

Local Interaction, Multilevel Selection, and Evolutionary Transitions

Peter Godfrey-Smith

Philosophy Department
Harvard University
Cambridge, MA, USA
pgs@fas.harvard.edu

Abstract

Group-structured and neighbor-structured populations are compared, especially in relation to multilevel selection theory and evolutionary transitions. I argue that purely neighbor-structured populations, which can feature the evolution of altruism, are not properly described in multilevel terms. The ability to “gestalt switch” between individualist and multilevel frameworks is then linked to the investigation of “major transitions” in evolution. Some explanatory concepts are naturally linked to one framework or the other, but a full understanding is best achieved via the use of both.

Keywords

altruism, complexity, evolutionary transitions, kin selection, multilevel selection, reaction norm

The starting point of this article is a distinction between two kinds of population structure that can make a difference to evolutionary processes. The distinction is between populations divided into discrete *groups* and populations in which individuals interact locally with their immediate *neighbors*, but where there are no group boundaries. In the first section, the distinction is described more precisely. In that section my goals are largely critical; I argue that the role of this distinction has not been recognized in some previous discussions. Neighbor-structured populations are sometimes described using a multilevel theoretical framework borrowed from work on group-structured populations. I argue that this is a mistake, and that this point also has consequences for our understanding of the evolution of altruistic behavior.

The second part of the article links the distinctions made in the first part to earlier discussions of “pluralist” treatments of levels-of-selection questions and to theorizing about the “major transitions” in evolution. Pluralists have argued that group structure can be seen both as a special kind of environmental *context* confronted by individual organisms, and in terms of the presence of a population of higher level *collectives*. This duality of perspective has a special role when thinking about evolutionary transitions that involve the binding together of lower level units into a higher level evolutionary individual. In this section I make connections to recent work by Carl Schlichting, Dan McShea, and Brett Calcott, as well as to less recent work by a long-dead Victorian.

1. Multilevel Selection and Two Kinds of Population Structure

The simplest models of evolution treat populations as unstructured; the evolving population is imagined as comprising a large, well-mixed soup. If interaction between individuals is important (in the treatment of mating, contests, and so on), then it takes place at random.

Real populations are structured in space, of course, and interaction between individuals is generally not random. There is a long tradition of modeling the consequences of such structure for evolutionary processes (Wright 1932; Levene 1953; Hamilton 1975; Wilson 1980; Wade 1985). In evolutionary biology, the main approach taken by theorists has been to look at consequences of the division of a population into discrete groups. These might be persisting “demes,” or shorter-lived aggregations. An alternative approach, often treated as secondary in the evolutionary literature, supposes that individuals are located on a spatial array, interacting locally with their neighbors but without group boundaries.

The relation between these two kinds of population structure has often been discussed fairly informally. Maynard Smith (1976) used the distinction to insist that kin selection is not always a form of group selection, because kin selection can

be important in neighbor-structured populations where group boundaries are not present. Hamilton (1964, 1975) coined the term “viscous population” for, roughly speaking, cases of the neighbor-structured kind where dispersal after reproduction is local. Wilson (1975, 1980) noted the distinction between the two kinds of population structure when he first developed his “trait-group” model of group selection. Wilson used the term “group” very broadly, however, distinguishing “discrete” as opposed to “continuous” trait-groups. The case he described in terms of “continuous trait-groups” corresponds to what I call a neighbor-structured population.

In theoretical discussion, neighbor-structured models were for some time often treated as secondary. (Nunney [1985] is an exception.) More theoretical effort has been devoted to the consequences of the partitioning of populations into groups (Wade 1985). But recent years have seen a surge of interest in models of behavioral evolution that employ spatial lattices and game-theoretic interactions between neighbors. This includes some striking work on cooperation and altruism (Nowak and May 1992; Wilson et al. 1992; Alexander and Skyrms 1999; Mitteldorf and Wilson 2000; Skyrms 2004; Werfel and Bar-Yam 2004). This new work has considerable importance for foundational questions, but it has sometimes been misdescribed. Theoretical principles developed for the group-structured cases are borrowed and applied to the neighbor-structured cases, even when their application to these cases is questionable. In a sense, the tools of theoretical description have not kept pace with the development of new models.

