

- What Are Units and Levels of Selection?
- Conflict and Cooperation Within and Between Levels of Selection
- The Evolution of Units and Levels of Selection

Selection: Units and Levels

Benard J Crespi, *Simon Fraser University, Barnaby, BC, Canada*

Analysis of units and levels of selection allows determination of where and how natural selection takes place, and how it causes evolutionary change in genes and organisms.

What Are Units and Levels of Selection?

Selection is the primary cause of adaptive evolutionary change. To understand how selection takes place, it is necessary to determine what biological units or entities, at what levels of biological organization, are subject to its effects, and how its prevalence and efficacy varies across levels. Selection itself can usefully be defined as the differential reproduction of biological units due to differences in form or character between these units. 'Units of selection' are defined here as the units whose frequencies are adjusted by natural selection across generations, and 'levels of selection' are defined here as the levels of biological organization where natural selection occurs, within generations. Biological units are arranged in a hierarchy (Table 1), with higher-level units subsuming lower-level ones, and units at the different levels exhibiting different properties with regard to how they reproduce and whether and how they interact with units at different levels and with aspects of the environment. These properties are critical to understanding how and why natural selection, and across-generation responses to selection, take place.

Units of selection

Genes are segments of DNA or RNA that may exhibit informational content coded in their nucleotide sequences. Some genes code for protein or RNA products that interact with the internal organismal environment, other genes have regulatory effects on biochemical processes, and others have no known function. Genes reproduce via the processes of mitosis and meiosis, and the fidelity of gene

replication is a function of the rate at which mutation and recombination produce new gene sequences. Genes cannot simply be considered as segments of DNA or RNA that code for single, specific effects, such as the production of a haemoglobin molecule: larger segments of genetic material can be inherited together across many generations, and these larger segments have stronger effects but are more likely to be altered by mutation and recombination. Thus, from an evolutionary viewpoint, genes are best considered as units whose fidelity of reproduction tends to decrease with increasing number of nucleotides (Williams, 1992).

Different genes exhibit different patterns of transmission across generations. Autosomal genes are inherited biparentally, sex-linked genes are inherited or not depending on the sex of the parents and offspring, and cytoplasmic genes (e.g. genes on mitochondria and chloroplasts) are inherited with the cytoplasm of gametes. These distinct inheritance patterns create circumstances whereby autosomal, sex-linked or cytoplasmic genes may have effects that increase their own rate of reproduction but decrease the reproductive rate of genes with the other modes of inheritance.

Genes are arranged in packages – chromosomes – that are normally transmitted as units. Chromosomes reproduce via meiosis and mitosis, using cytogenetic machinery such as the spindle apparatus that divides them among daughter cells according to the inheritance pattern of the chromosomes involved. Reproduction of autosomes, and sex chromosomes, via meiosis is normally equitable because each chromosome has an equal chance (one-half) being passed to a given gamete. However, the meiotic process provides opportunities for differential reproduc-

Table 1 The primary levels of biological organization, the units at each level, and the properties of the units

Level	Amount of variation	Turnover rate	Inheritance fidelity	Expression of traits	Nature of unit
Genes	High	High	Very high	No	Replicator
Chromosomes	High	High	Medium	No	Replicator
Genotypes	High	High	Low	No	Replicator
Gene products	High	High	N/A	Yes	Vehicle
Cells	Variable	High	N/A	Yes	Vehicle
Individuals	High	High	Low	Yes	Vehicle
Groups	Variable	Variable	Variable	Yes	Vehicle
Species	Variable	Very low	Variable	Yes	Vehicle
Communities	Variable	Low	Variable	Yes	Vehicle

N/A, not applicable.

tion of chromosomes with effects that increase their own reproductive rate and necessarily decrease the reproductive rate of their homologues.

