Making Populations: Bounding Genes in Space and in Time

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At least below the level of species, biological populations are not mind-independent objects that scientists discover. Rather, biological populations are pragmatically constructed as objects of investigation according to the aims, interests, and values that inform particular research contexts. The relations among organisms that are constitutive of population-level phenomena (e.g., mating propensity, genealogy, and competition) occur as matters of degree and so give rise to statistically defined open-ended biological systems. These systems are rendered discrete units to satisfy practical needs and theoretical preferences associated with specific contexts of investigation. While it may be possible to defend a realist position regarding biological relations among organisms, biological populations are "made" when contextual features determine which kinds and degrees of relations to privilege over others, and so how to bound genes in space and time. Consequently, the objectivity of population-based approaches to species genome diversity cannot rest in the mind-independence of populations themselves.

1. Introduction. Theodosius Dobzhansky once said that population geneticists study genes and populations. Both genes and populations are assumed to be mind-independent objects.[1] Biological populations are re-

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1. When I say 'mind-independent' here, I do so only in a sense that refers to the minds of researchers. There are additional questions to address in species like us where conscious choice and symbolic representation influence mating patterns. I am preparing to deal with these questions elsewhere.

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ferred to by terms like 'Mendelian population,' 'deme,' and 'isolate.' The basic notion that characterizes these populations is that organisms that belong to the same population are more likely to mate and share genealogical ties with one another than they are to mate and share genealogical ties with organisms that belong to other populations. Biological populations are distinct from other populations that may be found in biomedical research—especially groups constituted in virtue of properties that individuals share, for example, women with the BRCA1 gene. This is because they are conceived of as ontological individuals, and not classes of individuals, as in the BRCA1 example.

In this paper, I challenge the assumption that biological populations exist as mind-independent objects whose properties and relations scientists discover. I argue instead that populations are "made." Populations are pragmatically and variably constituted in different sorts of investigations of species genome diversity. Genes become bounded in space and time in ways that fulfil aims, interests, and values associated with particular explanatory contexts. Population boundaries are not fixed but vary from one context of inquiry to another.

Although most examples in the paper involve *Homo sapiens,* a reflection of my research interests, the conclusions, I believe, apply to zoological populations as well, where the biological individuality of species and organisms can be viewed as relatively unproblematic, at least in contrast to subspecific populations. Biologists and philosophers of biology are well aware that biological individuality is more readily recognized in some cases than in others. In many of the species we humans tend to be best acquainted with, the individuality of organisms is not in question, but this is not true, say, of slime molds. Similarly, species definitions in terms of reproductive isolation accept that isolation develops gradually and that hybridization does occur. Difficulties arise with subspecific populations that, as open reproductive systems, lack the reproductive isolation that individualizes species populations. Population-based approaches in genetics nevertheless treat these as mind-independent objects, the basic ontological units of species genome diversity.

2. Populations: Real or Ideal? The term 'Mendelian population' was not always understood to refer to a real, in contrast to an ideal, object. The term dates back at least to Karl Pearson's 1904 paper where he establishes that Mendelian principles of inheritance are consistent with biometric properties of populations with the assumption of random mating. Pearson did not presume that Mendelian populations occur in nature. The Mendelian population was a model for which statistical predictions were made based on a set of theoretical assumptions, assumptions that Pearson

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himself did not suppose to be true given that he rejected Mendelism. Once Mendel's principles became widely accepted among geneticists, the term 'Mendelian population' continued to refer to ideal, rather than real, objects—for example, in Sewall Wright's 1931 paper "Evolution in Mendelian Populations." As the ideal objects of mathematical models, Mendelian populations could possess such unrealistic attributes as the infinite size and random mating that are assumed by Hardy-Weinberg equilibrium.