The reasons for this phenomenon are interesting from a methodological point of view. Evolutionary change in a neighbor-structured population on a spatial lattice tends to be difficult to describe mathematically in analytic terms over many generations. This is because if reproduction is treated as a spatially local matter, then the “viscosity” of the population tends to affect *everything* in the model. It affects not just the fitness of individuals at one time-step, but also the future distribution of individuals on the lattice, and hence the future distribution of neighborhoods experienced by individuals. So work on these models is often done with simulations, and research of this kind has advanced rapidly as the technology of computer simulation has improved.

The features of neighbor-structured populations that I will focus on here, however, can be discussed using a simplified case that can be compared very directly to the familiar group-structured cases. We achieve the simplification by making the spatial distribution of individuals *ephemeral* rather than persisting. This is illustrated in Figure 1.

In the case depicted in Figure 1(A), any individual has fitness-affecting interactions with four other group members. In the case depicted in Figure 1(B), any individual has fitness-affecting interactions with its four edge-neighbors (also known

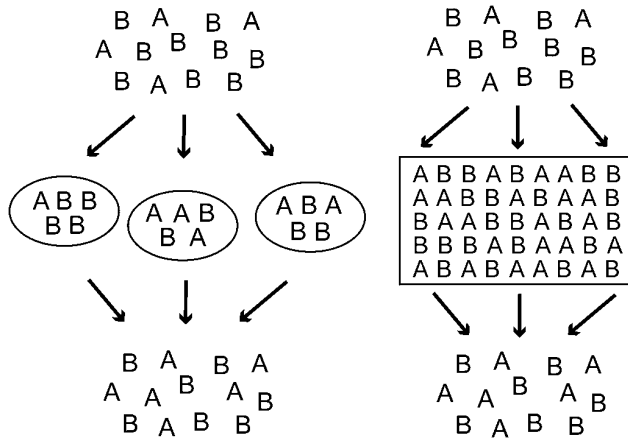


Figure 1. A, A discrete trait-group model and, B, an “ephemeral” neighbor-structured model.

as its “Von Neumann neighbors”). In both cases, the life cycle includes the regular formation and dissolution of population structure. In each case, population structure is generated (in the form of either groups or a lattice), selection then occurs, and asexual reproduction dissolves the population structure and creates a “pool” from which a new generation is formed.

In some ways, these two models are very similar. For example, various kinds of “altruism” can evolve in each. Roughly speaking, an altruist is an individual who donates benefits to other individuals around it, at some cost to the donor. Standard definitions of altruism for group-structured populations must be modified to be applicable to the neighbor-structured situation, but the core principles are the same in each case.¹ In particular, a positive association or “clumping” of types in the population helps the altruistic type in both kinds of population. Via this association, the benefits of altruistic behavior fall preferentially on other altruists.

There has been extensive discussion of how we should describe the process in Figure 1(A), where the population is divided into discrete groups. In particular, should we apply a “multilevel” approach that distinguishes processes of within-group and between-group selection? Provisionally, let us say “yes” to that question.

How should we then describe the neighbor-structured case? It is common to treat the neighbor-structured case as a messier, but fundamentally similar, version of the familiar group-structured case. As noted above, theoretical principles developed for the group-structured case are often borrowed for the neighbor-structured case. For example, the success of an altruist type is often explained in terms of a between-group force favoring altruism prevailing over within-group selection favoring the selfish type. This is seen, in slightly different forms, in Wilson (1980), Nunney (1985), Sober and Wilson (1998), and Okasha (2007).² I hold, however, that the multilevel description often borrowed for the neighbor-structured case

relies on features that are only present in the group-structured case.³

I will go through this argument in detail. The core of the multilevel framework, as noted above, is the distinction between selection within and between groups. Some groups do better than others, and some individuals do better than others within their groups. To apply this multilevel description, we need a *partition* of the total population into groups. These groups are collective or higher level entities, each made up of a number of lower level individuals. At least some of the groups should have more than one member, and each individual should be a member of only one group. (I will later discuss the possibility of a partial relaxing of this requirement.) Further, for there to be competition or selection *between* these groups, we need the population to contain more than one group. Lastly, if the groups recognized are nonarbitrary, there must be some real biological relation between individuals that determines who is in a group with who.

I will introduce a more formal framework for describing some of these requirements. Groups in the sense sketched above are *equivalence classes* of individuals.⁴ If groups are described by means of a relation *x is in the same group as y*, defined on the lower level individuals, we find that this relation is reflexive, symmetrical, and transitive.⁵ This is an “equivalence relation” and it collects entities into equivalence classes. We then face a key question: which facts about the biological interactions between individuals determine who is in the same group? What is the biological basis for the equivalence relation *x is in the same group as y*? If some single relation is supposed to determine the grouping, then it must also be an equivalence relation, given the nature of the structure it is supposed to generate.

