence claim does not follow from the content sensitivity claim. We have no more reason to think that the quality of empirical work depends on settling the individuality debate than we have to think that settling the individuality debate is a purely empirical matter. On the contrary, the fact that conceptions of individuality are sensitive to empirical work suggests that empirical work can contribute to discussions of individuality.

4.2. Inadequacy of Particular Conceptions of Individuality. The second strategy for defending the dependence account moves from the necessity of rejecting particular conceptions of individuality to the necessity of resolving the entire individuality debate. It points out that some conceptions of biological individuality are bad and would lead biologists to draw faulty conclusions if widely used. An easy example is the spatial boundaries cri-

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terion for individuality. The spatial boundaries criterion is one of many individuation criteria that have been raised in the literature (see Clarke 2010). While the most familiar biological individuals meet this standard, it fails miserably as a sufficient condition for individuality because it also includes regenerating body parts, such as lobster claws. Almost no one wants to classify single lobster claws as biological individuals, because even though they have spatial integrity, they do not do many of the other things we expect individuals to do. As a result, the spatial boundaries criterion has been soundly rejected, at least as a stand-alone criterion.

What defenders of the dependence account take from the lobster claw example is that we know that there are some bad conceptions of individuality and that we need to reject these bad conceptions if we want to avoid getting caught up in speculations about the possibility of evolving lineages of lobster claws. What is true of the spatial boundaries criterion is true of all inaccurate conceptions of individuality. Therefore, we need to weed out all such bad conceptions by resolving the individuality debate. Otherwise, biologists might study all kinds of pseudo-individuals without realizing it.

There are two problems with this strategy. First, it conflates a claim about the empirical disadvantages of particular conceptions of individuality with a claim about the empirical advantages of settling the individuality debate altogether. That the spatial boundaries criterion has bad consequences does not mean that all disagreement about individuation criteria has bad consequences. The quality dependence claim is true of certain conceptions of individuality, but it does not follow that the claim is true of the entire individuality debate. Second, this strategy does not explain why genuine multiplicity and disagreement over individuation criteria should be a problem for scientists in the first place. When scientists disagree about theoretical issues, they carry out empirical studies to shed light on the unanswered questions. The existence of disagreement often motivates exciting work. If anything, we should hope for biologists to involve themselves in the individuality debate rather than waiting it out.

4.3. Conflation of Practical and Theoretical Problems. The most recent work on biological individuality and scientific practice has gravitated toward a third defense of the dependence account. This strategy identifies problems that practicing biologists face and then attributes these problems to lack of consensus about what constitutes biological individuality. Haber (2013) and Clarke (2013) both present arguments of this sort. While they are correct in their identification of challenges that confront biologists, they are wrong to think that overcoming these challenges requires us to settle the individuality debate.

4.3.1. The Counting Problem. Clarke's worry is the counting problem. Uncertainty about biological individuality can lead biologists to count the

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wrong individuals, which can produce inaccurate measurements of evolutionary change. Clarke explains the counting problem using the following example. During warm weather, female aphids reproduce asexually, cloning themselves and giving birth to swarms of live offspring. When the weather turns colder, females begin to asexually produce both males and females, who then sexually reproduce with one another. Winter temperatures kill all of the mature aphids, but the batch of eggs laid at the end of the season survives the winter before hatching in the spring and beginning the cycle of reproduction again.

Suppose a biologist is studying aphid evolution. How should she count the aphids in her sample? On one view of individuality, only sexual reproduction makes new individuals, so each swarm of genetically identical insects is one individual. On the more liberal bottleneck view, individuals are produced when genetic material passes through a cellular bottleneck, and so a swarm of cloned aphids contains many individuals. These differing counts can generate further problems. When a genetic mutation occurs within a swarm and confers a fitness advantage on some aphid clones within the swarm, the within-clone genetic profile changes. Though such change is evolutionarily relevant, it will not be detected by a scientist who counts each clonal swarm as an individual, because she will not pay attention to genetic differences caused by mutations within what she considers to be a single individual.

In this example, there are two ways in which the counting problem can harm biological research. First, being wrong about individuality can mean being wrong about evolutionary processes. This happens when the community consensus on individuality is wrong. If there is no community consensus (which there often is not), this first bad consequence is still possible, but with the addition of the second worry–that a multiplicity of individuality concepts will give rise to unproductive arguments and misleading cross talk that would be avoided if a clear definition were available.

