

CHAPTER I

The major evolutionary transitions and Homo loquens

1.1 Introduction

The biological world contains creatures such as fungi, plants, self-moving animals and self-conscious and culture-creating humans. These are composed of cells and cell organelles that were separate in the evolutionary past. Cell organelles were originally cells but later joined other cells (they became endosymbionts) and formed a higher-level creature: the symbiotic unicell (i.e. the eukaryotic cell). In this higher-level unit cell organelles retained their capacity to reproduce. Symbiotic unicells later joined other unicells and formed another higher-level unit: the multicellular organism. In this unit, the somatic cells abandoned their capacity to contribute genes to the next generation.

The benefit of cooperation is the reason why cells (and later multicellular organisms) joined forces (Bourke, 2011; Buss, 1987; Maynard Smith and Szathmáry, 1995; 1999). But there have been conflicts among the different cells as well. Conflict occurs when units are capable of affecting a common feature and when natural selection favours different effects of the units. For instance, the cells forming the symbiotic cell were unrelated and had therefore different interests, creating the potential for conflict. And in a large multicellular organism there were opportunities for cells to pursue their own ends, selfishly disregarding the common goals of the higher-level unit (e.g. a cancerous cell). Because selfish subunits undermined the stability of the new unit, the potential for conflict was reduced through conflict mediation. Conflict mediation led to subunits that no longer favoured opposing effects on a common feature, but a similar effect. The association between the subunits was therefore further strengthened. Hence cooperation and subsequent mediation of conflict contributed to an increase in life complexity: associations between lower-level units led to higher-level units, and reducing conflicts led to stronger associations (i.e. the integration and coordination of processes). As the result of reducing

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conflict the collectives were able to evolve further: they became obligate collectives with a high degree of interdependence of their parts. As obligate collectives, they became themselves candidates for participation, as subunits, in the next evolutionary transition (Bourke, 2011). The symbiotic unicell, multicellular organisms and later animal societies are therefore composed of layers upon layers of cooperation.

The evolution of higher-level units out of lower-level units is explicable in terms of the framework of inclusive fitness theory. It is no exaggeration to say that this insight is one of the most important theoretical discoveries of the previous decades. It was made possible by three developments. First, the discovery of a complex subcellular world. Molecular biologists disclosed a natural world below the level of the cell that did not rank second in richness to the world already known to naturalists. The discovery of cell organelles (e.g. mitochondria and chloroplasts), of genetic parasites such as transposons and retroviruses, of the processes of cell differentiation and apoptosis, of protein synthesis and RNA splicing and so on and so forth, revealed an enormous diversity of molecules and biological structures interacting in an orderly manner. Just as in the world studied by naturalists, some molecules and structures were related because of common descent whereas others were not. These observations raised the problem of how we can explain the orderly interactions between molecules and structures. Second, the development of a general theoretical model of social evolution. Darwin showed that natural selection is capable of explaining patterns observed by naturalists. Elaborations of Hamilton's theory revealed that inclusive fitness theory has similar explanatory powers and is capable of explaining observable patterns in both the subcellular and supracellular world. Hence the same theoretical principles that explained the behaviour of organisms and the social life of animal societies, could also explain the behaviour of genes, cell organelles and cells. Third, the development of a coherent conceptual framework for understanding social evolution. Scientists and philosophers have elaborated the rules for the use of both technical and ordinary concepts that we use when we investigate the behaviour of humans and other organisms. These investigations revealed that mastery of a language is the mark of the human, rational mind. This conceptual insight raises the question of how linguistic behaviour evolved out of animal behaviour. Hence the challenge is to explain how *Homo loquens* evolved in terms of Hamilton's theory. The principles and concepts of a framework capable of explaining the social evolution of human nature are discussed and elaborated in this book.

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Table 1.1: Two kinds of major evolutionary transitions, adapted from Queller (1997, 2000).