It is easy to see how this works in the group-structured model in Figure 1(A). In models of this kind, the population is divided into collections or subsets, such that everyone inside a subset affects the absolute fitness of everyone else inside that subset, and no one outside a given subset (directly) affects the absolute fitness of anyone inside that subset.⁶ In models of altruism, for example, there might be a rule applying to the population such that each individual receives a fixed fitness benefit r from every altruist in its group, and from no one outside its group. (In these models, altruists usually are said to pay a fixed cost c regardless of the composition of their group.) In cases of this kind, the relation *x has its fitness affected by the character of y* is an equivalence relation. This relation is reflexive, symmetrical, and transitive.⁷ So in this case we can look at the pattern of relations by which one individual’s character affects the fitness of another, and use these facts to partition the population into a set of nonarbitrary groups, around which lines can be drawn as in Figure 1(A).

Things are different in the case in Figure 1(B). In some ways, the problem is obvious from inspection—there is no

nonarbitrary partition of the population. But it is worth working through the formal treatment to see how the problem arises.

As in the group-structured case, each individual has fitness-affecting interactions with a limited number of other individuals, its neighbors. But in the case where neighbor interactions affect fitness, the relation *x has its fitness affected by the character of y* is not an equivalence relation. The relation is reflexive and symmetrical, but not transitive.⁸ So the relation *x has its fitness affected by the character of y* cannot be used directly to partition the population into subsets, where all members of a subset have the relevant relation to all the others inside the subset and not to anyone outside.

Might there be a way to use the relations between individuals in Figure 1(B) in a more indirect way to do the required job? Suppose individuals might be placed in the same group in virtue of a *chain* of fitness-affecting interactions, as well as a direct interaction. Thus we make the relation that collects individuals into groups into a transitive relation. But then everyone in the population will be collected together into one big group, as everyone can be linked in such a chain to everyone else. There is then no possibility of competition between distinct groups in the population.

Another response might be to say that each individual is at the center of its own cross-shaped group; there are as many groups as individuals.⁹ Let us think through the details of this idea. We now say that every individual is both the “focal” member or center of one group, and also a nonfocal member of four other groups. We could define a collective output, or group-level fitness, for objects of this kind. Here, just as in the more familiar models of the Figure 1(A) type, we treat the collective output of a group as the combined or mean output of all individuals within it. A cross-shaped group is still a group, in this sense. Some crosses will be more productive than others, and some individuals within any cross-shaped group will do better than others. But each individual’s output now counts toward five different groups; everyone’s fitness is being quintuple-counted. And as each individual has its output affected by its own neighbors, nonfocal group members are *mostly* being affected by the character of individuals who are *not* in their group.

An example can be used to make this more concrete. Suppose the two types in the population, A and B, are described by the following fitness relationships (formally given in note 1). First, the B-type does better than the A-type in any given neighborhood. Second, it is true of both types that they have higher fitness in direct proportion to the number of A-types among their neighbors. The A-type is then an altruist, and the B-type is selfish.

Now consider a particular group, G, containing a focal individual of the selfish type surrounded by four altruist individuals. What contribution will these altruists make to the group fitness? We do not yet know. The nonfocal altruists will

make a big contribution to G’s fitness if *they* are surrounded by altruist types on their other three sides, and a small contribution if surrounded by selfish types. So three out of four of the neighbors whose character affects a nonfocal individual’s contribution to a group will not themselves be members of that group. Putting it differently, for four of the five groups that any individual is counted in, three quarters of its fitness-affecting interactions are with individuals outside that group.

By allowing for the quintuple-counting of each individual, and by looking constantly outside a group when determining an individual’s contribution to that group, it may be possible to recover a formal description of evolution in these cases that ostensibly uses the language of within-group and between-group processes. But the fact that the number of groups is the same as the number of individuals shows that, even aside from the great artificiality of this description, we have abandoned a core idea of multilevel selection theory, the idea of partitioning the lower level population into a range of competing higher level entities. I do not know of any attempt to actually present a mathematical analysis of selection in a purely neighbor-structured population by calculating between-group and within-group fitness differences. It is quite common to give informal summary descriptions of change in neighbor-structured populations using the language of multilevel selection theory, but the underlying calculations are done in individualist terms, and the viability of the informal descriptions is exactly what I am challenging here. In cases of the Figure 1(B) kind, population structure instead operates as an aspect of the *environment*, or *context*, confronted by individuals.

