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REGARDING THE CONFUSION BETWEEN THE POPULATION CONCEPT AND MAYR'S "POPULATION THINKING"

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ABSTRACT

Ernst Mayr said that one of Darwin's greatest contributions was to show scholars the way to population thinking, and to help them discard a mindset of typological thinking. Population thinking rejects a focus on a central representative type, and emphasizes the variation among individuals. However, Mayr's choice of terms has led to confusion, particularly among biologists who study natural populations. Both population thinking and the concept of a biological population were inspired by Darwin, and from Darwin the chain for both concepts runs through Francis Galton who introduced the statistical usage of "population" that appears in Mayr's population thinking. It was Galton's "population" that was modified by geneticists and biometricians in the early 20th century to refer to an interbreeding and evolving community of organisms. Under this meaning, a population is a biological entity and so paradoxically population thinking, which emphasizes variation at the expense of dwelling on entities, is usually not about populations. Mayr did not address the potential for misunderstanding, but for him the important part of the population concept was that the organisms within a population were variable, and so he probably thought there should not be confusion between population thinking and the concept of a population.

INTRODUCTION

THE GREAT biologist Ernst Mayr left his mark on several fields, not least at the interface of Darwinian history and philosophy. In considering Darwin's impact, Mayr developed his famous thesis that one of Darwin's greatest contributions was to cause a cognitive shift in the minds of scholars, a

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shift away from typological thinking and toward, what he called, population thinking (Mayr 1959, 1982a). According to this history, naturalists before Darwin viewed the differing organisms of a species as imperfect manifestations around a central Platonic type or ideal. Then, after coming to understand Darwin's theory and the evidence supporting it, biologists shrugged off this typological mindset and developed population thinking in which a species has no central type and in which the variation among organisms is not a kind of meaningless noise to be ignored, but rather the very raw material of natural selection and evolution. Importantly, this shift in thinking was not just for biologists, and Mayr argued that population thinking has helped to undermine typological tendencies in a wide variety of fields (Mayr 1988, 1995; Hull 1994). Mayr was correct about this broader impact, for the transition he described has indeed become recognized by economists, psychologists, and scholars in other social sciences (e.g., Buss 1984; Hodgson 2002; Mesoudi et al. 2006).

Population thinking has also been at the center of a common and basic confusion with another concept that emerged in the decades after Darwin, which is the biological concept of a population. This idea of an interbreeding community of organisms that share in an evolutionary process was developed in the early 20th century (see below), and it has become a centerpiece of the life sciences. A biological population has its own history; it can change in many ways, including going extinct; and it is a valid focus for scientific investigation. The population concept is frequently joined with other fundamental biological concepts (including gene, cell, and organism) to form a basic hierarchical scaffold for organizing knowledge in the life sciences (Gerard and Stevens 1958; Lewontin 1970; Wilson 1977; Bonner 1988; Hull 1988). Contemporary biologists who study evolutionary processes in real time as they occur out in nature often identify themselves as population biologists. For them, a population may be vaguely defined, but nevertheless it is where the action is at—it is an interbreeding unit of evolution, a gene pool wherein natural selection and other evolutionary forces play out. And yet, paradoxically, population thinking and the concept of a population, both of which were inspired by Darwin, are not directly related and are in some ways in conflict with one another.

What Exactly Is Population Thinking?

Mayr first wrote about biologists' "thinking" change in 1955 and then more fully in 1959 with the claim that Plato was the inspiration for pre-Darwinian typological thinking (Mayr 1955, 1959). Those papers roughly coincided with a paper by Arthur Cain who claimed that Linnaeus had drawn heavily from Aristotle, including not only the words "genus" and "species," but also Aristotle's idea of essences (Cain 1958). Both Mayr and Cain concluded that the views on species of the Greek-inspired pre-Darwinians were incorrect and that their respective appreciations of nature suffered for their reliance on a Platonic *eidos* (in Mayr's critique) and on Aristotelian logic (in Cain's critique). Later, Hull (1965) explicitly introduced to this context the term "essentialist," which was by that time pejorative thanks to Popper (1944), to describe pre-Darwinian thought. In this view, the key components of typological thought are that species have essences that exist and that the purpose of taxonomic science is to discover these essences. Finally, Mayr adopted the label "essentialism" as a synonym for what he had called "typological thinking" (Winsor 2006a). It is also noteworthy that the first half of Mayr's thesis, the essentialist part of the transition story, has come under focused questioning by historians (Sober 1980; Sloan 1985; Greene 1992; Amundson 1998; Winsor 2001, 2006b; Stevens 2002; Müller-Wille 2007).