	Egalitarian	Fraternal
Examples of cooperative alliances forged	Different molecules in compartments; genes in chromosomes; nucleus and organelles in cells; individuals in sexual unions	Same molecules in compartments; same organelles in cells; cells in individuals; individuals in colonies
Units	Unlike, non-fungible	Like, fungible
Reproductive division of labour	No	Yes
Control of conflicts	Fairness in reproduction; mutual dependence	Kinship
Initial advantage	Division of labour; combination of functions	Economies of scale; later division of labour
Means of increase in complexity	Symbiosis	Epigenesis
Greatest hurdle	Control of conflicts	Initial advantage

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The evolution of a higher-level unit out of lower-level units is called an evolutionary transition. The lower-level units constituting the new unit lack a high degree of conflict within the new unit and interact in a coordinated manner to achieve common goals. I shall later elaborate this general definition of an evolutionary transition, but first discuss two types. Queller (1997, 2000) subdivided the major transitions into *egalitarian* and *fraternal* transitions (see Table 1.1). He took these terms from the motto of the French revolution: ‘Liberté, égalité, fraternité’. The essential difference is that egalitarian transitions involve a union of unrelated units, whereas fraternal transitions involve related units. Units involved in an egalitarian transition do not sacrifice their reproductive capacities when the units cooperate (hence their egalitarianism). The evolution of the symbiotic cell is the paradigmatic example. Other examples are the grouping of unrelated genes in chromosomes and the union of the female and male halves in a sexual organism. The benefit of cooperation is that two different functions are combined. The fraternal transition, by contrast, consists of a union of related units (hence their fraternity). The evolution of a multicellular organism is here the paradigmatic example. Because the cells are related (identical if the organism is derived from a single cell), there are no benefits

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related to combining different functions. The initial advantage was probably related to an increase in size. When multicellular organisms started to compete with other organisms, selection favoured a division of labour within the organism, resulting in cells and organs performing different functions (as the result of epigenesis, i.e. through different gene expression different types of cells, tissues and organs evolved). An essential division of labour was between germ cells and somatic cells. Somatic cells are characterized by sacrificing their reproductive potential. Other examples of fraternal transitions are the cooperation of individuals in a colony and the grouping of the same molecules in a cellular compartment.

This distinction between fraternal and egalitarian transitions immediately explains why the transition from unicellular to multicellular organisms and from cells (prokaryotes) to symbiotic unicells (eukaryotes), faced different problems. In the transition to multicellular organisms *kinship* explains why lower-level units cooperated and why in small multicellular organisms conflict was absent, whereas during the transition from unicells to symbiotic unicells conflict between unrelated cells was the greatest hurdle. But since endosymbiosis combined unrelated entities capable of performing different functions, *mutual benefit* explains why the new entity had adaptive advantages. By contrast, the lack of a combination of different functions was the greatest hurdle for a multicellular organism.

The distinction between egalitarian and fraternal transition also clarifies why certain phenomena occur in only one transition. For instance, an egalitarian transition, in contrast to fraternal transitions, does not involve *altruism*, for altruism, according to the principles of social evolution, can only occur if the interacting units are related. This amounts to the earlier observation that sacrificing the ability to reproduce (e.g. the non-reproductive, somatic cells of a multicellular organism and the sterile workers of social insect societies) is absent in egalitarian transitions. The cooperation between endosymbionts and host cells is therefore only explicable in terms of mutual benefit (also called ‘narrow-sense cooperation’): both partners benefit because of the interactions and there is no indirect benefit (because of their relatedness) involved. Note that the framework of inclusive fitness theory is not restricted to explaining interactions between related individuals. It is also capable of explaining patterns of interactions between unrelated subunits, but uses then different principles. Hence inclusive fitness theory encompasses both kin selection theory (explaining cooperation among related individuals) and theories that explain cooperation between non-relatives.

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Table 1.2: Six major evolutionary transitions, adapted and modified from Bourke (2011).