So this first stage of my argument can be expressed in the form of a necessary (not sufficient) condition on the presence of multilevel selection in a structured population.¹⁰ Multilevel selection requires the presence of nonarbitrary equivalence classes of lowerlevel entities, or at least an approximation to this situation.

I emphasize the qualification “or at least an approximation.” Suppose a population consists of groups with reasonably clear boundaries, within which all individuals strongly affect each other’s fitness, but with some degree of overlap between the groups. Such a case would clearly approximate the simpler case where there are genuine equivalence classes, and that should be sufficient. But there are also cases of structured populations that do not approximate the required condition at all, and the purely neighbor-structured case in Figure 1(B) is a clear example.

These facts about the special role of neighbor-structured populations have been neglected, I suggest, because people tend to derive theoretical principles from analytically simpler group-structured models where there *are* equivalence classes.¹¹ The resulting theoretical principles are then applied generally. But there have always been clues around, pointing to the phenomena that I focus on here. The most important of

these clues is the fact that the Price equation, the most popular tool for the formal representation of multilevel selection, requires a partition of the population into equivalence classes when it is used for this purpose. So if, in some real-life case, there is partial overlap between groups, and hence only an approximation to the requirement of equivalence classes, using the Price equation requires that we “clean up” the partition, and suppose there is no overlap.

People may also sometimes resist the message of these arguments because they seem to show that in neighbor-structured populations only “individual selection” can exist. Altruism can evolve in neighbor-structured populations, and it may seem that pure “individual selection” is incapable of explaining how altruism could survive.¹² So it might then appear that dropping the language of multilevel selection in these cases involves dropping the key to the explanation of how altruism is possible. But to say this is to mistake the resources of a sophisticated individualist or contextualist treatment of how these cases work. The key to the evolution of strong forms of altruism is positively correlated interaction between individual types (Hamilton 1975; Michod and Sanderson 1985; Skyrms 1996; Frank 1998).¹³ The idea that correlation is essential to the evolution of strong forms of altruism is sometimes presented as a crucial principle *within* multilevel selection theory (e.g., Wilson 1977). I think that some people regard an emphasis on multilevel selection and an emphasis on correlated interaction as amounting almost to the same thing. But they do not amount to the same thing. Correlated interaction can exist in purely neighbor-structured populations that do not have group boundaries and cannot be partitioned nonarbitrarily into a set of higher level collective entities. So one key message that can be drawn from models of neighbor-structured populations is that correlation, which is in many ways the key to the evolution of altruism, does not require group structure.

More generally, my aim in this section is to urge the recognition of the different kinds of relational structures that populations can be embedded in. Some of these networks of relations linking individuals generate equivalence classes, motivating the recognition of a higher level population of groups, and some do not. When the relations between individuals do not generate (at least an approximation of) a partition into equivalence classes, it is a mistake to look for a multilevel description. Instead, we have a different kind of structure, motivating a different theoretical treatment.

2. Gestalt Switching and the Evolutionary Transitions

In the previous section I contrasted two cases:

(i) Populations divided into discrete groups, where there is no overlap between and no structure within the groups

versus

(ii) Neighbor-structured populations, with no divisions into groups or distinct regions.

The discussion so far has been idealized in two respects. First, it has only considered extremes. Either model, when used to describe a real empirical situation, will usually be a simplification. Generally, we will find a mixture or combination of both kinds of structure.

Secondly, so far we have imagined the population structure as imposed on the organisms by their circumstances. But in most cases, the pattern of interactions between organisms that affects fitness will be a product, in part, of the organisms' own behavior and other phenotypic characteristics. Population structure and the evolutionary response to it will often coevolve. An important case of this is seen in the creation and maintenance of *boundaries* by collections of living things, the creation of a division between a richly connected ingroup and the rest of the world.

Cells within a complex multicellular organism provide a useful illustration of the role of both idealizations here. For some purposes, an organism is a collection of cells that can be seen as forming an equivalence class. That is, in some contexts all that matters is whether or not a cell is part of the same organism as certain other cells. The total population of human cells can be partitioned (approximately) into those that are my cells, those that are your cells, and so on. Here, *cell x is part of the same organism as cell y* is an equivalence relation.