In metazoans, sets of chromosomes are assembled into haploid or diploid cells, and such complements of chromosomes are referred to as genotypes. To the extent that traits are differentially expressed in gametes (e.g. in the growth of pollen tubes), leading to their differential fertilization success, gametes may be subject to selection. Similarly, selection may occur among cells in a metazoan if differences between competing cells promote differences in their reproductive rates. Intercellular selection appears fundamental to the function of the B cells of the immune system, which undergo cycles of differential reproduction based on their abilities to bind antigen, and it may also provide a useful context for understanding the causes of cancer (Lewontin, 1970).

Genes, chromosomes, genotypes and cells are all found within individuals, units in our hierarchy that express phenotypic traits, interact directly with the external environment, and differentially produce new such units as a function of the traits that they express. Individuals are poised at a special place in our hierarchy, because they each contain genes, chromosomes, genotypes and cells; they normally live, reproduce and die as units; and they represent the components that in various combinations make up the levels above them.

Individuals of many species interact among themselves, and these interactions provide the basis for defining groups, sets of individuals that interact and thereby express trait variation that may influence their joint differential reproduction relative to other groups. Groups, which may be as small as two individuals, may be composed of related individuals (kin) that share identical genes by descent (Hamilton, 1964), or unrelated individuals. Groups may or may not exhibit spatial separation, since they are usefully defined with respect to the trait-related interactions of individuals rather than proximity (Sober and Wilson, 1998). However, because spatial structure enforces intragroup interaction, it provides the most effective situation for selection at the group level.

The next level in our hierarchy – species – is defined here on the basis of interbreeding between individuals in a population, whereby individuals share a common gene pool among themselves across generations but do not breed successfully with individuals of other species. The equivalent of differential reproduction for species is differential speciation and extinction (Williams, 1992), which may be due to differences between species in traits such as body size or degree of ecological specialization. An equivalent of species-level selection may also be construed for asexual lineages, such as parthenogenetic animals or mitochondria, whereby non-interbreeding lineages differentially proliferate.

Finally, sets of ecologically interacting species – communities – may represent a level of selection to the extent

that they form discernible entities that undergo differential reproduction (i.e. exhibit differential stability) as a consequence of variation in traits expressed at the community level (Lewontin, 1970; Sober and Wilson, 1998).

The degree to which the units at different levels in **Table 1** are units of selection depends on three conditions (Lewontin, 1970; Alexander and Borgia, 1978). First, the units must exhibit variation among themselves in their effects, and the potential strength of selection at that level increases with the magnitude of the expressed variation. Second, the units must have some rate of differential reproduction or turnover, which determines the frequency of selective episodes, and this differential reproduction must be causally linked to variation among units. Third, the units must exhibit fidelity of inheritance, such that they persist as unique, replicating variant units for a sufficient number of selective episodes to have their frequencies adjusted by natural selection.

How well do our potential units of selection in **Table 1** meet these three criteria? Relative to units at other levels, genes normally exhibit high levels of variation, in that variants are common at a substantial proportion of loci, and genes turn over every generation, so the potential rate of differential reproduction is high. Most importantly, genes exhibit very high fidelity of inheritance; barring mutation or intragenic recombination between heterozygous nucleotide sequences, which tend to be rare events, genes are replicated perfectly across generations. The same cannot be said for higher-level packages of sets of genes: although they exhibit considerable variability and the same turnover rate as genes, chromosomes are usually broken up and reassembled by recombination each generation, and genotypes are scrambled by both recombination and meiosis. Gene products or cell lineages in the immune system or cancerous tissues cannot be units of selection because the variants are not inherited. Individuals, groups, species and communities cannot be units of selection because, although they may reproduce, they do not replicate; their fidelity of inheritance is sufficiently low that variants do not persist though a sufficient number of selective events to have their frequencies adjusted in a systematic manner. Finally, phenotypic traits themselves cannot be considered as units of selection because they cannot replicate exactly; their form is virtually always more or less altered across generations as a result of changes in genes, chromosomes, and genotypes.