In his earliest full explanation of the transition away from typological thinking, Mayr wrote that for the population thinker:

> All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. Averages are merely

> statistical abstractions, only the individuals of which the populations are composed have reality (Mayr 1959:2).

Mayr emphasized that population thinking applies not just to organisms but also to "organic phenomena," and unless the reader misses the point, he repeats himself to say that populations are formed by "any kind of organic entities." Decades later in his 1982 book, he laid out the generality of his idea very clearly:

> This uniqueness is true not only for individuals but even for stages in the life cycle of any individual, and for aggregations of individuals whether they be demes, species, or plant and animal associations. Considering the large number of genes that are either turned on or turned off in a given cell, it is quite possible that not even any two cells in the body are completely identical. This uniqueness of biological individuals means that we must approach groups of biological entities in a very different spirit from the way we deal with groups of identical inorganic entities. This is the basic meaning of population thinking (Mayr 1982a:46–47).

In population thinking, a population is a group of biological entities, and in this passage Mayr specifically uses the words "deme" and "species" to make clear that by "population thinking" he is referring to groups of these kinds of things, or any other kind of biological thing. This is noteworthy because "deme" is in many contexts a pretty good synonym for "population," and yet Mayr makes it perfectly clear that such things are only a subset of what he is talking about. Yes, a deme could be an entity within Mayr's "population thinking," and one could have a group of demes (i.e., a population of demes, in Mayr's meaning of "population"), but it is just as consistent with Mayr's meaning to consider a population of cells or kidneys.

By engaging in population thinking one focuses on the variation among entities, and the larger group, the population, is an abstraction. The individual varying entities are real, but Mayr specifically avoided invoking existence for populations. Again, from his 1959 paper, "only the individuals of which the populations are composed have reality" (p. 2).

Misunderstanding Population Thinking

Mayr explained population thinking several times in print with a meaning that was consistent over decades (Mayr 1959, 1963, 1968, 1976, 1980, 1982b). But despite this repetition and consistency, many biologists refer to population thinking as if it is about the modern biological concept of a population. Today it is quite common for biologists and others to identify with the idea that populations are the units of evolution—but then to incorrectly identify this as the "population thinking" that Mayr wrote about:

> Population thinking rejects the idea that each species has a natural type (as the earlier essentialist view had assumed), and instead sees every species as a varying population of interbreeding individuals (O'Hara 1997:323).

> This long-term perspective is based on 'population thinking,' which defines populations as reproductively isolated and self-sustaining groups of animals within particular geographic areas (Bottom et al. 2005:22).

> [T]he outstanding conceptual revolution that has occurred in physical anthropology is the replacement of typological thinking by population thinking'. Nowadays the physical anthropology student . . . is made continuously aware that the units of evolutionary change are populations (Harrison 1967:29).

> The scientific theory of biological populations originated with Darwin and his 'population thinking' (*sensu* Mayr 1959)—population is the unit of evolution (Haila and Järvinen 1982:263).

> Remember that the essential feature of Darwin's theory of evolution is population thinking. Species are populations of individuals that carry a pool of genetically acquired information through time (Richerson and Boyd 2005:59).

All of these examples cite Mayr but then use "population thinking" as if it refers to thinking in terms of populations as evolving entities. Mayr's own precise explanation of population thinking, repeated many times, is not about biological populations, and it conflicts with the way each of these examples invoke the existence of populations. Under

Mayr's meaning, the center of the investigator's focus is on variation, and the reality of the aggregate (i.e., the population) is rejected in contrast to the reality of the varying entities. But under the modern biological meaning of population, the centerpiece is a real evolving dynamic entity.

