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Chapter 14

Population

Kevin M. Kelly

INTRODUCTION

Like other concepts encountered in this volume, **population** has a variety of meanings (e.g., demographic, Malthusian, ecological, genetic, statistical, evolutionary, Darwinian). For example, statisticians define a population as the entire set of items or measures of interest. Demographic uses of the term focus on individuals circumscribed by geopolitical boundaries (Howell 1975: 17–18; Kertzer and Fricke 1997; Levy and Lemeshow 1999). Similarly, population ecologists use the term to describe the aggregated members of a species within some defined area (e.g., Andrewartha 1971: 10; Sutherland 1996: 1–4). Population biologists (e.g., Hastings 1997: 1) define a population as "a group of individuals of the same species that have a high probability of interacting with each other." Population geneticists restrict the definition further, identifying a population as a group of interbreeding organisms of the same species (Futuyma 1997; Hanski 1999).

Underlying all of these manifestations is the fundamental notion of the population as a "defined collection." Grouped as populations, individuals (and items) exhibit collective properties (e.g., density, size, age structure, a life history, a distribution in time and space, gene frequencies). Populations can be of any size and although the elements need not be identical, they must share at least one measurable attribute. The presence (or absence) of a single attribute is the simplest form of specification. The variables used to identify population membership may be interval (e.g., weight, birth order, antiquity), categorical (e.g., gender, location, language, presence/absence), ordinal (e.g., more/less, older/younger) or ratio (e.g, age, length) (see LeCompte and Schensul, 1999a: 115–119; Sokal and Rohlf 1981: 10–

11, for brief discussions of variable types). These attributes identify who or what are the designated members of the population in question and should, by inference, also indicate the features of the population that are of particulate interest.

In anthropology and archaeology, for example, populations of interest have been defined as the individuals living in a particular village (e.g., Durham 1991; Neel and Weiss 1975; Welsch et al. 1992); the speakers of a particular language (e.g., Howell 1979; Kelly 1990); the members of a specific religious sect (e.g., Glass 1953); the members of a socially recognized ethnic minority (e.g., Madrigal et al. 2001); and the skeletal remains from certain sites or locales (e.g., Weiss 1973). In addition, populations have been inferred from the distributions of certain kinds of artifacts (e.g., Bar-Yosef and Kuhn 1999; Kirch 1997); the genes of living people (e.g., Kayser et al. 2000); ancient DNA (e.g., Kolman and Tuross 2000); ecosystems having certain definable characteristics (e.g., Clark and Kelly 1993); and even on the basis of single fossil skulls (e.g., Leakey 1959). Each of these examples is a "defined collection." However, none of these designated populations is inherently or necessarily a Darwinian population.

HISTORY

As we consider what it means to say that a "population" is a Darwinian population, it is important to remember that evolution—what Darwin called "descent with modification"—had been recognized as a historical process long before Darwin. More than a century earlier, Buffon (1749) argued that species change in response to their environment and he suggested that such change comes about as a consequence of natural processes rather than by divine intervention. Similarly, Charles Darwin's grandfather, Erasmus Darwin (1794–1796), was aware that members of a species both change through time and compete for resources. Still better known are the writings of Jean-Baptiste Lamarck (1809, 1815), who suggested that species adapt to changing environments by use and disuse of organs. According to Lamarck, organ systems develop in response to wants and needs of the organism. Thus, in Lamarck's view, evolution occurs because attributes acquired by parents are passed on to their offspring.

Before the works of these philosopher naturalists, species were not only thought to be immutable, but it was also believed that every organism possesses all of the qualities and conditions necessary to be a member of its species. Mayr (1991) has labeled this extreme position **typological essentialism**, since according to this view, every species—seen in an Aristotelian manner—has its own "essence," and how far the individuals in any given species may have deviated from this defining essence is seen as unimportant (see, e.g., Sober 1992: 247–278).

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win and Alfred Russel Wallace (1855, 1864) were predicated on this earlier recognition that intraspecific variation exists and change occurs. Lamarck and his contemporaries, for example, had correctly perceived the role of the environment in evolutionary change. However, they failed to produce a satisfactory explanation for how evolutionary change takes place. What Darwin (and Wallace) contributed was a convincing evolutionary mechanism, natural selection.

Darwin's notion of population as well as his inspiration for the idea of natural selection came from Malthus (1798). In *An Essay on the Principle of Population*, Malthus (1798) explains why the size of an animal population may remain stable over time. In nature, individuals tend to aggregate with other members of their species in order to exploit resources and to procreate. Malthus, an economist, observed that although the numbers of adult animals may remain more or less constant, many more offspring are born to these animals than reach maturity. He concluded that high infant mortality prevents most of their offspring from reaching adulthood. Malthus suggested that humans, like animals, are capable of overproducing, and he observed that poverty and famine are natural outcomes of unchecked population growth.