Even Ernst Mayr, more of a naturalist than a theoretician, expressed doubts in *Systematics and the Origin of Species* that populations actually exist in nature other than in exceptional cases where more-or-less discrete boundaries are present—for example, island populations in zoological species and isolates in humans:

> Normally the "population" is more or less an abstraction because there is a considerable interchange of individuals between neighboring populations, owing to the absence or incompleteness of physical barriers. Under ideal conditions a population consists of a small group of individuals clearly separated from other individuals of the species by a physical barrier. Examples of such isolated populations would be those on islands in the sea, or in oases of the desert, or on mountain tops, and the like. (1942, 24)

Around the same time, Dobzhansky, who conceived of races as breeding populations, referred to races as more abstract than species because they lack reproductive isolation. Hence, at least in the early 1940s, discreteness was an ontological criterion for both Mayr and Dobzhansky, and a property they believed populations to lack.

In 1950, however, Dobzhansky presented a realist definition of 'Mendelian population': "A Mendelian population is a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool" (1950a, 405). On Dobzhansky's definition, biological species are the largest and most inclusive Mendelian populations. Barriers to gene exchange, whether physical or social, structure species populations into subordinate units. Panmictic (randomly mating) units are the smallest Mendelian populations. In between panmictic units and species lie intermediate Mendelian populations, frequently referred to by such terms as 'subspecies,' 'races,' 'local populations,' and, in humans, 'ethnic groups.' On Dobzhansky's account, then, Mendelian populations are genuine biological units, discoverable in the natural world. But such units are rarely, if ever, discrete. This is because barriers to gene exchange, whether these are physical obstacles like oceans and mountains or social conventions like language and religion, are seldom complete.

In order to arrive at a realist definition of 'Mendelian population' by 1950, Dobzhansky needed to move away from discreteness as an onto-

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logical criterion. He had expressed earlier ambivalence about the significance of discreteness. In their popular book, *Heredity, Race, and Society,* Dunn and Dobzhansky argued that the arbitrariness frequently encountered in drawing racial distinctions does not mean that races do not exist:

> Do not conclude however that because the dividing lines between races are frequently arbitrary races are imaginary entities. By looking at a suburban landscape one can not always be sure where the city begins and the country ends, but it does not follow from this that the city exists only in imagination. Races exist regardless of whether we can easily define them or not. (1946, 110)

Dobzhansky's 1950 characterization of Mendelian populations as "reproductive communities" represents a significant conceptual shift away from "dividing lines" and boundaries. Ultimately, relations among organisms—for Dobzhansky, breeding and parental involvement in offspring; for David L. Hull (1965), genealogical ties; for Michael T. Ghiselin (1974), competitive interactions—replace discreteness as the criterion for the reality of biological populations. Such relations provide the glue, the spatial and temporal cohesion, to bind individual organisms together into population wholes.

Biological populations constituted by relations among organisms are statistically defined. On the breeding definition of populations, individuals belong to any number of populations where they may potentially find mates and the degree to which they belong to each of these varies depending on mating probabilities. On the genealogical definition of populations, individuals are always more or less related to one another. Although it is well recognized that populations are statistically defined, the implications tend to be downplayed. Consider these comments expressed by Dobzhansky:

> The probability that an individual taken from a given population will carry a given gene may be either greater or smaller than it would be for an individual from another population. . . . By and large, the more traits examined in an individual, . . . the more precisely can be inferred the part of the world from which these individuals came. (1950b, 116–117)

The assumption made here is that there is a single population to which any individual organism belongs, with probabilities involved only in the ability to discern which one. These probabilities are tied to the statistical distribution of genetic variability among populations and not to the statistical definition of populations themselves.

Yet, the relative boundaries of statistically defined populations mean that individual organisms are only more or less members of particular populations in the biological sense. It may be indeterminate whether a

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particular organism belongs to a given population and organisms may belong to more than one population at the same level of organization. It is an idealization to represent the porous nature of barriers among populations in terms of gene flow due to migration, a representation that assumes there is a unique population to which any organism belongs. If the concept of biological population picks out any objects in nature, it is unlikely that these will be discrete entities with well-defined boundaries and determinate, nonoverlapping parts.