The gene is the primary unit of selection because it is the only unit exhibiting high variation, high turnover rate, and ability to replicate or reproduce with extremely high fidelity. Chromosomes may be units of selection only if rates of recombination are very low or zero, and genotypes may be units of selection only in asexual forms where the absence of recombination and meiosis results in the inheritance of entire genomes intact. To be a unit of

selection, being a replicator is key (Dawkins, 1982), and only the lowest-level units can meet this stringent criterion.

Levels of selection

The conclusion that genes are the main units of selection begs the question of levels of selection, or where selection exerts its influences in the hierarchy of life. Selection requires the expression of trait variation at some level, and interaction of that trait variation with the environment in such a way that the units at that level, and necessarily at lower levels, differentially reproduce. Expressed traits include gene products or effects, such as RNA, proteins or DNA configuration or methylation, phenotypes of individuals, phenotypes of groups or communities that involve interactions between individuals, or phenotypes of species and asexual lineages. The terms 'vehicle' and 'interactor' have sometimes been used to describe these biological units that interact directly with the environment (Dawkins, 1982). To understand levels of selection, we must assess where interaction with the environment takes place, and how important interactions at different levels are in causing differential reproduction of units of selection.

Selection can occur among trait variants expressed in developing gametes, mature gametes, individuals, groups, species, asexual lineages, or communities. It may occur with varying strength at different levels, and it may occur in the same or opposing direction at different levels. The strength of selection increases with the amount of trait variation expressed at a given level, and with the rate or intensity of differential reproduction of the entities that is due to expression of the trait variants.

Replicators in developing or mature gametes, or developing zygotes, may express traits that increase their own relative frequency, such as by the destruction of vehicles that do not exhibit the trait and the replicator that codes for it. Such cases of 'ultraselfish DNA' are discussed below. Individuals exhibit considerable trait variation, and a usual high intensity of differential reproduction that is linked to the variation; as a result, they have long been considered as the level of selection that is most prevalent and important for the evolution of adaptations. The amount of variation expressed among groups of individuals will depend upon whether the groups are formed assortatively by trait variant, and whether or not movement of individuals between groups erodes the variation. The intensity of group selection depends on how strongly the among-group trait variation is associated with differential group reproduction, and how frequently group-selective events take place (Alexander and Borgia, 1978). This topic of 'group selection' has a long history in evolutionary biology and it is discussed below. Species may vary considerably in phenotypic traits that affect their rates of speciation and extinction, but their rates of differential

reproduction are extremely low, relative to selection within species. As a result, species-level selection cannot be expected to yield adaptation, where adaptation is defined in terms of a close fit between the form of a trait and some aspect of the environment (Williams, 1992). Selection among species may, however, lead over macroevolutionary time to an increased frequency of traits that cause increased speciation rate and decreased extinction rate.

Although individuals are normally the most important level of selection, the levels above and below them may also be subject to strong selection. As a result, analysis of questions regarding levels of selection always requires consideration of multiple levels, and how they may jointly influence evolutionary change.

Conflict and Cooperation Within and Between Levels of Selection

Vehicles of selection are expected to cooperate or compete, depending upon whether the replicators coding for their phenotypes exhibit positively correlated inheritance (reproducing via the same vehicles), or negatively correlated inheritance (reproducing by vehicles that differ in some way, such that increased reproduction of one replicator leads to lower reproduction of the other). For example: (1) all autosomes normally replicate via the production of offspring by the individual that contains them; as a result, autosomes are normally expected to produce effects that interact harmoniously in the production of the best possible phenotype; (2) sex chromosomes that are inherited via one sex only may exhibit effects that increase the production of that sex by the individual that contains them, but such overproduction of one sex may decrease the reproductive rate of the autosomes; and (3) if individuals in a social group cooperate, they may maximize the number of offspring produced by the group as a whole, but any individual in the group that eschewed cooperation could exhibit increased reproduction relative to fellow group members; as a result, alleles that code for cooperation would be selected for at the among-group level but selected against among individuals within groups.

