



Recent Work in Individualism in the Social, Behavioral and Biological Sciences *

ROBERT A. WILSON

*Department of Philosophy, University of Alberta, 4–115 Humanities, TG6 2E5 Edmonton,
Canada; E-mail: rob.wilson@ualberta.ca*

1. Individualism and individualisms

The social, behavioral, and a good chunk of the biological sciences concern the nature of individual agency, where our paradigm for an individual is a human being. Theories of economic behavior, of mental function and dysfunction, and of ontogenetic development, for example, are theories of how such individuals act, and of what internal and external factors are determinative of that action. Such theories construe individuals in distinctive ways – in the above examples, as rational agents, as folk psychologists, or as creatures with a (more or less) fixed stock of innate rules and representations, together with a sophisticated toolkit for responding to interactions with the world.

The various sciences subsumed under the rubric “social, behavioral, and biological” – what have been called the *human sciences* (Smith 1997) – concern themselves with more than the whys and wherefores of the behaviors of such individuals, to be sure. To continue with our examples, they are concerned with institutional phenomena, such as exchange fluctuations and monetary policy, with group decision-making and dysfunction, and with the operation of biological and psychological modules that contribute to the development of the individual. Indeed, particular economists, psychologists, or geneticists may (and do) spend their whole careers focused on such extra- or sub-individualistic phenomena. Thus, these sciences are not simply to be identified as the study of individuals, in their various guises. Yet it remains true that individuals occupy center-stage for much of the social, behavioral, and biological sciences.

* The material in sections 2–5 of this paper are modified from the discussion in chapters 2, 7, and 10 of my *Genes and the Agents of Life* (New York: Cambridge University Press, 2004). The material in section 6 develops some nascent discussion in the final sections of the last chapter of my *Boundaries of the Mind* (New York: Cambridge University Press, 2004).

Various positions within these sciences have been called “individualistic”. Methodological individualism has traditionally divided social scientists, with methodologies such as rational choice theory typically viewed as individualistic, and as problematic for that reason by some (see Little 1991; Kincaid 1997). By contrast, several approaches to understanding mental representation and the embodied and embedded nature of cognition have been critiqued for *not* being individualistic (Adams and Aizawa 2001; Grush 2003). The labeling of such theories or approaches as individualistic implies more than that they concern themselves – too much or too little, as the case may be – with individuals. Rather, it implies a broader perspective on the nature of the phenomena to be explained, and the role of individuals and what is intrinsic to them in explanations of those phenomena.

There is a huge swath of work across these sciences that invokes the “individualism” label, and much diversity in it. Individualism arises as a self-consciously methodological position in both the social sciences and in psychology; with revolutionary fanfare in characterizing views of the nature of species in systematics and evolutionary biology; and implicitly in taking a stance on debates over nativism in the cognitive sciences. What I shall suggest in the next section is that, despite the diversity that exists between these appeals to individualism, there is a common framework for understanding individualistic positions. With that framework in place, I then turn to three issues within the biological sciences to which one or more debates over individualism are central: the levels of selection (section 3), genocentrism and developmental systems theory (sections 4 and 5), and, more speculatively, the relationship between cognition, sociality, and evolution (section 6).

Our thinking about the complexities to each of these issues is facilitated by keeping an eye on debates over individualism in other areas, and although I will keep a focus on the biological sciences here, I shall draw on other sciences, particularly the cognitive sciences, where appropriate.

2. Characterizing individualism across disciplines

Let me begin with psychology and the cognitive sciences more generally, where individualism has received its most detailed treatment. Individualism about psychology is the thesis that psychological states should be construed without reference to anything beyond the boundary of the individual who has those states. Put loosely, it is the view that for the purposes of scientifically understanding the mind, the individual is the boundary for cognition. Minds are located inside individuals, and we need not venture beyond the boundary of the skin in characterizing any individual’s mind. Thus, if one is an individualist about the mind, then one should abstract away from an individual’s

environment in characterizing her psychological states (see Wilson 2003a for a more detailed treatment).