But when we are thinking about these cells for other purposes, we will recognize, of course, that an organism is internally organized, and many important relations between cells are intransitive and asymmetric. One cell is next to another, which is next to others again. One cell is nearer to the periphery of the system than another. The same will apply in many other cases of important collective entities—genes on a chromosome, or individuals within a social group, for example.

A connection can be made here to the “gestalt-switching pluralism” about some levels of selection debates defended in Kerr and Godfrey-Smith (2002). There we argued, for the simple case of discrete groups, that it is often good to switch between two ways of thinking about the higher level structure in a population. We can think of groups both as *collectives*, as the bearers of group-level fitness values, and also as aspects of the *context* or environment experienced by lower level individuals. Each of these ways of describing group structure, collectively versus contextually, tends to highlight some facts at the expense of others.¹⁴ Consequently, it is useful to be able to freely switch between these two ways of looking at a single system. This position is a relative of earlier “pluralist” views developed for trait-group models by Dugatkin and Reeve (1994) and Sterelny (1996). In the previous section of this paper I conceded the value of a multilevel description of the group-structured cases, but that concession should

be understood within the larger framework of gestalt-shifting pluralism. So the overall argument of the previous section can be summarized in this terminology by saying that trait-group structure can be thought of in both collective and contextual terms, but the neighbor-structured case can only be treated contextually.

In the rest of this section I will argue that this gestalt shifting between different ways of looking at population structure will be especially important when thinking about the “major transitions” in evolution (Maynard Smith and Szathmáry 1995; Michod 1999).¹⁵

The distinction discussed earlier has two kinds of relevance to the transitions. First, understanding the major transitions is, in many cases, understanding the evolution of higher level collectives from a state in which the relational structure was different. This is clearest in cases where transitions include appearance of new boundaries, creating a divide between members of a collective and the environment.

But second, during the process of transition itself, both ways of thinking about population structure may be important, each giving us conceptual purchase on distinct aspects of the situation. One reason for this is the fact that some theoretical concepts that are relevant here bring with them a “logic” that goes with one viewpoint or the other, contextual or collective.

I will discuss this by means of a particular example, Carl Schlichting’s recent work on “developmental reaction norms” (Schlichting 2003). Consider an idealized situation where we have a collection of cells, or other lower level units, coming together to form a coordinated higher level entity.¹⁶ As Buss (1987), Calcott (unpublished), and others have emphasized, such an evolutionary process is affected by two factors that pull in different directions. Using a terminology employed by Calcott, the evolution of a higher level collective must simultaneously achieve both the *alignment of reproductive interest* and the *generation of benefit*.

The problem of the alignment of reproductive interest is the evolutionary reflection of the more general problem of conflict, free riding, and subversion in collective enterprises. In the evolutionary case, the relevant forms of subversion tend to involve unconstrained reproduction by lower level entities, at the expense of the collective. Homogeneity in the collective, of some relevant kind, helps avoid this problem. Close genetic relatedness between the potentially reproducing components, for example, can bring about an alignment of reproductive interests.

However, this homogeneity often reduces the benefits that make the collective worth entering into. That is why the alignment of reproductive interest can pull against the generation of benefit. Although size per se can be a useful feature of a collective (Bonner 1988), often the benefits of membership in a collective derive from the division of labor, and the coordi-

dination of disparate activities. These require some relevant *heterogeneity* of parts. So one aspect of the overall problem pulls in the direction of homogeneity and the other pulls toward heterogeneity. In the case of multicellular organisms, as Buss and Schlichting emphasize, this is a key theme in the evolution of development and cellular differentiation.

Schlichting suggests that we can make conceptual progress on this problem by using the *reaction norm* concept (Schlichting and Pigliucci 1998). The reaction norm concept is usually applied at the level of whole organisms; here we apply it at the suborganismal level. Suppose we are thinking about a collection of genetically identical or very similar cells. It is easy to fall into the habit of thinking that this genetic similarity implies phenotypic similarity. But strictly, what these cells have in virtue of their genetics is a common reaction norm. The cells will have the potential to produce various different states and activities, given different environmental stimuli. The *absence* of this sensitivity—a “canalized” phenotype that is not conditional on environmental stimuli—is something that takes evolutionary “work” to evolve. It is not the natural, prior, or default state.

So a collection of genetically identical cells will usually have some capacity to differentiate, via the role of different stimuli interacting with their common reaction norm. But what is the source of the different stimuli that generate these different “realized” phenotypes in the lower level entities?