Charles Darwin saw the implications of Malthus' observations for his own work. Darwin knew from Malthus (1798) that under favorable environmental conditions, most offspring will survive, and consequently, the number of individuals in a population tends to increase geometrically. Also drawing from Malthus, Darwin recognized that anything in the natural environment that works to check population growth thus limits the biological variability of populations. From these observations, Darwin concluded that most offspring die as a result of a "struggle for survival."

At the same time, Darwin recognized from his own careful and extensive observations that individual physical variations can be observed within virtually every plant and animal species. These differences—however minor they may seem to be—are real. Moreover, although Darwin was uncertain how the environment could influence the development of biological variation, he judged that such variation must be inherited.

Darwin understood that inherited variation was critically important to his theory. Expanding on Malthus' environmental checks on population size, Darwin suggested that the environment favors organisms whose "individual differences" make them better able to survive and pass on their own characteristics to the next generation. In contrast, physical variations that are not as adaptive tend to be eliminated—not simply by the bearer's own death but also due to the bearer's diminished capacity to produce offspring. This is the process that Darwin called **natural selection**.

Key here is the idea that natural selection happens because some individuals, being better adapted to their environment, give rise to more progeny than others. Darwin understood, in other words, that an individual's evolutionary success cannot be measured only in terms of survival; it must be measured in terms of the capacity to leave offspring.

Thus the concept of a **Darwinian population** is intrinsically tied to the idea of "the environment" and to the fact of biological procreation. By positing the heritability of physical variation and by incorporating the environment as a driving force of change, Darwin defined populations as collections of individuals created by the act of procreation and maintained over time by the biological fact of descent.

In his day, Darwin's concept of evolution was widely accepted. However, the theory of natural selection was also widely criticized because Darwin knew little of the basic principles of heredity (Bowler 1997: 316; Eiseley 1961: 233–253). Although he was certain that individual difference could be inherited, he was decidedly unclear about the mechanics inheritance involved. The fundamentals of genetics were discovered by a Moravian monk, Gregor Mendel [1822–1884]. Mendel's research (1866), however, received little attention until its rediscovery in 1900 and thus had no effect on evolutionary theory until it was championed by William Bateson (1909) and Thomas Hunt Morgan (1915) in the early 1900s (Marks 1997: 418–419). In the twentieth century, the work of Sewall Wright (1921, 1922, 1933, 1968, 1969, 1977, 1978), R. A. Fisher (1930), J.B.S. Haldane (1932), Theodosius Dobzhansky (1970), and others established that the forces of evolution act not on individual genes as such but instead through the survival and reproductive success of individuals. But by the same token, as Darwin saw, individuals in our species can be thought of as being clustered together into small, local populations within which matings are most likely to occur. Nonetheless, matings also happen *between* such local populations, and in the case of Homo sapiens, they happen often enough to keep our kind of animal intact as a single, widely dispersed species.

Using our own species as an example, therefore, we can see that the size of a Darwinian population can be defined by a probability distribution, and local populations by this definition do not have discrete boundaries. Population geneticists refer to the subdividing of a species in this way as its **population structure**, and today it is becoming increasingly common to refer to the aggregate of such locally recognizable grouping of individuals as a **metapopulation** (Hanksi 1999; Hanski and Gilpin 1991; Hanski and Simberloff 1997; Levins 1970). From this perspective, a species can be thought of as a "highest order" metapopulation, and its component local populations are generally referred to as local populations, subpopulations, breeding populations, or demes.

CONTEMPORARY USES

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clouds its contemporary use as an analytical tool. In its most common and familiar usage, a population is defined simply as (or is assumed to be) a group of individuals living in some more or less well-defined area. Thus anthropologists and archaeologists routinely write about populations identified as the current or former members of various socially recognized ethnic or linguistic groupings (e.g., Durham 1991; Howell 1979; Kelly 1990; Madrigal et al. 2001; Neel and Weiss 1975; Weiss 1973; Welsch et al. 1992), or as the makers of particular kinds of artifacts or archaeological features found in some more or less well-specified locale or region (e.g., Braun 1996 [1987]; Kirch 1997; Minnis 1985: 50–54; Spriggs 1997). However, it is not self-evident how "populations" defined in these ways non-biological correspond to Darwinian populations, even when investigators then go on to invoke certain evolutionary principles (e.g., Braun 1996 [1987]; Johnson and Earle 1987; Pearsall 1995). Despite its importance as an evolutionary concept—or perhaps because of its status as a familiar demographic category—when the term "population" is used by archaeologists and anthropologists, precisely what kind of population is intended is often left unspecified. Indeed, it seems to be routinely taken for granted by many authors that every reader knows how "populations" are *always* defined.