Historians and philosophers have sometimes commented on the conflict between the two meanings. Sober (1980) highlighted the potential for confusion, and noted that Mayr's insistence on individual reality and the rejection of population reality, could be interpreted as meaning that "much of population biology has its head in the clouds" (Sober 1980:352). Historian Grene (1990) tried to connect the two different meanings and expressed puzzlement:

> Now if populations are the units of evolution, and populations are simply aggregates of particulars, in no way to be placed into types or judged in accordance with archetypes or essences, it seems to follow that there are no natures (p. 238).

In another example, philosopher Walsh questioned Mayr's invocation of "population thinking" and said that

> the basic unit of organisation should not be seen as the population but the individual. Individual thinking—not population thinking—is crucial to any understanding of adaptation (Walsh 2000:151).

Paradoxically, Walsh and Mayr agree, but Walsh misunderstood Mayr's usage of "population thinking" and concluded that they disagree.

Misunderstanding of Mayr's meaning, and attribution of an incorrect meaning of population thinking to Darwin, has at times distorted our understanding of how Darwin's theory has shaped our thinking. Consider Sinclair and Solemdal's (1988) history of population thinking in fisheries biology. They say that

> [t]he development of population thinking involved the shift from the species to the population as the appropriate unit of study for many ecological questions (p. 190).

But Mayr's population thinking did not mean using "population" to refer to a part of a species. Mayr was using "population" in an essentially statistical sense, i.e., that which is represented by a sample of individuals. The story that Sinclair and Solemdal tell is of how Friedrich Heincke set out in 1875 to help resolve a bitter debate among British and northern European ichthyologists over variation in herring stocks. Over a period of 25 years, Heincke applied careful statistical analyses of herring variation and discovered that the single herring species actually included multiple varieties distinguishable on the basis of morphological variation. But according to Sinclair and Solemdal, the "population thinking" lesson is that Heincke and others associated with the herring fishery came to appreciate the reality of the varieties (i.e., populations) that Heincke had discovered. This was indeed one of his lessons, but it is not the population thinking part of what Heincke did. This is because in Mayr's meaning of "population thinking," reality belongs to the individuals being studied (i.e., Heincke's individual fish) not to the populations from which they come. Heincke's classic work may have been an inspiration for the idea that populations within species are real entities (Sinclair and Solemdal 1988), but again that is not what Mayr meant by "population thinking."

Looking For the Roots of the Population Concept and Population Thinking in Darwin's Writings

In Darwin's time, the usual meaning of the word "population" was that of Malthus (*An Essay on the Principle of Population,* 1798) in reference to the number of individuals, as exemplified in an early dictionary: "[t]he state of a country with respect to the numbers of people" (Johnson 1812:486). Malthus's ideas played a key role in Darwin's development of his theory of evolution by natural selection, and so we might wonder just how Darwin used "population." With the aid of online search engines it is easy to find that Darwin never actually used "population" or "population thinking" in any of the various editions of *On the Origin of Species.* Searches of his other writings reveal that he occasionally used "population" to refer to a multitude of people or organisms (consistent with Malthus's usage), but not necessarily by species and not at all in reference to interbreeding (e.g., several times he used the construction "animal population"). Nor did Darwin use terms that we would recognize as a synonym for anything that a modern population biologist might recognize as their subject of study. He did use "race" and "variety," but in reference to types of organisms within species. He also frequently used "community," but very broadly (e.g., "community of language," "community of species," and "community of descent"). Moving beyond Darwin's choice of individual words, I have not been able to find that Darwin ever articulated any idea that much resembles the modern population concept of an interbreeding community of organisms that exists as an evolving entity.

Mayr gave Darwin full credit for causing the transition away from typological thinking and to population thinking. Darwin did of course reject fixed species and he clearly articulated the evolutionary role of variation within species. Regardless of just how essentialist his contemporaries were, they did receive from Darwin the idea that the seeds for adaptations and for new species lie in the variation that occurs among organisms within species. However, Darwin did not write about variation with the kind of abstract and existential language that Mayr used in the many times that he explained the meaning of "population thinking." For that matter, Mayr's writings on the existence of individuals, and not of aggregates, seem to draw upon 20th-century debates over nominalism (Mayr 1969).