A more precise expression of individualism says that psychological states should be taxonomized so as to supervene on the intrinsic, physical states of the individuals who instantiate those states. (A property, A, supervenes on another, B, just if no two entities can differ with respect to A without also differing with respect to B.) This has usually been taken to mean that if two individuals are physically identical, then they must also be *psychologically* identical. For this reason, individualism about psychology has often been presented as a view that follows from the acceptance of materialism or physicalism about the mind, and viewed as an instance of a general constraint on taxonomies across the sciences.

Three essential characteristics of this view of cognition are also shared by individualistic theses in the biological sciences. First, individualism is a normative thesis about how we ought to conduct our science. In the case of cognition, it proscribes certain views of our psychological nature, and so imposes a putative constraint on the sciences of cognition. Second, this constraint itself is claimed to derive either from general canons governing science and explanation or from entrenched assumptions about the nature of the subject matter of some particular science. It meshes with existing explanatory practices that have met with considerable success, and is an empirical rather than an *a priori* constraint on the sciences of the mind. Third, approaches to science that flout individualism are both methodologically and metaphysically misguided. In cognitive science, they go methodologically awry in that the most perspicuous examples of explanatorily insightful research paradigms for cognition – computational approaches – have been individualistic. They go metaphysically awry in a corresponding way, relinquishing the insights into mental causation afforded by computational views of cognition. In short, individualism about a particular science is a normative, empirically grounded constraint that guides how that science is practiced.

In the biological sciences, we can readily see individualism as an issue that arises in the debate over the levels or units of natural selection. Here individualism is the view that the organism is the largest unit on which natural selection operates. Thus, proponents of genic selection who claim that natural selection can always be adequately represented as operating on genes or small genetic fragments are individualists about the units of selection, as are those who adopt the traditional Darwinian view that allows only (near enough) for organism-level selection. To embrace higher levels of selection, such as group selection, is to reject individualism. Like individualism in psychology, individualism about the levels of selection is a putative normative constraint that

derives from existing explanatory practice, and whose violation, according to its proponents, involves both methodological and metaphysical mistakes.

First, individualism about the levels of selection implies that individual organisms act as a boundary beyond which evolutionary biologists need not venture when attempting to theorize in considering the nature of what it is that competes and is subject to evolutionary change through natural selection. Second, by focusing on what lies within the individual, one can best understand the dynamics of adaptive change within populations of organisms, whether it be via population genetic models, through the deployment of evolutionary game theory, or by means of the discovery of the forms that individualistic selection takes. This constraint builds on the specific explanatory successes of models of kin selection, reciprocal altruism, and other processes that articulate strategies that individuals might adopt in order to maximize reproductive success. Third, flouting individualism creates both methodological and metaphysical problems avoided by individualistic approaches. Methodologically: given that individualistic models of selection putatively explain the full range of observed behaviors in evolutionary terms, to reject individualism is to abandon real explanatory achievement. Metaphysically: just how does natural selection transcend the level of the individual and go to work directly on groups? Common (even if incompatible) responses to claims of group selection are that the appropriate model of group selection really boils down to a variant on an existing individualistic model of selection, and that it requires assumptions that rarely hold in the actual world. In the former case, we simply have individualism by another name; in the latter, our models are mere models and fail to correspond to how the world actually is.

In several places, I have argued that although there are strong *prima facie* reasons to think that individualism is a constraint on the sciences of cognition, and much cognitive science has been individualistic, in fact individualism should be rejected (Wilson 1995, 2003a). More positively, there are contrasting *externalist* views within the cognitive sciences worth developing further. These require re-thinking many concepts central to the philosophy of mind and cognitive science, such as physicalism, computation, and representation. While these views about cognition are not directly relevant to individualism about biology, they at least caution against an unreflective acceptance of individualism. The plausibility of individualism more generally depends in part on how the debate over individualism is generalized or transformed in moving from the cognitive to the remainder of the human sciences. There are at least three ways of doing so.