That this was not always the case is illustrated by Howell (1979). Writing soon after anthropologists had begun to embrace the union of demographic methods and evolutionary models (e.g., Swedlund 1975; Ward and Weiss 1976), Howell (1979) demonstrates an understanding of the importance of population both as a demographic and as an evolutionary concept. In particular, she took great care to provide definitions for demographic (Howell 1979: 17–18) as well as genetic usages of the term (pp. 355–358).

CASE STUDIES

Two examples illustrate the varied manner in which the population concept has been applied to archaeological phenomena within a Darwinian framework. At issue in the first case is how well archaeological evidence can be used to define Darwinian populations. The example I use is the spatio-temporal distribution of a particular kind of artifact found in the southwest Pacific called "Lapita" pottery. Skeletal remains associated with this pottery exist; however, the human remains are fragmentary, and the sample sizes are statistically quite small. Thus, as is often the case in archaeology, the population affinities of the long-dead peoples associated with this archaeological phenomenon must be inferred from non-biological traits.

Lapita's importance in the archaeological record arises from several features, not the least of which is the fact that the people currently occupying Lapita site localities in the Fiji-West Polynesia region are arguably the descendants of the ancestral Polynesian population (Green 1992; Kirch and

Green 1987). In addition, the peoples of Polynesia, in common with numerous populations of island and coastal Melanesia as well as populations of Southeast and East Asia, speak one of the languages assigned to the linguistic taxon known as Austronesian. In fact, many Pacific archaeologists and prehistorians believe the people who made Lapita ceramics were Austronesian-speakers (e.g., Bellwood 1979, 1991; Kirch 1997; Shutler and Marck 1975; Spriggs 1997). Due in large part to these geographic and linguistic associations, the term "Lapita," although technically a ceramic style, is commonly applied to the people who made those pots (e.g., Kirch 1997).

Ceramics are the product of human action and in that sense are associated with a human population. However, the ceramics themselves are a collect (i.e., a population) whose elements are defined by the presence of certain geometric designs and the manner of creation. What is often forgotten is that this population (i.e., Lapita ceramics) is defined by specific attributes that are relevant within a particular paradigm or model. Whether the populations relevant to one realm of inquiry (e.g., ceramics) are equivalent or comparable to others (e.g., humans) will be discussed below.

The second example concerns recent attempts to apply Darwinian principles to the evolution of cultural attributes (e.g., Dunnell 1980, 1985, 1995; Jones et al. 1995; Teltser 1995). Although its relevance may not be readily apparent, it provides another study of the fit of the Darwinian concept of population to archaeological inquiry. In particular, Dunnell (1980: 63) has argued that

> [i]*f a given trait is heritable to a measurable degree* (the mechanism need not be known) *and if it also affects the fitness of organisms possessing the trait to some measurable degree* (recognizing the possibility of neutral or stylistic traits), *then the trait must be subject to natural selection* and will be fixed in populations. (emphasis in original)

In that sense, culture attributes might be analyzed as traits (memes) that spread through social units like the alleles of a gene spread through the population (Dawkins 1976).

In defense of this application, Teltser (1995: 4), citing Dunnell (1980) and Lewontin (1970), notes that "[e]volutionary theory is a framework for understanding the differential persistence of variation." Indeed, although there is a general sense in which memes are analogous to genes, the genetic metaphor for cultural transmission quickly breaks down. Whereas genes can only be transmitted from parent to child (**vertical transmission**), memes can be transmitted between any two individuals (**horizontal transmission**). Since one can acquire and transmit cultural attributes at any point in life, cultural evolution is, at best, Lamarckian and decidedly non-Darwinian.

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Two recent publications (Boone and Smith 1998; Dunnell 1995) reveal something of archaeology's inattention to the Darwinian population concept, and more generally, how the evolutionary archaeology versus evolutionary ecology debate has focused almost exclusively on the "role of natural selection," to the detriment of discussions of other important Darwinian principles and concepts. In a chapter curiously titled "What Is It that Actually Evolves?", Dunnell (1995) makes what is ostensibly the benign argument that artifacts are evolutionary units subject to variation and selection. Boone and Smith (1998: S142–S144) soundly criticize this notion, arguing—under the unfortunate heading "What is evolving? Replicators and phenotypes"—that Dunnell's (1995) thesis ignores the replicator-phenotype distinction and the problems with the transmission of cultural traits briefly described above. Specifically, Boone and Smith (1998: S143) note that "selection can act on phenotypic variation . . . only to the extent that it is heritable."