Elliott Sober (1984, 157–159) nonetheless argues that populations, no less than organisms, are concrete individuals. He points to these analogous characteristics: organisms have physiological boundaries and populations have reproductive boundaries; as organisms and populations persist through time, their characteristics change, due to developmental or evolutionary processes, without compromising the integrity of the whole; populations are born by budding off from the parental unit, like some kinds of organisms; populations and organisms alike will cease to exist through the functional disintegration no less than the destruction of their component parts. Sober believes that populations vary in the degree to which they are individuals because, like organisms, their parts can be more and less functionally integrated. But he does not believe that the overlapping or sharing of parts, as happens with the occurrence of hybrid zones, threatens the ontological status of populations as individuals. This is analogous, he contends, to accepting that "Siamese twins" are two separate organisms and that the United States, France, England, and the Soviet Union shared political control of Berlin after World War II.

I am unconvinced by these examples. As political entities, Berlin, Britain, France, the Soviet Union, and the United States have reasonably well-defined boundaries, which biological populations usually lack. We recognize conjoined twins as two distinct individuals that share parts for a number of reasons, but these reasons, again, do not apply to biological populations. Conjoined twins are rare occurrences and, like cities and nation-states, the individuality of human organisms is generally not in doubt. In addition, the assumption that conjoined twins are two distinct individuals that share parts becomes less evident were the shared part to be a brain; this is because we privilege consciousness and do not treat all body parts as ontologically equivalent. At the species and organism levels, hybridization and conjoined twins do not present challenges to individuality because these are exceptions to what is generally the case. For biological populations below the species level, however, individuality is dubious, discreteness is rare, and no parts (organisms) are privileged.

One might interject to say that recognizing that biological populations are not discretely bounded objects but defined statistically need not lead us to impugn their reality. Recent work in metaphysics could provide a basis

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upon which to argue that populations are "vague objects," that the biological world is complicated and messy, and that the precision that is misleading us in the discussion thus far is introduced by language. The philosophical literature on vagueness deals with whether vagueness is linguistic, ideational, or ontic, that is, whether it is a feature of words, concepts, or objects. There is also the epistemological alternative that approaches vagueness by assuming that the world is perfectly precise but that we humans are limited in our cognitive ability to discern this precision. The dominant view seems to be that the world is precise and vagueness is introduced by language. Michael Tye, though, is prepared to defend the minority view that vague objects, like countries, mountains, deserts, and islands, really do exist.

For biological populations, the precision of the associated concepts is not in question; we can clearly delineate the abstract Mendelian populations of mathematical models. There is no basis either for assuming that biological populations are precise but that knowledge of their boundaries lies beyond our epistemic capacities; subspecific populations are open reproductive systems and not discretely bounded. Our concern, then, is ontic vagueness. On Tye's account (1990, 536), a biological population might be considered to be a vague object because (i) it has borderline spatiotemporal parts and (ii) it is indeterminate whether there are objects other than those that are parts, borderline parts, or nonparts of the object. Consider Tye's candidates for possible "vague objects": countries, mountains, deserts, and islands. From a biological perspective, island populations are as clear-cut an example of populations as there is, and yet these are rare. How vague can a "vague object" be and still be an object? For an ontology of biological populations as "vague objects" to be helpful, it must be possible to ascertain the population to which *most* organisms belong, even if it is difficult to determine where one population ends and another begins and impossible to discover the population to which *some* organisms belong. In other words, most parts (organisms) must belong to unique wholes (populations), despite the existence of borderline spatiotemporal parts (organisms which may or may not be counted as belonging to a given population).

Consequently, an ontology of biological populations as "vague objects" can be of only limited help. The approach shared by Dobzhansky, Hull, and Ghiselin, that treats relations among organisms as constitutive of populations, seems correct to me, at least in species where the individuality of organisms is relatively unproblematic. Patterns of relations among organisms give rise to higher-order structures, and, as a matter of historical contingency, these structures will be ephemeral, overlapping, or coherent to varying degrees. Sometimes, then, populations we could feasibly conceive as "vague objects" do come into (and pass from) existence and,

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on such occasions, the laws of population genetics "lie" a little bit less, in Nancy Cartwright's (1983) sense, than they usually do. Although this ontology casts organisms and their interrelations as more fundamental than populations, by portraying populations as emergent structures, features of importance to the holism of "population thinkers" such as group selection and frequency-dependent selection are accommodated. The relations singled out by Dobzhansky (mating propensity), Hull (genealogy), and Ghiselin (competition) are also recognized for their causal, not just constitutive, role in determining how properties are distributed from one generation to the next.[2]

If the appropriate ontology for species genome diversity treats organisms and their interrelations as basic and populations as emergent, at least in sexual species where the individuality of organisms is unproblematic, this challenges population-based approaches that assume that populations exist as mind-independent objects across all parts of the species' distribution, both geographical and historical. In the next section, I argue that populations are "made," that is, pragmatically constituted. Genes are bounded in space and time in ways that are determined not only by patterns of relations among organisms but by specific contexts of investigation.