The first, exemplified by the above example of the debate over the levels of selection, is simply to transpose the issue of whether the individual organism serves as a boundary of some kind that constrains the form of the corre-

Table 1. Individualism: Cognition and biology

	Cognitive	Biological
Individualistic constraint	Individual as a boundary for cognition	Individuals as largest unit acted on by selection
Empirically ground explanatory practice	Appeal to scientific taxonomy in general or to specific features of psych. (e.g., computational theory of mind)	Principle of parsimony; success of individualistic theories, such as kin selection, reciprocal altruism
Denials:		
Methodological:	Abandoning best research programs	Abandoning best research programs
Metaphysical:	Giving up on mental causation and mechanisms	Group selection mysterious

sponding science (see Table 1). This form of generalization takes a bird's-eye view of the individualism debate over the mind, abstracting away from the metaphysical complexities – expressed in terms of realization, determination, and intrinsic properties, for example – that talk of supervenience brings in its wake. Call this form of individualism in the biological sciences *organismic boundary* individualism.

It is *prima facie* extremely plausible to think that at least some areas within the biological sciences, such as physiology, genetics, and developmental biology, are individualistic in this sense. Such sub-disciplines are concerned with units that are parts of, sometimes very small parts of, individual organisms. Since the systems that such units constitute can be understood in abstraction from much of the rest of the body of the organism, it is difficult to see why the same should not be true of the world beyond the individual. Thus, at least these parts of biology would seem to be constrained by organism boundary individualism.

A second way to extend the debate over individualism from the cognitive to the biological domain is to adapt the supervenience formulation of individualism and explore whether *biological* properties supervene on the intrinsic, physical properties of organisms. Call the position that holds that biological properties do so supervene *organismic supervenience* individualism. Although I implied above that one motivation for individualism in psychology was the idea that individualism held more generally in the

sciences, there are many examples of biological properties that *prima facie* flout organismic supervenience individualism. (In fact, such examples have provided one basis for challenging the presumption of individualism about the mind.) These examples include evolutionary fitness, being highly specialized, and being a predator, all properties of individual organisms or species, as well as properties of phenotypic traits or behaviors of individuals, such as being an adaptation, a homology, or a spandrel. All of these biological properties are *relational* or *contextual*, such that something can gain or lose the property simply through a change in that thing's relations, or in the context in which it exists.

To take one of these examples, whether a given trait, such as a wing of a particular shape and structure, is an adaptation (say, for flight) depends in part on the history of that structure. When evolutionary biologists argue about whether a wing-shaped structure is an adaptation for flight, this sort of historical consideration is paramount, and the lineage history is itself individuating. Lineage history is not simply an epistemic clue to discovering something intrinsic to the organism or trait itself, but part of what makes a given structure an adaptation for flight. Without the right kind of history, wing-shaped structures are not, cannot be, adaptations for flight, no matter what else is true of them, any more than pieces of paper lacking the right kind of history can be dollar bills. Two pieces of paper that were not just indistinguishable but identical in their intrinsic, physical properties could differ with respect to the property of being a dollar bill simply because only one of them was produced by the government treasury, the other by your neighbor. Likewise, of two wing-shaped structures identical in their here-and-now physical features, only the one that resulted from a lineage in which flying had been naturally selected would be counted as an adaptation for flight.

Given that it is common for the biological sciences to explore properties that metaphysically depend on more than the intrinsic, physical features of the agents that have them, can there be a serious debate over organismic supervenience individualism? One reason to think so comes from reflecting on individualism about cognition.

Individualists about the mind have conceded that there are many common (and commonsense) ways of describing mental states that are relational. They hold, nonetheless, that something like organismic supervenience individualism is true because of some sort of special relationship between such states and the intrinsic, physical states of individuals. Thus, the *narrow content program* is based on the idea that although ordinary, propositional content is not individualistic, it can be factored into narrow content, which is individualistic. This program thus aims to preserve a privileged causal role for the intrinsic, physical properties of individuals (see, e.g., Fodor 1987: ch. 2).

Something similar is true of those who have suggested an isomorphism of some kind between representational and computational or “syntactic” states (see, e.g., Stich 1983: ch. 8).