	Social group formation	Social group maintenance	Social group transformation
1. Separate replicators (genes) → cell enclosing genome	Origin of compartmentalized genomes	Control of selfish DNA	Evolution of large, complex genomes
2. Separate unicells → symbiotic unicell	Origin of eukaryotic cells	Control of organellar reproduction	Evolution of hybrid genomes through transfer of genes from organelles to nucleus
3. Asexual unicells → sexual unicells	Origin of zygotes	Control of meiotic drive	Evolution of obligate sexual reproduction
4. Unicells → multicellular organism	Origin of multicellular organisms	Control of selfish cell lineages (cancers)	Evolution of a segregated, early-diverging germ line
5. Multicellular organisms → eusocial society	Origin of societies	Control of conflict with dominance, punishment or policing	Evolution of dimorphic reproductive and non-reproductive castes
6. Primate societies → human societies	Origin of language	Control of cheating	Reciprocating, evolution of social norms

I distinguish here six major evolutionary transitions (see Table 1.2): (1) the evolution of genomes, (2) the evolution of eukaryotic cells, (3) the evolution of sexual reproduction, (4) the evolution of multicellular organisms, (5) the evolution of societies, and (6) the evolution of human societies (language). Maynard Smith and Szathmáry (1995; 1999) defined eight transitions. They subdivided the first transition in Table 1.2 into three separate transitions. Their table has been criticized and modified by Bourke (2011) whom I am following here. But whereas Bourke defines the evolution of the origin of interspecific mutualism (cooperation between separate species) as the sixth transition, I return to the evolution of language defined by Maynard Smith and Szathmáry as the, for the time being, final transition. There is only one reason: this book discusses the problem of how we can understand the transition from primate to human societies. Bourke focuses on another no less interesting problem, but this problem is not under discussion here. However, he has an important

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argument for excluding language evolution: it does involve the evolution of – what he calls – individuality, i.e. a new biological entity. I include language evolution here because it enables humans to create new bonds (reciprocity, social norms) resulting in new collectives consisting of individuals interacting in a coordinated manner to achieve common goals. One can argue that language evolution did not result in a transition but in a transformation of primate societies. This would meet the objection that the resulting collectives are not strict biological entities, but has the disadvantage that language evolution and its consequences are not comparable to the many transformations in the animate world (e.g. the metamorphosis of a caterpillar into a butterfly). Language evolution created new (types of) bonds between organisms and led to cultural evolution: symbolic information was transmitted from one individual to the other. The problem discussed in this book is of how we can expand the framework of inclusive fitness theory so that it is capable of explaining the sixth transition.

However, it is important to note that speaking about language evolution as an example of an evolutionary transition does not mean that human societies are, or are predicted to become, biological entities (as Bourke correctly noticed). This has the important consequence that human societies are not and will not evolve into *obligate* collectives. In obligate social groups the lower-level entities can only replicate as part of the group. For example, in the case of multicellular organisms, it means that cells in obligate multicellular organisms can only replicate as part of an organism, whereas in *facultative* multicellular organisms (e.g., in social amoeba, see section 1.3) they have the capacity to replicate independent of the higher-level entity. There is evidence that obligate social groups evolve when $r=1$, for there are no examples known of obligate social groups when $r<1$ (Fisher, Cornwallis and West, 2013), i.e. when social groups are formed out of an aggregation of cells that are not always identical. Interestingly, there is a similar story to tell in the case of insect societies: obligate insect societies (with sterile females) only evolve when there is monogamy (Boomsma, 2009), leading to a potential worker being equally related to her own offspring and to the offspring of her mother ($r=1/2$ in both cases; the relation to the offspring of her mother is the average of three-quarters (to the daughter of the mother) and one-quarter (to the son of the mother)). Any small efficiency benefit for rearing siblings (offspring of the mother) over their own offspring will then favour eusociality (i.e. a division of labour resulting in an obligate insect society). Hence it appears that a bottleneck is essential for the formation of obligate collectives: they

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evolve when a multicellular organism is derived from a single cell, and when an insect society is started by a single queen fertilized by a single male.

Yet although current human societies are not obligate societies, social groups evolved. One can argue that the stability of human societies requires a social-cultural explanation, but that does not exclude inclusive fitness theoretical explanations. I shall argue in this book that inclusive fitness theory applies here because the use of a language evolved as an extension of non-verbal, communicative behaviour. But I shall also argue that to use cultural and historical explanations becomes more and more important when humans are able to use a complex language.