Clarke argues that we solve the counting problem by getting individuality right. If we resolve the controversial cases and settle on some individuation criteria, biologists will not count the wrong individuals or unintentionally talk past one another. The problem with this solution is that it prescribes a theoretical remedy for a practical problem. The counting problem does not exist because of a crisis in biological theory, and it is not the sort of problem that a complete resolution of the individuality debate can address. Luckily, there is a practical solution to this practical problem, so biologists need not look to the individuality debate for help.

The two worries Clarke identifies are that biologists will incorrectly measure evolutionary change and miscommunicate with one another. Though she works hard to connect these worries to the individuality debate, neither of them bears any necessary link to it. Consider the aphid case. As soon as

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a biologist realizes that evolutionary change can occur within a swarm of clones, she can infer that counting swarms rather than single aphids is a bad method of investigation. This inference is available to her regardless of the relative merits of the sexual or bottleneck individuation criteria. She can count single aphids even if she and others have unanswered questions about the biological status of single aphids. All the biologist needs in this case is the ability to reason about the process of genetic mutation and the way it works in populations.

Similarly, the worries about cross talk and unproductive arguments do not really have anything to do with the question of biological individuality. If biologists are clear about what counting methods they use and why, it will not cause problems if other scientists in other labs use different counting methods. As long as biologists communicate clearly about the conceptions of individuality they use in their own work, they can avoid engaging in useless debates and getting caught up in misplaced criticisms of alternative approaches.

Not only is it a mistake to construe the counting problem as a theoretical rather than practical matter, but resolving the theoretical debate about biological individuality will not address the features of the counting problem that generate Clarke's concerns. Biological individuality is an evolved character, and there will always be marginal cases of biological individuals, no matter what individuation criteria we adopt. A clear and unanimously accepted set of individuation criteria will never tell us exactly which objects are and are not biological individuals, because borderline individuals are an ineliminable feature of the biological world. The most we can ever hope for is agreement about individuation criteria, but it would be a mistake to think that such agreement entails agreement about individuals. As long as there is room to disagree about whether certain candidate individuals meet the individuation criteria well enough to be counted as individuals within the scope of a particular research project, the counting problem will remain as a challenge that biologists must confront. Since no solution to the question of biological individuality will make it easy to classify the borderline cases, we should not expect ending the individuality debate to end the counting problem.

Biologists have already developed the practical tools they need to deal with the counting problem. After all, scientists have been dealing with the challenges of divergent methodologies and fierce disagreement for quite some time. They can rely on good communication practices to avoid unproductive debates, and they can consider the particular goals and demands of their research projects to avoid making wrongheaded counting choices. In cases where it is genuinely unclear how they should count individuals, they can acknowledge the problem and compare the results of different empirical strategies in order to eliminate bad counting methods. Finally, there

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may be instances in which employing different counting methods makes no empirical difference at all, in which case the individuality debate is even farther removed from the counting problem. Though the counting problem is real, and Clarke is right to flag it as a potential obstacle to good empirical work, it is not the kind of problem to which the individuality debate can provide a remedy.

4.3.2. The Problem of the Paradigm. Unlike Clarke, Haber focuses on the process of choosing a research question, rather than that of answering a research question. He calls his concern the problem of the paradigm. The problem of the paradigm is our pretheoretical tendency to think of organisms as paradigm individuals. We know that not all biological individuals are organisms, but even trained biologists have a tendency to foreground organisms simply because they are the most familiar individuals. Haber worries that until we have the right conception of individuality, biologists will be guided by their pretheoretical, organism-based view of individuality even though it does not accurately represent the biological world. If they work from this misleading theoretical perspective, biologists are liable to overlook important questions and phenomena.