Here we need to think in terms of a particular set of relations linking the lower level entities. Think of the cells arrayed as a group in space. Some cells will be near the periphery, some near the center. This fact alone will imply that they experience somewhat different microenvironmental conditions. Peripheral cells will be more directly affected by external conditions; cells in the center will be affected more by products of other cells in the group. Those different conditions will interact with the common reaction norm to produce different realized phenotypes. So differentiation per se is not something that needs explanation, once we remember to think in terms of reaction norms, and once we note the ubiquitous nature of microenvironmental differences for collections existing in space.

In some ways this argument is very old. Reasoning of this kind was central to the elaborate evolutionary speculations of Herbert Spencer (1866, 1872). Spencer held that homogeneity, an undifferentiated condition in a system, is inherently unstable. Natural tendencies will produce differentiation, and this will be seen in all systems. One of Spencer’s examples was exactly the case of an initially homogeneous collection located in space, with some elements subject more to influences from the external environment than others. The result, for Spencer, will be the inevitable differentiation of parts.¹⁷

Here as elsewhere, Spencer greatly over-played this argument. He saw the phenomenon as applicable on too many

scales and with too much reliability. But such reasoning may be quite useful in some cases. In recent work, McShea (2005) has sought to extract a useful core from Spencer's reasoning, and has applied a moderate "instability of homogeneity" principle to problems involving macroevolutionary trends toward greater complexity. For McShea, the indefinite retention of a simple, homogeneous condition is not a default state, which evolutionary forces must work against. The opposite is true. Natural tendencies will tend to produce increases in a basic kind of structural complexity, for general reasons of the kind sketched above. Most of this complexity will be maladaptive, mere noise or worse. Selection may be pushing *against* complexity most of the time. But of course, some rare increases in complexity are valuable and will be retained.

McShea's argument is more ambitious than the line of reasoning that we see in Schlichting's use of reaction norms. Schlichting's core point is that differentiation itself, in a genetically homogeneous collective, is not something that must take evolutionary "work" or a special kind of explanation. It is the nature of genetic systems to be sensitive to environmental stimuli, and collections existing in space will inevitably be subject to microenvironmental differences. Thus, we should regularly expect collectives of this kind to show the beginnings of a developmental sequence. Differentiation per se is not the same as adaptive, coordinated, differentiation, of course. That requires mutation and natural selection acting on the reaction norms themselves.

It is interesting that McShea and Schlichting have both, in different contexts, been pushing against the same set of informal assumptions about the explanation of complexity and differentiation.¹⁸ My primary example here, however, is Schlichting's line of thought. What sort of thinking have we applied, in working through his argument? We have been moving back and forth between collective and contextual modes of thinking, as a consequence of the different kinds of relations that are relevant at different points in the story. To apply the reaction norm concept we look at nontransitive and nonsymmetric relations that link a biological entity to its environment, its surroundings, its context. It does not matter whether this environment is biotic or abiotic. That is part of the logic of the reaction norm concept. The explanation it generates here works *because* the cells we are describing are not connected only by relations that are transitive and symmetrical, relations that merely group the cells into a collective. If they were, the mechanism Schlichting describes would not apply. To explain differentiation in a collection of cells using the reaction norm concept, we apply a contextual mode of thinking. But our aim, of course, is to explain the evolution of a higher level collective—something with boundaries, division of labor, and the ability to suppress internal conflict. The aim is to explain what Michod (1999) calls a "transition in individuality."

The main themes of this paper can be summarized as follows. Owing to the rich theoretical development of multilevel selection theory as applied to group-structured populations, it has often been tempting to apply these concepts to other kinds of population structure as well. The temptation is especially strong when cooperative and altruistic behaviors are the focus of explanation. But the key to the explanation of strong forms of altruism—positively correlated interaction between types—can operate in neighbor-structured cases where higher level collectives are absent. Though cooperation itself does not require the presence of higher level collectives, higher level collectives of various kinds are often what we see. Evolution has conspicuously included the evolution of various higher level bounded collectives, including both loose social aggregations and tightly integrated products of "transitions in individuality." Why has the evolutionary process tended to "package" cooperating entities in this particular way? In understanding these transitions, gestalt switching between contextual and collective ways of thinking about population structure is exactly the kind of thinking that will often be useful.

Acknowledgments

This article was presented at the ISHPSSB Meetings in Guelph, 2005. I am grateful to those present and to Ben Kerr for helpful comments.