The six major evolutionary transitions took time (see Bourke, 2011). It is estimated that the first cell arose around 3,500 million years ago (mya). Many events must have occurred between the origin of self-replicating molecules and the origin of the first cell. For example, there has been a switch from RNA to DNA as the primary replicator, and the genetic code and protein synthesis evolved during this period. The first symbiotic unicell arose 2,000 mya. The eukaryotic cell was 1,000 times larger by volume than its prokaryotic predecessors. It acquired not only cell organelles (mitochondria, in the later animals, and chloroplasts, in the later plants) as the result of the symbiotic fusion of two cells, but also possesses several structures which are absent in prokaryotic cells, such as a nucleus and internal cytoskeleton. It is unclear when the transition from asexual unicells to the sexual unicell occurred, but it can be placed between the origin of eukaryotes (2,000 mya) and the origin of multicellular organisms (1,200 mya), because it has not preceded the origin of eukaryotes. Prokaryotes (e.g. bacteria) transfer genetic material to one another, but sexual reproduction in eukaryotes involves the formation of haploid gametes from a diploid cell and the fusion of the gametes to form a zygote. Multicellular organisms arose 1,200 mya and there is evidence that multicellularity evolved at least sixteen times independently in eukaryotes. Simple multicellular eukaryotes are slime moulds (social amoeba); complex multicellular eukaryotes are animals and plants. The first eusocial societies (a social system with non-reproductive workers) consisting of multicellular organisms arose 150 mya; the first steps resulting in language evolution were taken about 2 million to 3 million years ago.

Bourke (2011) subdivided the stages of evolutionary transitions into three principle stages (see Table 1.2). First, social group *formation*: i.e. the initial formation of a higher-level unit as the result of the spread of genes for social behaviour through the population. Kinship and mutual benefit explain why units join forces. Second, social group *maintenance*:

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i.e. the stable persistence of higher-level units once they have originated (e.g. through mediation of potential conflicts between subunits). Because the stability of the new-formed unit depends on the coincidence of fitness interests, fraternal unions are maintained through self-limitation, whereas egalitarian unions are maintained through shared reproductive fate. A well-known example of the latter principle is the uniparental inheritance of mitochondria: they are transmitted through the female gamete reducing the potential of conflict. For if mitochondria are transmitted only through the female germ line, a mitochondrial variation occurring in the male will not be passed on to the next generation, and the success of a mitochondrial variation arising in the female depends on the success of the female (see further in Chapter 3). Third, social group *transformation*: i.e. the process that transforms the facultative higher-level unit into an obligate one. For example, in a simple, facultative multicellular organism, somatic cells are totipotent (in insect societies workers have reproductive potential), whereas in a complex, obligate multicellular organism all somatic cells lost totipotency and the organism displays a segregate, early-diverging germ line (in insect societies workers have low reproductive potential and the society displays high queen–worker dimorphism).

Units coordinate their actions in order to achieve common goals. Inclusive fitness theory explains these goals in evolutionary terms, i.e. goals are defined in terms of reproductive fitness. I shall later explain why another interpretation of ‘common goals’ is essential for understanding the transition to human societies, but first discuss the evolutionary view. The advantage of the evolutionary definition is that it enables us to see the common principles of social evolution. For example, compare a multicellular organism consisting of interacting cells with an insect society consisting of interacting organisms. In both cases kin selection explains why new levels of social organisation evolved consisting of lower-level units (cells or organisms) coordinating their activities or actions so that fitness is maximized. There is, of course, an important difference: in the case of multicellular organisms the cells are identical ($r=1$ if there are no mutations) if they are derived from a single cell; in the case of an insect society the relatedness between sisters is three-quarters if the society is founded by a single queen fertilized by a single male. Because males develop out of unfertilized and females out of fertilized egg cells, the sisters share the common genome of their father but only one of the genomes of their mother; hence the relatedness is $(1+\frac{1}{2})/2=\frac{3}{4}$. Yet kin selection explains why cells coordinate their actions and why females are the cooperative part of the insect society, and why somatic cells and workers sacrificed their

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reproductive potential. Kin selection theory also predicts that both transitions are contingent upon suppression of conflict between lower-level units. One can predict that conflict was more abundant during the transition to insect societies because of the lower value of r (see Ratnieks, Wenseleers and Foster, 2006).