It is perhaps illuminating that when Mayr wrote a new index for *On the Origin of Species* (Darwin [1859] 1964) he inserted a heading for "population thinking" and then cited just two of Darwin's pages under that heading. Page 212 describes variation among bird nests within species. Page 459 is the beginning of the summary chapter, and Darwin succinctly emphasized the role of slight variations in the evolutionary process. In short, Darwin did not provide us with any text that directly resembles Mayr's explanation of population thinking. Darwin certainly did emphasize the importance of variation and this does hold center place in Mayr's articulation of population thinking. However, Mayr went further by adding a significant and fairly precise philosophical component to the idea. Mayr was criticized for his highly synthetic and progressive approach to history (e.g., Bynum 1985); to which he responded by embracing those charges and vigorously defending his methodology (Mayr 1990).

Francis Galton and the Statistical Meaning of "Population"

Sober observed that the emergence of "population thinking," as defined by Mayr, actually involved an initial stage of statistical thinking that was part of the methodology developed by Francis Galton (Sober 1980). Galton, the pioneer of the statistical study of inheritance, appears to have been the first to articulate the investigator's abstract statistical point of view and to use "population" in this context. At that time, the usual meaning of the word was that of Malthus (1798), and of Darwin in his letters. Galton departed from this and took on the approach of defining his own population for the purposes of an investigation. In *Hereditary Genius*, the text focuses on just one specific subset of the citizens of a nation, that being the men of Great Britain (Galton 1869). In *Natural Inheritance,* Galton was strict about how he used the term, defining it as not more than "a unit of study," albeit in practice he always used it with regards to some selected members of a single species (Galton 1889).

A paradox of statistical thinking, and of using "population" in the abstract sense of Galton (and as Mayr meant by population thinking) is that once you start to conduct a study then, regardless of what makes up the target population, that population tends to be reified and to be referred to with a connotation of some reality (e.g., rhetorically, "who would study something that did not exist?"). Thus, it is possible to read Galton and to suppose that because he is referring to populations and to studying them, that he also makes some existential commitment. But if that were true then we might expect to also find that he wrote about the things that populations do, and yet this kind of language does not appear in Galton's writings, at least in *Hereditary Genius* and *Natural Inheritance.* In neither of these works did Galton use "population" to mean anything like an interbreeding community. Rather, he consistently used it to refer simply to the group of individuals under investigation.

In Galton, rather than Darwin, we find a historical figure who articulated a usage of "population" that is close to Mayr's meaning for "population thinking." For Galton in his major works, a population was a necessary tool of the investigator; what mattered was the variation, and "population" was required in order to refer to the aggregated groupings of those individuals that varied. Philosophically and statistically this closely resembles Mayr's idea of population thinking.

To what extent were Galton's mathematical studies of variation and inheritance inspired by Darwin's book? Galton and Darwin shared a grandfather in Erasmus Darwin, and Galton later wrote that when his cousin's book came out he "devoured its contents and assimilated them as fast as they were devoured" (Galton 1908:288). Apparently, Darwin's work fed into a long-standing interest on Galton's part:

> I was encouraged by the new views to pursue many inquiries which had long interested me, and which clustered around the central topics of Heredity (Galton 1908:288).

So it seems fair to say that Galton's population thinking was indeed strongly, if not entirely, inspired by Darwin (Hilts 1973).

Early References to Interbreeding Units

In the sixth edition of *On the Origin of Species* published in 1872, Darwin cited his debate with Moritz Wagner over the role that interbreeding could play in the prevention of species formation. Wagner had argued that interbreeding could prevent a single species from diverging into two in the absence of geographic barriers (Wagner 1873), whereas for Darwin the lack of such barriers was a basic component of his "principle of divergence." In the years following, the role of free interbreeding or "free intercrossing," in the evolutionary process came under increasing scrutiny (Romanes 1874, 1897; MacLaren 1876). The language in these contexts used "forms," "varieties," "races," or "species," for example:

> the Reviewer does not seem to estimate at its full amount the influence of free intercrossing in retarding changes in races (MacLaren 1876:141).

The earliest full articulation that I could find and that directly connects interbreeding to the idea of an evolutionary unit, belongs to Edward Poulton, the prominent naturalist and biographer of Darwin. Poulton was ahead of his time in some important ways (he coined the words "sympatry" and "sympatric") and he clearly grasped the modern conception of populations as real evolving entities, when he wrote

> [t]he individuals of an interbreeding community form a biological whole, in which selection inevitably keeps up a high standard of mutual compatibility (Poulton 1903:105).