3. "Making" Populations. If reproductive isolation defines species populations, it makes sense that subspecific populations, as open reproductive systems, increase in reality as they diverge and become increasingly isolated from one another. In fact, this was Dobzhansky's belief in the early 1940s when his ontological criterion for the reality of populations was discreteness. Yet, interestingly, scientists seem quite confident in the reality of panmictic units—the smallest breeding populations within species. The majority of human population geneticists and biological anthropologists, though they reject the race concept because of the arbitrariness of racial divisions, are prepared to divide the entire human species into more or less discrete panmictic units or demes despite the extensive continuities in breeding patterns and allelic distributions that exist. Biological anthropologist Jonathan Marks, for example, rejects the "typological" division of humans into a small number of discrete races because, circling the globe, one finds that traits are distributing continuously. He argues instead that it is the "small biopackages" called popu-

2. Philip Kitcher has defined species as "sets of organisms related to one another by complicated, biologically interesting relations" (1984, 309). I believe that Judith Crane (2002) is correct to point out that the contribution made by spatio-temporal relations among organisms (as parts) to the structure of the species (as whole) is lost in this representation. There is also the problem of the discreteness of sets which "fuzzy sets" overcome only to the extent that "vague objects" improve on an object ontology.

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lations, not races, that are the "real units of human diversity" (1995, 274, 116). Similarly, human population geneticist L. Luca Cavalli-Sforza treats panmictic populations as real but characterizes attempts to classify "clusters" of populations into races as a "futile exercise" (Cavalli-Sforza, Menozzi, and Piazza 1994, 19).

In this section, I argue that biological populations are not mind-independent objects discoverable by scientists. Rather, biological populations are pragmatically and variably constituted within specific contexts of scientific investigation. I discuss three areas of contention that arose during planning stages of the Human Genome Diversity Project (HGDP): choosing which populations to sample, securing informed consent from sampled subjects, and sampling strategy. All of these debates took place against a background that assumed the mind-independent reality of biological populations. I believe that a pragmatic account of populations better explains the sources of tension that divided parties to the controversies.

3.1. Choosing Populations. In October 1992, a planning meeting for the HGDP was held at Pennsylvania State University. The meeting brought various experts together to reach agreement on which populations would be sampled as part of the project (Roberts 1992). Embedded in the organizational aims of the meeting was the assumption that populations are real "discoverable" objects. Organizers recognized that negotiation would be necessary because different research questions and priorities would lead to the inclusion of different groups. This is not because they assumed that populations are constituted differently depending on what research questions are asked. It is simply because only a subset of all existing populations could be sampled and it was important to select those that would enable a range of questions to be addressed. The operative assumption was that there is a definitive collection of demes that exist in the world that is entirely independent of researchers' practical needs and theoretical interests. This assumption is mistaken. Asking different research questions results in different *populations,* not simply in a different *list* of populations. Populations are variably constituted in different contexts of investigation because different theoretical interests determine what particular sets of relations are privileged.

Population geneticists ask a wide range of questions, about genealogical relations, the adaptive values of particular alleles, mechanisms of evolutionary change, etc. Underlying these questions are realist assumptions about populations: that they are constituted by breeding relations; that they exist now, and have existed in the past, as (relatively) discrete units; that they have been shaped by a unique sequence of past events; that their future evolutionary behavior can be predicted. Yet, populations are con-

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stituted differently when different questions are asked. Take a researcher who wishes to predict what a particular population's gene pool will look like in the future given the population's current size, genetic composition, and breeding structure, and rates of mutation and migration. Now take another researcher who wishes to compare adaptive differences within the same population. For the first researcher, it does not matter if the current breeding population has multiple origins. But for the second researcher, it does. This researcher will consider the population to be "mixed" and will divide it into several populations on the basis of ancestral relations, perhaps even combining these with related populations in other parts of the world. Dynamic breeding units and genealogical units are not identical. Each kind of unit is constituted by ostensibly biological criteria, but there is no principled reason to prefer one set of criteria over the other. It depends on the question.