Likewise, in biology we might concede that folk and scientists alike often ascribe properties in ways that violate organismic supervenience individualism, but hold that there remains some special relationship between such properties and the intrinsic, physical properties of organisms. For example, even if we concede that a certain evolutionary history is needed for some structure to be a wing (or an adaptation for flying), there remains a biological natural kind of entity – call them *narrow* wings – that includes both wings and structures just like wings except for their history. Wings and narrow wings, after all, will bring about the very same causal effects when placed in the same context – they have the same causal powers – and a powerful intuition that supports the idea that there is more than word-play at issue here is that the biological sciences should attend to entities vis-à-vis their causal powers.

So the dialectic over organismic supervenience individualism is more complicated than it initially appears. On the one hand, given that relational properties are widespread in the biological sciences, particularly in the evolutionary and ecological aspects of biology, biology appears not to be individualistic in this sense. But individualists have a strategic response here, one that has been popular in thinking about cognition. To move beyond the appearances we have to return to metaphysical complexities bypassed by the first construal of individualism. (In particular, we need to attend to the nature of relational properties and the contrast between them and intrinsic properties, and philosophical notions foreign to the ear of many a biologist, such as determination and realization.) Further reflection on organism supervenience individualism may also provide reason to reconsider the apparent organism boundary individualism of physiology, genetics, and development, and to explore the relationship between our two senses of individualism.

In considering whether biological properties supervene on an individual’s intrinsic, physical properties we have maintained a focus on our paradigm individuals, human agents and organisms. A third way to transpose the individualism issue from the domain of cognition to that of biology drops this focus, and generalizes on the notion of an agent or individual. Thus, we move from our paradigm individuals, organisms, to other kinds of thing that are treated as individuals. In the biological sciences these include groups and species, but also living things that are contained within paradigmatic individuals, such as bodily organs and obligate parasites, and other biological entities, such as pathways and systems. Such biological agents are often construed as individuals in their own right.

Table 2. Three construals of individualism in biology

Construal	Characterization	Sample issue
Individual as a boundary (Organism boundary)	Can bracket off or ignore world beyond the individual in doing biological science	Are physiology, genetics, and developmental biology individualistic?
Biological properties as supervenient on the organism (Organism supervenience)	Intrinsic physical properties of organisms constitute a supervenience or realization base for biology	What is the significance of the prevalence of relational and historical properties in ecology and evolutionary biology?
Biological properties of X as supervenient on what's inside X (Generalized supervenience)	A generalization of the second construal, from organisms to individuals more generally	Do intrinsic, causal powers play a special role in characterizing biological kinds and taxonomies?

Individualism in the biological sciences on this third construal is the view that biological taxonomy at *any* level is by the intrinsic, physical properties of the entities taxonomized. Call this *generalized supervenience* individualism. It says that what makes any biological entity the kind of thing it is are facts about what is inside its boundary, what it is physically constituted by, or what causal powers it possesses. For example, what makes something a gene (or a specific type of gene), or a protein, or a heart, are facts about that thing's constitution or the causal powers that it has.

Generalized supervenience individualism can also avail itself of the narrow content strategy of argument in the face of a variety of putative counter-examples. It is particularly relevant as we move "up" and "down" from the organism to examine other kinds of biological agents. Table 2 provides a summary of these three ways to construe individualism within the biological sciences.

Keeping the parallel between the cognitive and biological sciences in focus, I shall call those who deny any one of these individualistic positions within biology *externalists*, using the corresponding adjectival modifications where appropriate (cf. Godfrey-Smith 1996: ch. 2). Thus, proponents of group selection are organismic boundary externalists, and the name is descriptively apt in that they posit agents of selection that extend beyond the boundary of the organism – groups, species, clades, for example. (They are also externalists about organismic supervenience, since they appeal to causal

factors – population density and structure, dispersal mechanisms, resource limitations – that do not supervene on the intrinsic, physical properties of organisms, that are not “causal powers” of organisms, as themselves subject to the mechanism of natural selection.)

In denying one or another form of individualism, externalists are not, however, proposing their own version of a normative constraint on the corresponding science. This is in part because they adopt a more pluralistic view of scientific taxonomy, one that allows for a place for causal powers and intrinsic properties, but that also recognizes a taxonomic or individuating role for the relational and historical properties that individuals possess. Externalists are likely to view scientific taxonomies and scientific explanation as sensitive to a range of factors, and to be skeptical about the prospects for recipe-like prescriptions or generalizations regarding proper scientific taxonomy of the sort that individualists propose. Thus, a consideration of the positive forms that externalism takes will raise the issue of pluralism in the biological sciences.