Although I concur with this critique, I am troubled by the fact that Boone and Smith (1998), like Dunnell (1995), blur the distinction between the units of selection (phenotypes) and the unit of evolution (the population). While it is true that artifactual characteristics vary over time (and space) and that artifacts are subject to selection, there is no Darwinian sense in which artifacts (or for that matter, phenotypes) should be thought to evolve. Darwinian evolution occurs within populations. Although characteristics of cultural attributes clearly change over time and in that sense evolve, we can only know whether the frequencies of these attributes change with reference to a population. Does a comparable evolutionary unit exist for cultural attributes? How does one discern a population of memes? What is the appropriate population within which to study the evolution of cultural phenomena? Answers to these questions will clearly have to wait for another discussion. However, as Dunnell (1995: 44) cautions, "until the matter of units is taken more seriously . . . there is no reason to expect that evolutionary accounts will be anything more than just another story."

FUTURE IMPORTANCE

It is impossible to write about evolution or diversity without reference to the concept of population. The population (however defined) is the group that one wishes to describe and about which one wishes to draw conclusions. Unfortunately, although the population is the primary focus, investigators are often forced to study a sample. Samples are used because the population is either too large to conveniently study or simply unavailable to study in its entirety. In fact, archaeologists and other evolutionary scientists are often forced to employ a kind of reverse sampling strategy, aggregating the elements in order to infer the existence of a population. The question is often not how to choose a sample to represent our population but rather, what population does our "sample" represent? (I have placed the term sample in quotes because a sample properly only exists in relation to a population.) Collections of discovered items (e.g., artifacts) only become samples when one relates them to a population. Over time, these relationships often change as the investigator's and the discipline's focus of interest evolves. For example, consider the changing relationships among fossil hominids as new discoveries lead to the lumping and splitting of taxa. In other words, the population is often abstracted from the sample rather than the sample having been drawn from the population.

The difference between a population and a sample is that with a population our interest is in defining the population's characteristics, whereas with a sample our interest is in making inferences about the characteristics of the population from which that sample was drawn. A critical feature of any scientific investigation is the testing of hypotheses by statistical criteria. By studying a sample, the investigator hopes to reach valid conclusions about the population.

However, in order to draw inferences from the sample, the investigator must make certain assumptions about both the population which the investigator is generalizing and the sample being used. The process of using a sample to make inferences about a population is called a **sampling strategy** (see LeCompte and Schensul 1999b; Pelto and Pelto 1978; Weir 1990). Those assumptions convenient by divide into two categories: (1) those with which the investigator is fairly confident and is willing to accept and (2) those about which the investigator is somewhat doubtful and is therefore interested in testing. The assumptions with which the investigator is confident are the basis for the model, while those about which the investigator is interested in testing are the **hypotheses**. Examples of model assumptions include the use of linguistic reconstruction as standard for ordering and interpreting genetic and archaeological data (e.g., Kirch 1997; Spriggs, 1997); and the premise that natural selection operates on cultural phenomena (e.g., Dunnell 1980) as well as the investigator's acceptance of the study sample as adequate representation of the population. Examples of hypotheses include the suggestion that the dispersal of Lapita ceramics is associated with spread of Austronesian languages (e.g., Clark and Kelly 1993) as well as the assertion that post-contact artifact change reflects natural selection as opposed to acculturation (e.g., Ramenofsky 1995).

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it is important that only one of the assumptions (preferably the hypotheses) is in doubt. However, all of the assumptions made by the investigator (model and hypotheses) have the same logical status (i.e., they are unproven). Indeed, one can easily imagine a time or place where the investigator may choose to the test the assumptions of the model. Given their indeterminate status, erroneous model assumptions (e.g., a biased sample) may lead the investigator to accept false hypotheses. At the same time, any test that rejects the hypotheses also calls into question the assumptions of the model.

In order to understand evolutionary relationships within a Darwinian paradigm, one must remain keenly aware of the assumptions of the model, for as with any model, to failure to attend these assumptions may lead to erroneous conclusions. Of particular concern to this discussion is the fact that one's ability to draw valid inferences is predicated on the assumption that the sample is representative of the population.

As we have seen, populations are collections defined by selected attributes for specific reasons. Thus, a Darwinian population is a collection of individuals defined by procreation and common descent for the purposes of understanding variations in the spatial and temporal distributions of physical variations. Whether populations defined on the basis of archaeological attributes are comparable to Darwinian populations remains open to debate. However, the reality is that the comparability of populations defined using different attributes can rarely, if ever, be demonstrated and thus must always be treated as an assumption. For this reason, it is important that the researcher carefully and completely defines the population. Without a clear definition of the population, it is impossible to know what the sample represents. For example, some of the issues and consequences of relying on historic names and categories to identify genetic populations are discussed by MacEachern (2000) and Terrell (2001; Terrell et al. 2001). At the same time, without a clear definition of the population how does one judge what is relevant? How is one to know what one means? How does one know what one is interpreting? How does one know whose history one is writing?

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