The dynamics of situations involving cooperation and conflict among biological entities are complex, and depend upon the strength of selection at different levels and the power, or magnitude of influence, of the phenotypic traits that interact. The two primary conflict zones are gene-effect level selection versus individual selection, and individual selection versus group selection.

Gene-effect level selection versus individual selection

The effects of some genes increase the replication rate of the gene coding for them, relative to other alleles, but decrease

the reproductive rate of the individual that bears them, relative to individuals that do not. Such genes are sometimes called ‘ultraselfish’, because their effects will be in conflict with the effects of genes that interact harmoniously owing to their joint interest in maximizing individual reproduction. Ultraselfish genes can be either cytoplasmic or nuclear, and nuclear genes can be autosomal or sex-chromosomal (X or Y in most species). Ultraselfish elements may be genic, comprised of a DNA segment that is a small part of a chromosome, or they may consist of an entire chromosome. Conflicts occur between the effects of cytoplasmic and autosomal nuclear genes because cytoplasmic genes are normally (in most taxa) inherited only via females, whereas autosomal nuclear genes are inherited via both sexes. As a result, a cytoplasmic gene may be selected to express effects that increase the number of females in a brood, but, if this effect decreases total brood size, then it will engender selection for nuclear autosomal genes that increase brood size by suppressing it. Examples of ultraselfish cytoplasmic elements include cytoplasmic male sterility in plants and some vertically inherited bacteria such as *Wolbachia*. Similarly, a sex-chromosomal (e.g. X- or Y-linked) gene with effects that increase the number of an individual’s offspring that bear it will be selected for, but if such sex ratio bias involves decreased individual reproduction then autosomal genes with effects that suppress it will be favoured by selection. So-called ‘supernumerary’ autosomes, such as B chromosomes, may exhibit similar dynamics, increasing their representation in the next generation at a cost to the individual, and thereby to all chromosomes inherited in an equitable manner. Finally, the effects of autosomal genes at unlinked loci may be in conflict if a gene increases its replication rate by directly decreasing the replication rate of its alternative allele at the same locus, via killing developing gametes or individuals that contain the alternative allele. Alleles at all loci unlinked to such a gene will be selected to suppress its effects if these effects include reduced individual reproduction. Examples of such genes include segregation distorter in *Drosophila*, and the t-alleles found in some mice.

The different forms of ultraselfish genetic elements described above exert their phenotypic effects in myriad ways. Some elements, such as segregation distorter in *Drosophila* or ‘Medea’ in *Tribolium*, exhibit a ‘poison–antidote’ system, whereby chromosomes with the genic element produce an effect that kills chromosomes (and, as a consequence, developing vehicles) without the antidote, but are themselves protected (Hurst *et al.*, 1996). Chromosomal elements such as B chromosomes may enjoy a transmission advantage via altered chromosome–spindle interactions during mitosis or meiosis, or they may cause condensation and loss of potentially competing chromosomes (apparently also via a poison–antidote system) after fertilization of an egg, as in the PSR element found in *Nasonia* wasps. One genic autosomal drive element has even evolved to use adult individuals as executioners of the

alternative allele: in a species of ant, workers with the ultraselfish allele kill the queens in their colony that lack it.