3. The levels of selection

Even though the affinity between externalist views and pluralism mentioned above is worth keeping in mind, we can see that matters are more complicated by turning to recent work on the levels of selection. Here pluralism has been endorsed by both philosophers and biologists – often as a way of resolving debate over the level(s) at which natural selection operates – and many of these pluralists are individualists about the levels of selection. Since there are a number of perceptive overviews of recent work on the levels of selection in general (see, e.g., Sober and Wilson 1998, ch. 1–2; Lloyd 2001; Okasha 2001, 2003a), I shall concentrate here on the interaction between individualism and pluralism about the levels of selection.

Pluralism is just the view that there are many different levels at which natural selection operates, and as in other areas of philosophy, it is contrasted with monistic views. The multi-level selection theory defended by Elliott Sober and David Sloan Wilson, particularly in their *Unto Others*, represents a pluralistic view of the levels of selection that exemplifies the affinities between pluralism and externalism about the levels of selection. Sober and Wilson deny that there is any single level at which selection operates; rather, selection can, and often does, operate at multiple levels, levels that often pull in opposite directions. That is, there is a plurality of units of selection – gene, individual, group – with the inclusion of group selection implying the rejection of organism boundary individualism. This form of pluralism suggests *realism* about the existence of the units of selection, in the sense that there are,

independent of our particular perspectives, distinct units of selection in the natural world, with their own distinctive properties and subject to particular processes (see also Wilson and Sober 1994).

I have elsewhere called this form of pluralism *unit pluralism*, since at its core is the idea that there is a plurality of units of selection in the biological world itself (Wilson 2003b; see also Wilson 2004c). Clearly unit pluralism could be combined with an individualistic view of the levels of selection. Indeed, one might take the extension of the standard, organism-centered view of natural selection associated with Darwin that was articulated by George Williams and popularized by Richard Dawkins that introduced the idea of *genic* selection to exemplify such a form of unit pluralism. Genes or organisms can be units of selection, but we should remain skeptical of the idea that natural selection can or does operate on units larger than the organism.

Alongside this form of pluralism, however, is another, one that has received its most sophisticated articulation in the recent work of Benjamin Kerr and Peter Godfrey-Smith (2002). This is what I have called *model pluralism*, since it identifies a plurality in the models that evolutionary biologists adopt, rather than in the reality that those models depict. Model pluralism is also manifest in Sober and Wilson's work, particularly when they consider the relationship between the theory of group selection and putative alternatives to it. They say,

In science as in everyday life, it often helps to view complex problems from different perspectives. Inclusive fitness theory, evolutionary game theory, and selfish gene theory function this way in evolutionary biology. They are not regarded as competing theories that invoke different processes, such that one can be right and the others wrong. They are simply different ways of looking at the same world. (1998: 98)

Model pluralists hold that while there may be strategic or pragmatic advantages to using one rather than another model in a particular case, these models do not compete for the truth about the nature of natural selection.

Like unit pluralism, model pluralism has been endorsed not only by friends of group selection, such as Sober and Wilson, but by those who adopt a more sanguine view of this form of externalism, such as Sterelny (1996) and Dugatkin and Reeve (1994; see also Reeve and Keller 1999; Reeve 2000; Dugatkin 2002). Model pluralism has also proven popular recently amongst biologists working on the social insects and the origins of eusociality (Bourke and Franks 1995; Crozier and Pamilo 1996), and on the evolution of multicellular and social life from simpler forms (Frank 1998; Michod 1999). In general terms, these theorists adopt the view that models positing higher-level processes, such as group selection, do not differ significantly or fundamentally from models positing lower-level processes, such as genic or

kin selection. As Bourke and Franks say in summarizing a chapter devoted to this topic, "... colony-level, group, individual, and kin selection are all aspects of gene selection. This means that the practice of attributing traits to, say, either colony-level selection or kin selection is illogical" (1995: 67). As this quotation illustrates, model pluralism is sometimes combined with the denial of unit pluralism in that it suggests that there is a sense in which one of these levels – typically, that of the individual or the gene – is more fundamental than the others. While this is not quite monism about the units of selection, it suggests that models of genic selection carry with them something more fundamental as a way or representing the process of evolution by natural selection (cf. also Sterelny and Kitcher 1988; Dawkins 1989: 258).