Notes

1. The most natural definition of altruism for neighbor-structured populations is a hybrid of the "focal-complement" definition and the "individual-centered" definitions of altruism discussed in Kerr et al. (2004). Suppose that α_i is the fitness of an A-type individual with i neighbors of the A-type, and β_i is the fitness of a B-type individual with i neighbors of the A-type. Then A is an altruist if these three conditions hold:

- (1) $\alpha_i < \beta_i$, for $i \in \{1, 2, \dots, n\}$;
- (2) $\alpha_i < \alpha_{i+1}$, for $i \in \{1, 2, \dots, n-1\}$;
- (3) $\beta_i < \beta_{i+1}$, for $i \in \{1, 2, \dots, n-1\}$.

2. I include Okasha here because of his treatment of contextual analysis (Damuth and Heisler 1988). For Okasha, contextual analysis is overall superior to the Price equation and other methods for detecting group selection in group-structured populations. This method can also be applied to neighbor-structured populations. As I understand Okasha (2007), his conclusion is that contextual analysis detects a kind of group selection in these cases too.

3. For an informal version of this argument, which was the germ of this article, see also Maynard Smith (2002).

4. The term comes from set theory and related parts of mathematics.

5. Relation R is reflexive if and only if for all entities x in the relevant domain, x has R to itself. Symmetry: if x has R to y , then y has R to x . Transitivity: if x has R to y and y has R to z , then x has R to z .

6. Absolute fitness, not relative. Otherwise, it is trivial that everyone affects everyone else's fitness.

7. Perhaps the reflexivity is not as obvious as the other features. The idea is that any individual's character affects its own fitness; it would have a different fitness if it switched from altruist to selfish, or vice versa, whatever its group context.

8. In Godfrey-Smith (forthcoming), I discuss a case where the problem arises from the symmetry requirement. It would also be possible (though more

implausible) to generate a case where the reflexivity requirement creates the problem.

9. This is how D. S. Wilson sometimes describes these cases (1980: 38–39).

10. More precisely, this is a condition on “MLS1.” See Damuth and Heisler (1988) and Okasha (2007).

11. Wade (1985), for example, gives an influential theoretical summary of the relations between hard selection, soft selection, kin selection, and group selection using a Pricean framework that assumes a partition into equivalence classes. There is no discussion of other kinds of population structure.

12. A version of this principle is at work in Nunney’s valuable (1985) treatment of this issue.

13. Hamilton’s (1975) paper is usually interpreted as an endorsement of multilevel selection theory. In some ways it is, but Hamilton also explicitly notes that the crucial role of correlation can operate in fostering altruism in a “viscous” population where groups are absent; see p. 337.

14. This sense of “contextual” is different from the sense seen in the “contextual analysis” of Damuth and Heisler (1988), though there are interesting relations between the two.

15. Here I follow up a brief comment at the end of Kerr and Godfrey-Smith (2002). See also Sterelny (forthcoming).

16. For an empirically oriented review of recent work on this topic, see King (2004).

17. For a very short summary, in Spencer’s own words, of his biological views, see chapter 15 of Belew and Mitchell (1996). I give a longer summary in chapter 3 of Godfrey-Smith (1996).

18. The fact that they are thinking along similar lines is seen in this quote from the McShea paper: “We are used to thinking of complexity as hard to produce. The [Spencerian] internal-variance principle shows it to be easy. . . .” (p. 155). Contrast Queller (1997: 186), who is thinking about the problem very differently.