3.2. Group Consent. The plans of HGDP organizers to conduct a worldwide survey of genetic diversity that would collect DNA from individuals belonging to up to 500 indigenous populations soon encountered opposition from representatives of these groups. Scientists and bioethicists associated with the project responded with a human-subjects protocol that required researchers to obtain informed consent from groups as well as from individuals (Reardon 2002). Related discussions of group consent found in Eric T. Juengst (1998) and the 1997 National Research Council (NRC) report *Evaluating Human Genetic Diversity* assume the mind-independent existence of well-defined biological populations or demes. Juengst and the NRC report hold that human population geneticists should obtain informed consent from the groups as well as the individuals they study because these groups are socially defined and the results obtained will have implications for any member of the group. But group consent is seen as a temporary requirement because of the belief that, once adequate data on DNA differences are compiled, it will be possible to identify existing biological groups or demes based on patterns of these differences. When "technology to infer deme membership exists," the authors of the report write, it will not be necessary to "continue to rely on socially defined human groups as surrogates for human demes" (NRC 1997, 68). This assumes that demes are more-or-less discrete entities; otherwise, it would be impossible to "infer deme membership." I would argue instead that biological populations are pragmatically constituted *as* discrete objects in order to satisfy practical aims and theoretical preferences that are particular to specific contexts of investigation.[3]

3. For a different argument why a priori social and political categories of classification may not be expendable in human genome diversity research, see Gannett and Griesemer (2003a).

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Practically speaking, populations are named and delimited as discrete entities for methodological convenience so that resampling can take place. In Drosophila research the name of a canyon or a mountain range might be used. In human research, as the NRC report notes, investigators may rely on "socially defined groups" as "rough markers of human biologic lineages" (1997, 56). The mathematical machinery is also limited in its ability to deliver panmictic units through the detection of statistical differences in gene frequencies among groups because X^2 and Hardy-Weinberg tests assume large populations and only small populations are likely to be panmictic. So merely postulated barriers to gene exchange become reified as population boundaries; in humans, this means that wholly social boundaries are used to delimit these ostensibly biological objects.[4] Then, there is the simple problem of language. What Jean Hiernaux wrote in his critique of the race concept many decades ago can be easily extended to the concept of population: "there is no escaping it: if you put a label, be it a name, a letter or a number, on something, you make it discrete" (1964, 39–40).

Theoretically speaking, diverse aims and interests lead to the bounding of genes in populations. Evolutionists study changes that occur in the genetic composition of populations over time, the genealogical relations that exist among populations, and the ways in which populations causally interact with one another; all of these inquiries require that populations be treated as well-defined biological units. Merely to offer a genetic description of a population in terms of frequencies of various alleles, perhaps to make predictions about future evolutionary changes or hypothesize about past evolutionary history, assumes the existence of an entity with discernible boundaries and determinate parts. Similarly, because the theoretical populations of mathematical models are discrete, such models cannot be applied to actual populations unless these are assumed at least to approximate discreteness. Theoretical preferences also dictate whether statistically defined populations are to be rendered discrete. This has been demonstrated by the ways in which changing theoretical interests shaped the course of Dobzhansky's work on the natural populations of *Drosophila pseudoobscura*. The role played by random drift in determining the genetic characteristics of a population cannot be determined without an accurate estimation of population size. In contrast, assessing the role of selection

4. This is seen in Cavalli-Sforza, Menozzi, and Piazza's (1994) *The History and Geography of Human Genes*. Because the authors used already-published data to investigate genealogical relations among various human groups, they were faced with the task of ascertaining whether populations identified and sampled by other researchers were indeed panmictic units. Unable to rely on X^2 and Hardy-Weinberg tests to determine this, they ultimately decided to include data obtained from groups called "tribes" as the best approximation to demes.