Conflict between the gene-level effects of ultraselfish elements and individual level effects can yield several possible outcomes (Hurst *et al.*, 1996). First, the ultraselfish element can be suppressed so that its effects are lost. The means whereby the negative effects of ultraselfish elements are suppressed by other genomic elements are as yet poorly understood, but in linked poison–antidote systems they may include breaking the system apart by recombination, the evolution of loss of sensitivity to the poison, or the evolution of an alternative antidote. Second, some elements, such as sex-ratio-distorting chromosomal elements, have the potential to drive populations or species extinct, and this effect has been demonstrated for an artificial Y-linked drive system in a laboratory population of *Drosophila*. Such potentially suicidal genocide has been proposed as an explanation for the general lack of gene expression on Y chromosomes of animals (Hamilton, 1967). Third, in some cases not involving XY sex determination, the evolution of a novel sex-determination system that favours the ultraselfish element but is not selected against at the individual level may eliminate the genetic conflicts (Hurst *et al.*, 1996). Finally, the conflict may reach a stalemate whereby the element is maintained at some frequency owing to opposing selective forces at different levels. Many ultraselfish elements cause reduced fertility or viability of individuals homozygous for the element, as well as lowered reproduction of heterozygous individuals. As a result, gene-effect level selection for increasing the frequency of the element can, in subdivided populations, be counterbalanced by group-level selection against populations that carry the element at a relatively high frequency (e.g. for the PSR element in *Nasonia*, and possibly for the t-alleles of mice).

Individual selection versus group selection

Many phenotypic traits involve interactions between individuals. These interactions can influence the reproduction of each interacting individual, and they can also affect the reproduction of multiple individuals taken collectively (a group), such that their total reproduction is increased or decreased in some manner that is associated between them (Wade, 1978). Group selection of traits, and consequent differential reproduction of the replicators that code for them, may operate in the same direction as individual-level selection or in the opposite direction. Moreover, traits can be close to neutral at one level but favoured by selection at the other level. To determine how important individual and group selection are in trait evolution, it is necessary to assess their relative prevalence and efficacy in causing evolutionary change via processes at the two levels.

The conditions most favourable to evolution by group selection are high among-group variation relative to

within-group variation in the trait, a relatively small individual-fitness cost to the trait within groups, a relatively large among-group fitness advantage to groups exhibiting the trait, and a high rate of group turnover, such that individual selection does not have time to extinguish the trait within each group. One difficulty with the simultaneous presence of these conditions is that high among-group variation is likely to be antagonistic to high rates of turnover, unless the temporal pattern of group formation and dissolution precludes among-group movement during most of the life cycle (Alexander and Borgia, 1978; Sober and Wilson, 1998).

When groups are composed of two or more kin, they differ genetically by definition. In this situation, individuals may be selected to engage in altruism – behaviours that have a reproductive cost to themselves as individuals but that increase the reproduction of their kin group and thereby lead to a higher rate of replication of the genes that code for the trait (Hamilton, 1964). In particular, genes for such acts are expected to increase in frequency where the benefit to the recipient of the act, multiplied by the relatedness of the actor to the recipient, is greater than the cost of the act to the actor (Hamilton's rule). Hamilton's theory of 'kin selection', or 'inclusive fitness maximization' can be shown to be mathematically equivalent to a group selection model (Queller, 1992), and it has been well supported by numerous studies of organisms that interact socially.

The process of group selection among non-kin is theoretically plausible (Sober and Wilson, 1998) and it has been demonstrated artificially in laboratory populations (Wade, 1978), but its prevalence in nature is not yet known. Four examples have commonly been set forth as evidence for such group selection in nature. First, female-biased sex ratios in some insects have been considered the result of a balance between within-group frequency-dependent selection for a 1:1 sex ratio and among-group selection for highly female-biased sex ratios (Sober and Wilson, 1998). However, the evolution of these female biases can also be construed as the result of kin-group selection, because the biases require selection for a reduction in competition between brothers. Second, the evolution of reduced virulence of parasites, such as the myxomatosis virus, may provide examples best understood as group selection, since separate hosts create pronounced population structure, and among-host selection for reduced virulence can be strong relative to within-host selection for increased virulence. Third, in some ant and bee species, non-kin cooperate in colony foundation or in defending the nest, and selection among groups (colonies) for these traits, mediated by competitors or predators, is quite strong. Finally, groups of humans delineated by cultural traits and cohabitation of territory rather than close kinship ties appear to provide ideal conditions for selection of social traits at the group level, because intense intergroup competition and intragroup

cooperation may often lead to extremely high among-group fitness differences (Alexander and Borgia, 1978; Sober and Wilson, 1998).