References

- Alexander J, Skyrms B (1999) Bargaining with neighbors: Is justice contagious? *Journal of Philosophy* 96: 588–598.
- Belew R, Mitchell M, eds (1996) Adaptive individuals in evolving populations: Models and algorithms. *Proceedings of Santa Fe Institute Studies in the Sciences of Complexity*, Vol. 26. Reading, MA: Addison-Wesley.
- Bonner JT (1988) *The Evolution of Complexity*. Princeton, NJ: Princeton University Press.
- Buss L (1987) *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Calcott B (unpublished) Selection, variation, and development in major evolutionary transitions. Presented at ISHPSSB 2005, Guelph, Canada.
- Damuth J, Heisler L (1988) Different formulations of multi-level selection. *Biology and Philosophy* 3: 407–430.
- Dugatkin L, Reeve HK (1994) Behavioral ecology and levels of selection: Dissolving the group selection controversy. *Advances in the Study of Behavior* 23: 101–133.
- Frank S (1998) *Foundations of Social Evolution*. Princeton, NJ: Princeton University Press.
- Godfrey-Smith P (1996) *Complexity and the Function of Mind in Nature*. Cambridge: Cambridge University Press.
- Godfrey-Smith P (forthcoming) Varieties of population structure and the levels of selection. *British Journal for the Philosophy of Science*.
- Hamilton WD (1964) The genetical evolution of social behavior, I and II. *Journal of Theoretical Biology* 7: 1–16 and 17–52.
- Hamilton WD (1975 [1998]) Innate social aptitudes of man: An approach from evolutionary genetics. In: *Narrow Roads of Gene Land: Collected Papers of W. D. Hamilton*, Vol. 1, 329–251. Oxford: Oxford University Press. [Reprint]
- Kerr B, Godfrey-Smith P (2002) Individualist and multi-level perspectives on selection in structured populations. *Biology and Philosophy* 17: 477–517.
- Kerr B, Godfrey-Smith P, Feldman M (2004) What is altruism? *Trends in Ecology and Evolution* 19: 135–140.
- King N (2004) The unicellular ancestry of animal development. *Developmental Cell* 7: 313–325.
- Levene H (1953) Genetic equilibrium when more than one ecological niche is available. *American Naturalist* 87: 331–333.
- Maynard Smith J (1964) Group selection and kin selection. *Nature* 201: 1145–1147.
- Maynard Smith J (1976) Group selection. *Quarterly Review of Biology* 51: 277–283.
- Maynard Smith J (2002) Commentary on Kerr and Godfrey-Smith. *Biology and Philosophy* 17: 523–527.
- Maynard Smith J, Szathmáry E (1995) *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- McShea DW (2005) The evolution of complexity without natural selection, a possible large-scale trend of the fourth kind. *Paleobiology* 31 (Suppl.): 146–156.
- Michod R (1999) *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.
- Michod R, Sanderson M (1985) Behavioral structure and the evolution of social behavior. In: *Evolution: Essays in Honor of John Maynard Smith* (Greenwood J, Slatkin M, eds), 95–104. Cambridge: Cambridge University Press.
- Mitteldorf J, Wilson DS (2000) Population viscosity and the evolution of altruism. *Journal of Theoretical Biology* 204: 481–496.
- Nowak M, May RM (1992) Evolutionary games and spatial chaos. *Nature* 359: 826–829.
- Nunney L (1985) Group selection, altruism, and structured-deme models. *American Naturalist* 126: 212–230.
- Okasha S (2007) *The Levels of Selection Debate*. Oxford: Oxford University Press.
- Queller D (1997) Cooperators since life began. *Quarterly Review of Biology* 72: 184–188.
- Price G (1972) Extension of covariance selection mathematics. *Annals of Human Genetics* 35: 485–490.
- Schlichting CA (2003) Origins of differentiation via phenotypic plasticity. *Evolution and Development* 5: 98–105.
- Schlichting CA, Pigliucci M (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland: Sinauer.
- Skyrms B (1994) Darwin meets the logic of decision: Correlation in evolutionary game theory. *Philosophy of Science* 61: 503–528.
- Skyrms B (2004) *The Stag Hunt and the Evolution of Social Structure*. Cambridge: Cambridge University Press.
- Sober E, Wilson DS (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.
- Spencer H (1866) *Principles of Biology*, 2 vols. New York: Appleton.
- Spencer H (1872) *First Principles of a New System of Philosophy*, 2nd ed. New York: Appleton.
- Sterelny K (1996) The return of the group. *Philosophy of Science* 63: 562–584.
- Wade M (1985) Soft selection, hard selection, kin selection, and group selection. *American Naturalist* 125: 61–73.
- Werfel J, Bar-Yam Y (2004) The evolution of reproductive restraint through social communication. *Proceedings of the National Academy of Sciences of the USA* 101: 11019–11024.

- Wilson DS (1975) A theory of group selection. *Proceedings of the National Academy of Sciences of the USA* 72: 143–146.
- Wilson DS (1977) Structured demes and the evolution of group-advantageous traits. *American Naturalist* 111: 157–185.
- Wilson DS (1980) *The Natural Selection of Populations and Communities*. Menlo Park, CA: Benjamin/Cummins.
- Wilson DS, Pollock G, Dugatkin L (1992) Can altruism evolve in purely viscous populations? *Evolutionary Ecology* 6: 331–341.
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth International Congress of Genetics* 1: 356–366.