As both quotations from Sober and Wilson and from Bourke and Franks suggest, one of the attractions of model pluralism is that it provides a way to bypass putative disagreements about the levels of selection. But despite the recent enthusiasm for model pluralism, I remain skeptical about its broader significance. The chief reason is that I think that at the heart of the debate over the levels of selection are different views about the ontology of the biological world – what entities it contains, how these entities are related, and what sorts of properties these entities have. Model pluralism is concerned primarily with the relationship between models (equations, variables, postulates) and as such it is poorly positioned to make sense of the ontological differences that underlie different models. There are many rich traditions of philosophical analysis that have attempted to show that some kind of talk (about material objects, about arithmetic, about theoretical entities) can be reformulated in terms of some other kind of talk (about sensory appearances, about logic, about observables). There is, of course, the question of whether any particular one of these translations or reconstructions is successful, but there is also the more fundamental question of whether, even if successful, they would shed light either on the debate between (say, to take the last case) scientific realists and empiricists or on the ontological issues that separate them. By way of support for my general pessimism about model pluralism, let me return to externalism about the levels of selection itself.

Suppose that one were to accept the kind of unit pluralism and externalism that Sober and Wilson have defended. This is not yet to take a position on which kinds of group are units of selection. For example, Kim Sterelny (1996) has argued that only superorganism-like groups, such as ant or bee colonies, and not the trait groups that Wilson (1975) first modeled under that name, are units of selection. Samir Okasha (2003b) has more recently argued that monophyletic clades are not the right sort of entity to be units of selection; this is so despite the fact that clade selection is often presented as a natural extension of species selection (see, e.g., Williams 1992; Gould 2002). Since

proponents of group selection have typically not distinguished between these kinds of groups – between trait groups and superorganism, or between clades and (say) species – in these ways, these positions imply that externalism about the levels of selection may be significantly more limited than group selectionists themselves have often thought.

I think that such views, and disagreements about them, are largely ontological; they turn on what one thinks “groups” are like, and what kinds of properties they have. Sterelny (1996), for example, thinks that trait groups are not objectively vehicles or interactors: what counts as a trait group, and which organisms belong to that group, is not a part of the structure of the world but depends, in part, on *us*. Superorganisms do not suffer from this kind of arbitrariness. Sober and Wilson disagree with this view because they take the crucial property for group selection to be *sharing a common fate*, which short-lived trait groups and superorganisms can both possess. Those who talk of species and clade selection in one breath have stressed similarities between both species and clades and organisms, as exemplified by Stephen Jay Gould’s “grand analogy” (Gould 2002: 703–744). Okasha drives a wedge between species and clade selection because clades, unlike species, cannot reproduce themselves in any meaningful sense.

Thus, those departing from organism boundary individualism about the levels of selection themselves disagree about the nature of the groupish entities they are prepared to countenance. Model pluralists have at least that much apparent ontological disagreement to resolve. But no matter how effectively trait group models can represent superorganismic groups, or how extensive the analogy between organisms and clades, there remain ontological differences that model pluralism itself cannot explain away or resolve. I think that the same is true of the application of model pluralism to the broader debate over the levels of selection.

4. Supervenience individualism about genetics and development

I said earlier that there were areas of the biological sciences for which organism boundary individualism would seem to be a safe bet, namely, those areas concerned primarily with the parts of organisms and how those parts function: physiology, genetics, and developmental biology, for example. But even in those disciplines there remains the question of whether either form of *supervenience* individualism holds about the properties they explore. Are genes, for example, individuated by the intrinsic causal powers of the DNA that, in some sense, constitutes them (see Beurton et al. 2000; Moss 2003)? Does the taxonomy of particular kinds of genes, such as Hox genes in mammals or specific homologues of these genes in insects, such as *lab* and

pb, supervene on the intrinsic, physical properties of either organisms or of some smaller entity, such as a strand of DNA (see Walsh 1999; Wilson 2000)? In what follows I shall concentrate on generalized supervenience individualism about genes before returning to reconsider whether organism boundary individualism is as safe a bet as I have been thus far supposing.