It is noteworthy that Poulton succinctly captures the biological concept of a population and that he did not use the word "population." A few years later, Orator F. Cook expressed the same idea, and as with Poulton's writings, Cook's book made no use of "population," although he did use "species":

> Another cause of evolution is free interbreeding among the members of a species to maintain a broad network of descent. A species is an evolutionary unit because its members travel together along the path of development. Unless new characters were distributed through the species by broad interbreeding there would be no such evolution as that shown in nature (Cook 1908:22).

Clearly by the early 20th century some naturalists where making use of the idea, which later became strongly associated among biologists with the word "population," but were doing so without using that word.

The Rise of "Population" Following the Rediscovery of Mendel's Laws

The trigger for the next step in the evolution of "population," on its way to meaning a real interbreeding and evolving entity, seems to have been the rediscovery of Mendel's laws of inheritance in 1900 by Correns, de

Vries, and von Tschermak-Seysenegg. In the confusion over what those laws meant for inheritance and for evolution, Wilhelm Johannsen played an important role by defining key terms such as "genotype" and "phenotype" (Johannsen 1903a) and "gene" (Johannsen 1905). Johannsen also adopted Galton's definition of "population" (i.e., a unit of study), and wrote how it could be a useful term to apply to a group of related organisms under investigation: "A race, a people, a stock of any kind—let us call it from now on a 'population'" (Johannsen 1903b:174). He also imagined the idea of random mating within a population:

> In a population where the choice of mates is more or less free—as in human society—or where entirely pure random mating or fertilization occurs, as is the case with many animals and with cross-pollinated plants (Johannsen 1903b:178).

Johannsen's original work defining "population" was in Danish, but that same year a German translation appeared, as did a commentary in English (Yule 1903) and Johannsen's work quickly became very well known in the young field of genetics (Provine 1971). Interestingly, Mayr, in his 1982 history, was dismissive of Johannsen for "losing the very meaning of 'population'" by specifying a narrow definition (Mayr 1982a:41). But Johannsen was just codifying a usage he received from Galton and from Karl Pearson, and it seems the case that in 1903 there did not exist any other usage of "population" among those inquiring of evolution. Mayr's complaint makes sense in so far as Johannsen's meaning departs from Galton's narrow usage, but there does not appear to have existed a broader usage of the term by biologists at that time.

In 1904, Pearson, the student and biographer of Francis Galton and the leading biometrician of the age, wrote what may have been the first paper that explicitly used "population" in a model of Mendelian inheritance. Over the previous decade, Pearson had been developing mathematical models of evolution that drew upon Galton's work on inheritance, but without the benefit of Mendel's theory (Pearson 1894, 1895). In those papers, Pearson used "population" as Galton had and as Johannsen later did. Then, in this seminal paper from 1904, Pearson articulated in words and mathematics the idea of a Mendelian population in which Mendel's rules apply and within which there is "random cross fertilisation" (Pearson 1904:60). Pearson's idea was a mathematical one, yet even as such a Mendelian population is clearly an entity that is enjoined by the intermingling of genes.

For the early geneticists, the idea of a random mating population was a theoretical breakthrough allowed them to envision what Mendel's laws might mean for the frequencies of inherited traits in nature, outside of the laboratory and garden. And yet to articulate the idea was to also imply some sort of entity within which random mating occurred. Although his paper was not mathematical, Udny Yule was the first to use the idea of random mating to consider the relationship between gamete frequencies and genotype frequencies for a locus with two alleles (Provine 1971):

> what, exactly, happens if the two races *A* and *a* are left to themselves to inter-cross freely *as if they were one race*? (Yule 1902:225).

Castle (1903) and then Pearson (1904) were the first to develop the mathematics that showed the relationship between genotype frequencies and gamete frequencies under random mating, followed by Weinberg (1908) and, most accessibly of them all, by Hardy (1908). From there the theoretical idea of an entity that is a random mating population went on to become a lynchpin of the new field of population genetics (Fisher 1930; Wright 1931; Provine 1971).