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can be done with more qualitative methods. Dobzhansky, when interested in random drift as the major force of evolutionary change in *pseudo-obscura,* focused on small, geographically delineated groups. When his interests became focused on adaptive evolutionary change, group boundaries became less important (Gannett and Griesemer 2003b).

3.3. Grids and Clines. At the first HGDP planning meeting held at Stanford University in June 1991, a debate arose over what DNA sampling strategy would be best to use. Cavalli-Sforza proposed a population-based approach where populations deemed of particular scientific interest would be identified and DNA samples obtained from individuals belonging to these groups. Allan Wilson preferred to lay a geographic grid across the globe and to sample indigenous individuals found at intersections of the grid in order to avoid making perhaps unwarranted assumptions about the existence of populations (Roberts 1991). In the end, Cavalli-Sforza's population-based strategy prevailed. The 1997 NRC report on the HGDP agreed with this decision. The report concluded that nonpopulation-based sampling is unable to address many important scientific and clinical questions and yet does not minimize the ethical risks associated with population-based sampling because naming geographic locations suggests the identities of populations likely to have been sampled. It is indeed true that nonpopulation-based sampling cannot address many scientific and clinical questions. But the report incorrectly represents concerns about population-based sampling as ethical and nonscientific when it treats questions that require the apportionment of human genome diversity into intrapopulational and interpopulational components as theoretically valid. This takes the mind-independence of populations for granted. I would say instead that populations come into existence *because,* without them, scientists could not answer questions they deem important.

Implicated in the grid vs. population debate is a controversy over whether patterns of species genome diversity are best explained by adaptive clines and/or isolation by distance or by isolation in breeding groups.[5] In 1964, C. Loring Brace argued that, because of clinal variation, there can be no "typology of groups," even breeding populations. This extended Frank Livingstone's earlier claim: "There are no races, there are only clines" (1962, 279). Similarly, John H. Moore contends that the "human species is best considered as a fabric, not a mosaic. The boundaries of

5. Where environmental factors vary along a continuous gradient, traits that have arisen in adaptive response to these factors are likely to be distributed along a coincident gradient referred to as a 'cline' (Mayr 1942, 95). Similarly, in isolation by distance, distance alone can account for why a particular allele is found in one area of the species distribution and not another; it need not be due to the presence of isolating barriers, either physical or social (Wright 1943).

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human polities, ethnicities, marriage pools and language communities are, always and everywhere, very fuzzy'' (1996, 226). Moore favors a geographical approach to human genome diversity that investigates the spatial distribution of genes across the entire ''fabric'' of the species. This cline/isolation by distance challenge to population-based approaches appears to confront us with a realist choice: either the species is substructured into more-or-less discrete populations, Moore's ''mosaic'' ontology, or the species is composed of a mass of interacting and interrelated organisms, Moore's ''fabric'' ontology. Despite appearances, there are pragmatic factors at work. The methodological privileging of clines over populations is conceptually tied to the theoretical privileging of selection over migration or drift. It is no accident that when Brace made his ''no populations, only clines'' argument he believed that natural selection, not random drift, is responsible for human differentiation. It may not be that Wilson's preference for grid sampling reflects an a priori commitment to this theoretical extreme; he may have simply wished not to assume that populations exist where they do not. Still, the plan to sample only indigenous people at points of the grid shows that Wilson did not altogether eschew a population-based approach. Bounding individuals (and their genes) in one way rather than another makes some evolutionary narratives and explanations possible and others impossible. How boundaries are drawn depends on context, on what matters, and to whom.

4. Conclusion. Complicated tangles of webs of relations connect all parts of a species and these relations occur as a matter of degree. It is possible to view these relations in realist terms: for example, James R. Griesemer's (2000) work on units of reproduction focuses on the material overlap that occurs between parents and offspring. In this paper, I have argued that biological populations are pragmatically constituted according to aims, interests, and values that are particular to specific research contexts and wind up privileging some kinds and degrees of relations among organisms over others. Such choices are not wholly arbitrary. Relative to the practical and theoretical stakes of particular contexts of investigation, objective reasons can be supplied for a preference to investigate certain kinds and degrees of biological relations instead of others. Objectivity about biological populations does not rest in the existence of populations as mind-independent objects. This is an objectivity without objects.

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