Haber offers the practice of referring to social insect colonies as superorganisms as an example of the problem of the paradigm. When we say that social insect colonies are superorganisms, we are recognizing that they, no less than single ants or humans, possess features that make them biological individuals in their own right. Unfortunately, we are often also claiming that the features that make colonies individuals are the same features that make organisms individuals. In the case of colonies, we often have in mind individuation criteria such as functional organization or division of labor. The problem here, according to Haber, is not that colonies are not individuals. Instead, the problem is that there is a tendency to decide that colonies are individuals based on their similarities to organisms. This is to assume that what makes organisms individuals is necessarily, rather than incidentally, due to their organismal characteristics. In making this assumption, we risk excluding some true individuals because we are using an inappropriate paradigm. Further, even if we do correctly identify individuals that are not organisms, we are liable to focus on their similarities to organisms, even if it is not by virtue of those similarities that these objects are individuals. In the case of social insect colonies, comparisons between colonies and paradigmatic organisms lead us to focus almost exclusively on selection processes in colonies while neglecting other important processes, such as developmental or metabolic or ecological ones.

Haber argues that we solve the problem of the paradigm by finding the appropriate conception of individuality. The appropriate conception will

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identify the general characteristics of individuality and allow biologists to work from that starting point, rather than relying on characteristics of organisms. There is a problem with this solution, however. In order to choose their particular research questions, biologists need more than a conception of individuality. They also need more specialized tools that enable them to gain epistemic access to phenomena that they do not yet understand. The problem of the paradigm arises in the context of employing these tools, and as a result, settling the individuality debate will not address the problem.

One of the important tools for studying poorly understood phenomena is analogical reasoning, or comparative thinking (see Gentner 1983; Nersessian 1992, 2008). Comparative thinking is especially crucial when the object of study is some unfamiliar individual. For example, it can be very useful to compare a controversial candidate individual such as a social insect colony to an organism. The reason is not that colonies are fundamentally like organisms, but rather that the questions that are fruitful when we ask them about organisms might also be fruitful when we ask them about colonies. Regardless of how similar organisms and colonies turn out to be, comparative thinking allows us to improve our epistemic access to the unfamiliar.

Of course, there are pitfalls associated with comparative thinking (Goodman 1972), and the problem of the paradigm is one of them. The solution is clearly not to avoid comparative thinking altogether (a point on which Haber surely agrees), so we need to deploy comparative thinking carefully. Settling the individuality debate is of no help here, because agreeing on individuation criteria does not tell us how best to compare two individuals. Even if we do resolve the individuality debate, biologists will still face the challenge of thinking comparatively while avoiding the problem of the paradigm.

Fortunately, the problem of the paradigm is like the counting problem in that it is a practical problem for which biologists have developed practical solutions. For example, the best social insect research does not study similarities between organisms and colonies by assuming that colonies have organismal features, but rather by identifying questions that have been fruitful when asked about organisms and then asking these same questions about colonies. In a recent paper, Johnson and Linksvayer (2010) look at the way organisms have developed anatomical and physiological systems to solve the functional problem of specialization of and communication between their parts. They reason that the functional problems facing multicellular organisms are structurally similar to those facing social insect colonies. Given this similarity, they then ask whether there is any analogous distinction between anatomy and physiology in social insect colonies. Johnson and Linksvayer avoid the problem of the paradigm because they (*a*) make a comparison with substantial theoretical grounding (Weisberg 2012) and (*b*) use the specified similarity to develop testable questions, rather than to make further, untested, assumptions. These methodological points offer general insights

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into how researchers have learned to sidestep the problem of the paradigm, regardless of their preferred conception of individuality.

5. Conclusion. Not only do these three defenses of the dependence account fail, but they also reveal a problem with the entire approach. Embedded in the dependence account is the idea of priority of the theoretical over the empirical. It requires that there be a theoretical resolution to the individuality debate in order for many areas of biology to progress. Priority in this sense implies that there are problems in scientific practice that have no solution other than the resolution of the individuality debate. I have examined two such problems and found that in both cases a resolution to the individuality debate is irrelevant to solving them. The counting problem and the problem of the paradigm have solutions that operate on an entirely different level than the individuality debate does. I suspect that other problems facing practicing biologists are similar: dealing with them requires coordination, communication, and clarity in response to a biological world that perpetually resists neat classification. Resolving theoretical debates does not alter this reality. As a result, there may be no problem of scientific practice to which resolving the individuality debate provides a solution.

As an alternative to the dependence account, we should accept the sensitivity account. It takes the relationship between the individuality debate and scientific practice seriously, but it resists the priority assumption. In addition to avoiding this dubious assumption, it has the advantage of promoting engagement with empirical biology. The best approach to better understanding biological individuality is to recognize the mutual dependence between empirical and theoretical biology and investigate them together.

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