The record of Theodosius Dobzhansky's usage of "population" is revealing because of how influential he was to biologists, including Mayr, and because it reflects the transition from the idea of an abstract unit of study to an idea of a real entity in nature (Gannett 2003). In his first papers written after arriving in the United States, he used "population" in much the way that Johannsen proposed to refer to a grouping of genetic strains (Dobzhansky 1927, 1930a,b). But just a few years later, in his first papers on the distribution of variation in nature, he was using "population" with seemingly more existential commitment; for example, writing about the evolutionary differences of different populations and using the idea of a panmictic population (Dobzhansky 1933, 1935a,b). A kind of capstone to the conceptual transition from populations as abstractions to being real evolving things comes in 1950 when Dobzhansky revisited "Mendelian population." The term had come in to wide usage among population geneticists since Pearson (1904), however, Dobzhansky defined it as "*a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool*" (1950:405). For Dobzhansky at this time, Mendelian populations really did exist out in nature (Gannett 2003), whereas for Pearson when he coined the term in 1904, they were a mathematical idea (Pearson 1904). Importantly, Dobzhansky also recognized the distinction Mayr was making with his articulation of "population thinking." In a book chapter from 1967, Dobzhansky begins with a philosophical preamble in which he repeats with precision Mayr's meaning for population thinking and then later in the chapter he turns to using "population" more broadly in reference to evolving entities (Dobzhansky 1967).

The Discovery of Random Mating Populations

It is interesting to ask of the extent to which the idea of a random mating population actually needed empirical support in order to be found useful. The concept of a biological population became very popular in the 20th century, but it has often been used quite loosely and it seems to serve as a conceptual crutch—a necessary idea, but one that in specific contexts is often used without precision or without empirical support (Millstein 2009). At least part of the vagueness stems from empirical practicalities. Populations of the same species need not be distinct from one another, and they can be difficult to study. Until recently, populations have been difficult to identify on strictly genetic grounds, so investigators have often resorted to identifying them in geographic terms suggesting, but often without actually knowing, that the organisms in a geographic region constitute a population in some genetic sense.

In fact none of the early articulations of the idea that were found in the course of this study, including those by naturalists Poulton and Cook, by geneticists Johannsen and Castle, and by biometricians Yule and Pearson, drew in any direct way upon empirical observations to bolster the idea of an interbreeding unit, and none addressed whether there actually exist such things as random mating populations. It was as if the theoretical idea was so useful that it could stand on its own for some time, with little reference to what actually occurs in nature.

Eventually of course the idea did come to be very widely used in empirical contexts. One of the most important consequences of Pearson's mathematical idea of a Mendelian population was that it opened the door for biologists to use genetics to quantify the departure from random mating out in nature. In principle, all that was needed to identify populations genetically was a trait that exhibited countable genotypic types in nature; although in fact such variation was very difficult to come by outside of the laboratory for a long period of time after the rediscovery of Mendel's laws (Lewontin 1974). The earliest papers that I could find that connected allele and genotype frequencies in nature, using the idea of random mating, are by Geroud (1923) on wing color in *Colias* butterflies and by Bernstein (1924, 1925; see Crow 1993) for the study of ABO blood group inheritance in humans. The earliest report of Hardy-Weinberg equilibrium for *Drosophila* chromosomal inversions was by Dobzhansky and Queal (1938).

Why Did Mayr Choose "Population Thinking"?

Why did Mayr create a term specifically to draw attention to scholars' shifting away from a preoccupation with entities, and use as part of that term a word that had recently come into wide usage to mean a kind of biological entity? The choice of "population" seems odd, particularly considering that an alternative such as "individual thinking" (Walsh 2000) or "variation thinking" (a suggestion from Dan Dykhuizen) would probably have served Mayr's meaning without causing confusion with the population concept. However, I have been unable to find in Mayr's published books and papers that he ever wrote directly about the confusion between these two versions of population thinking.

In at least two ways there should be no confusion. First, one can certainly apply population thinking to biological populations (i.e., focusing on the individuality of, and variation among, populations). Recall that Mayr used "deme" as a specific example of a kind of individual that can the focus of population thinking (Mayr 1982a). But in this sense a population is just an example of a one kind of entity that may vary, and so this seems an unsatisfactory justification for the label "population thinking."