Hence in both cases kin selection explains the evolution of a new entity consisting of lower-level entities interacting to maximize reproductive fitness, either as parts physically joined to one another (a multicellular organism), or as parts that remain and tend to remain in close proximity (an insect society). Note that only humans can create bonds between individuals even if they are not living in close proximity to each other. Note also that there is no separation between altruistic and reproductive functions in human societies, and that language evolution enabled humans to form intentions and, hence, to choose between selfish and altruistic behavioural options. It is, therefore, a challenge to extend the conceptual framework of inclusive fitness theory so that this extension (1) highlights the common principles of social evolution and (2) is capable of accommodating the transition made possible by language evolution.

Fraternal and egalitarian unions are two extremes and it is possible to characterize the major transitions, as described in Table 1.2, as fraternal, egalitarian, or both. For example, the evolution of workers in social insects is a characteristic of a fraternal union, while the union of the female and male halves in the genome of sexual organisms is an example of an egalitarian union. The evolution of genomes probably involved both egalitarian and fraternal elements, because it included identical genes and unrelated ones.

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Inclusive fitness theory solved the problem of altruism through invoking indirect fitness effects. For example, a cell of the immune system displays ‘suicidal altruism’ (apoptosis) when the cell is infected by a virus. It exhibits this behaviour because it promotes the survival and reproduction of its relatives in the whole organism. For the effect of apoptosis is not only that the cell dies, but also that the virus present in the cell is degraded by enzymes. Hence apoptosis is part of a defence mechanism: it reduces the survival and replication of the virus and enhances therefore the survival and replication of the genes (of the cell committing suicide) because copies of those genes are also present in the germ line of the

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organism. Suicidal altruism is therefore explicable in terms of inclusive fitness theory because of its indirect fitness effects.

Inclusive fitness theory teaches us that the ultimate goal of genes is to maximize their transmission to future generations. This can be calculated and modelled, for this definition of the (ultimate) goal can be described as the effect of genes on the (expected) offspring numbers. Evolutionary biologists are not concerned with the goals or intentions of an organism when they study goals: they only investigate fitness effects. This clarifies why they also attribute goals to cells and talk about the ‘suicidal altruistic behaviour’ of the cytotoxic T-cells of the immune system (see further in Chapter 3). Note also that when they talk about ‘selfish genes’, the resulting behaviour displayed by cells or organisms may be either altruistic or selfish. I shall later elaborate this view, but first discuss three well-known examples illustrating how inclusive fitness theory explains cooperation and conflict at the subcellular level (see Burt and Trivers, 2006; Keller, 1999; Stearns and Hoekstra, 2005, chapter 9).

1.3.1 Transmission of bacterial plasmids

Many bacteria carry circular DNA molecules called plasmids. These have genes important for their own propagation, but they also contain genes which are beneficial for the bacterial cell, like those that code for antibiotic resistance. Plasmids are transferred vertically, i.e. at bacterial cell division they are transmitted to the daughter cells. If this was the only possibility, then their long-term fate would be coupled to that of the bacterial host: the more successful the host, the more successful plasmids are. Inclusive fitness theory explains then why the possible actions of plasmid genes coincide with those of the host. However, horizontal transmission occurs too. The genes of many plasmids are able to induce their host to conjugate with another, uninfected cell. During conjugation the recipient acquires a plasmid while the donor retains a copy. The consequence of horizontal transmission is that the long-term fate of plasmids is no longer coupled to the success of the host cell. Models show that, if the horizontal transfer occurs frequently enough, plasmids can invade and establish themselves despite a negative effect on the bacterial host. Hence horizontal transmission creates the potential for conflict between the host and plasmids. If plasmids have negative effects, natural selection at the level of the host will favour the loss of plasmids, since plasmid-free bacteria do not bear the costs. Natural selection also predicts then the evolution of counteractions of plasmids.