The Evolution of Units and Levels of Selection

The units of biological organization (Table 1) have all themselves evolved, owing to selection at levels below them (whereby they originate) and selection at their level (whereby their properties evolve). The emergence of each higher level of organization has involved the evolution of mechanisms that facilitate cooperation and reduce competition among vehicles at lower levels, and serve as adaptations for competition between vehicles at lower and higher levels. Some examples are presented below.

1. The presence of chromosomes ensures that sets of genes are normally inherited together, such that their synergistic effects can be selected for jointly and each gene has a common stake in chromosomal reproduction. Multiple chromosomes, recombination, and independent assortment during meiosis can be seen as adaptations that counter the effects of meiotic drive, via minimizing the size of linkage groups (i.e. evolutionary 'genes') (Hurst *et al.*, 1996).
2. Uniparental inheritance of organelles may have evolved via selection to prevent the spread of ultraselfish organelle genes (Hurst *et al.*, 1996).
3. The usual inviolate segregation of the germline from the soma in multicellular individuals may have evolved in the context of suppressing intercellular competition, and thereby fostering synergistic cooperation of cells in the evolution of individuals.
4. Social cooperation and altruism within groups has evolved via selection for maximization of inclusive fitness by each individual, whereby within-group individual selfishness is countered more or less successfully by between-group advantages to cooperating (Hamilton, 1964). Mechanisms helping to enforce cooperation include recognition of group membership and joint suppression ('policing') of selfish individuals.

Hypotheses concerning the evolution of levels and units of selection are testable (Hurst *et al.*, 1996), and their analysis will provide insight into all areas of the life sciences, from genome structure through macroevolution.

References

- Alexander RD and Borgia G (1978) Group selection, altruism, and the levels of organization of life. *Annual Review of Ecology and Systematics* 9: 449–474.

- Dawkins R (1982) Replicators and vehicles. In: King's College Sociobiology Group (eds) *Current Problems in Sociobiology*, pp. 45–64. Cambridge: Cambridge University Press.
- Hamilton WD (1964) The genetical evolution of social behavior, I and II. *Journal of Theoretical Biology* **7**: 1–52.
- Hamilton WD (1967) Extraordinary sex ratios. *Science* **156**: 477–488.
- Hurst LD, Atlan A and Bengtsson BO (1996) Genetic conflicts. *Quarterly Review of Biology* **71**: 317–364.
- Lewontin RC (1970) The units of selection. *Annual Review of Ecology and Systematics* **1**: 1–18.
- Queller D (1992) Quantitative genetics, inclusive fitness, and group selection. *American Naturalist* **139**: 540–558.
- Sober E and Wilson DS (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, CA: Harvard University Press.
- Wade MJ (1978) A critical review of the models of group selection. *Quarterly Review of Biology* **53**: 101–114.
- Williams GC (1992) *Natural Selection: Domains, Levels and Challenges*. Oxford: Oxford University Press.
- Further Reading**
- Alexander RD (1979) *Darwinism and Human Affairs*. Seattle, WA: University of Washington Press.
- Alexander RD (1987) *The Biology of Moral Systems*. Hawthorne, NY: Aldine de Gruyter.
- Buss LW (1987) *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Dawkins R (1989) *The Selfish Gene*, 2nd edn. Oxford: Oxford University Press.
- Keller L (1999) *Levels of Selection in Evolution*. Princeton, NJ: Princeton University Press.
- Maynard-Smith J and Szathmary E (1999) *The Origins of Life: From the Birth of Life to the Origin of Language*. Oxford: Oxford University Press.
- Werren JH and Beukenboom LW (1998) Sex determination, sex ratios, and genetic conflict. *Annual Review of Ecology and Systematics* **29**: 233–261.
- Williams GC (1966) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, NJ: Princeton University Press.