Second, and more importantly for understanding Mayr, one can use "population" with the statistician's meaning as Galton did. Mayr certainly did write as if channeling Galton's use of "population" when he explained population thinking; and Mayr appreciated Galton's historical role in the rise of population thinking:

> Francis Galton was perhaps the first to realize fully that the mean value of variable biological populations is a construct (Mayr 1982a:47).

> He was a strong proponent of population thinking, appreciating the uniqueness of the individual more clearly than any of his contemporaries (Mayr 1982a:697).

In the 1940s and 1950s, when Mayr was first articulating the story of the transition from typological to population thinking, his concept of a population was primarily of a sample of varying individuals. In his 1942 book, he wrote of the population as a taxonomic unit below that of the species:

> The population or rather an adequate sample of it, the 'series' of the museum worker, has become the basic taxonomic unit (Mayr 1942:7).

Later he described the growing use of the idea of a population in systematics, and of what he described as a "population concept," the idea that a species is composed of variable populations (Mayr et al. 1953:15). By itself, "variable populations" is ambiguous because it could mean that populations vary, or that a population includes varying individuals, but earlier in that same source Mayr emphasized the importance of the variation among individuals within populations:

> The typological concept of the species, which was already shaky in the preceding period, was abandoned and replaced by a dynamic, polytypic concept. Interest reverted to the fauna of local areas and to the study of variation within populations and the slight differences between adjacent populations (Mayr et al. 1953:9-11).

Therefore, it seems that the most likely reason that Mayr did not address the potential for confusion is that he did not think there was cause for confusion. Mayr's own primary concept of a population was that it is the container of the variation that is found among organisms in a species. With this focus on variation as the key part of the population concept, rather than the idea of a population as a kind of evolutionary entity (as others had emphasized), Mayr did not find conflict between population thinking and the concept of a population. Mayr was certainly fully aware of the idea of a population as a kind of evolutionary unit, as we see, for example, in Chapter 7 (The Population, Its Variation and Genetics) in his 1963 volume. But even in these pages, Mayr writes as if the population is noteworthy mostly as the place within which organisms are variable.

Summary

Darwin developed a tremendously successful theory in which species do not exist as types and in which variation within species is the raw material for adaptation and speciation. So to the extent that population thinking means appreciating the importance of variation at the expense of typological thought, Darwin was indeed the great teacher of population thinking. This emphasis on variation is the kernel of Mayr's population thinking. However, he also articulated a fuller more complex meaning of population thinking that has often been confused with the biological concept of a population that emerged in the early parts of the 20th century.

- Mayr's meaning for "population thinking" was highly synthetic and included statistical and philosophical language for which it is hard to find counterparts in Darwin's writings. In particular, Mayr invoked an ontological component to "population thinking" in which individuals and their variation are real, but the population is an abstraction.

- Darwin rarely used "population," and never did so with meanings having anything to do with variation and evolution. "Population" first appeared in the context of variation and inheritance when Francis Galton adopted it to refer to the collection of individuals under investigation.

- The idea of a random mating unit of evolution—what would come to be called a population—emerged in the early 20th century among naturalists. However, they did not at first use the word "population." Simultaneously, geneticists and biometricians, who were inspired by Galton and who were considering the implications of Mendel's laws on variation in nature, began to use "population" in an abstract or mathematical sense to refer to units of randomly mating organisms. Thereafter, in a time period that is coincident with the modern evolutionary synthesis (Mayr and Provine 1980), the term came into wide usage among both empirical and theoretical population geneticists.

- The idea of a population as an evolutionary unit is often mistakenly cited as Mayr's population thinking. In fact the two ideas share little in common, although they have an interesting historical connection through Galton, who used "population" in a way that is quite consistent with Mayr's population thinking and who also inspired the early geneticists and biometricians.

- Mayr thought primarily in terms of the population as a holder of variation, as a taxonomic level below the species within which organisms are variable. Under this viewpoint, the study of a population means studying the variation of the organisms within it, rather than studying the population per se. So Mayr probably did not think there was much cause for confusion between population thinking and the biological concept of a population.

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