Generalized supervenience individualism about genes says that the properties of genes supervene on the intrinsic, physical properties not just of organisms but of the smaller physical entities that coincide with or physically constitute genes. Whether this view is true turns on just what properties genes have. Many of the more striking (but now classic) claims about genes – that they are both “law-code and executive power” (Schrödinger 1944: 19), that collectively they contain an organism’s “entire future: the stages of its development, the shape and the properties of the living being that will emerge” (Jacob 1973: 1–2), that they encode anything from proteins to phenotypes – suggest individualism.

But this relatively strong form of individualism is also manifest in more mundane claims. Consider the “central dogma” of molecular biology, articulated by Francis Crick in 1958, which says that information begins in DNA and flows (via RNA) to proteins, and not vice-versa. This dogma presupposes a conception of protein synthesis as information flow, and information can flow from A to B only if it is already in A to begin with.

Many biologists would, I think, follow John Maynard Smith (2000) in regarding the informational metaphor as solidly grounded in the biology of organisms themselves, rather than simply in disciplinary-specific ways of talking about that biology (but see also the commentaries by Sterelny 2000; Godfrey-Smith 2000; and Sarkar 2000, as well as Griffiths 2001). Suppose that we grant this. At issue here is just what the biological base of genetic information is. Consider not Crick’s central dogma, but its companion, the sequence hypothesis, which Crick defended together with it. The sequence hypothesis says that the “specificity of a piece of nucleic acid is expressed solely by the sequence of its bases, and that this sequence is a (simple) code for the amino acid sequence of a particular protein” (Crick 1958: 153). This means that the property of coding for, say, lysine is determined by the nucleotide triplet AAA (as well as by AAG), which corresponds to a sequence of three adenine molecules (or two adenines followed by a molecule of guanine).

The obvious problem for this fairly mild view of genetic encoding is that since only about 1.5% of the human genome codes for proteins, nucleotide sequences code for proteins only in certain contexts (Baltimore 2001). Apart from non-coding regions (introns), there are also a variety of regulatory functions, including those of promotor, repressor, and activator sequences. Perhaps we simply need to update the sequence hypothesis in order to take

account of the last 45 years of molecular biology, and thus extend the range of basic structures and functions that nucleotide sequences code for. The problem with this view, however, is that the very sequences that code for proteins in one context either themselves code for, in whole or in part, regulatory functions in other contexts, or for nothing at all. What it seems that the increase in molecular knowledge has done, in effect, is forced biologists to look beyond the physical boundary of the gene in order to more fully understand just what it is that genes do. Thus, I would suggest, that an externalist view of even protein coding (let alone of phenotypic or organismic coding), fits better with the biological facts than do the individualistic views that have, by and large, generated the work that led to those facts!

Individualists can, of course, avail themselves of some version of the revisionary strategy outlined in section 2 that is familiar from the narrow content program and computational views of representation in the cognitive sciences. (Or they can, especially if they are biologists, just throw up their hands at all this mere metaphysically haggling and get on with their experiments.) My aim here is not to resolve this aspect of the debate over genetic coding but to suggest that there is at least a strong *prima facie* case for individualists to answer.

5. Organismic individualism and developmental systems theory

The critique of the metaphor of genetic encoding to which I alluded above has also been at the center of a more wide-ranging attack on the perceived genocentrism of much of biology, that associated with *developmental systems theory* (hereafter “DST”; see the essays in Oyama et al. 2001). While much of DST has been negative and critical in nature, here I want to examine DST as an externalist research program within developmental biology and theories of biological inheritance.

The basic claim of DST is that organismic development should be understood in terms of a pair of notions, that of a *developmental resource*, and that of a *developmental system*. Genes are an important example of a developmental resource and a part of many developmental systems, but they are not unique, special, or privileged in the role they play within an organism’s development. Proponents of DST may themselves be organism boundary individualists about developmental resources and systems (see, e.g., Keller 2001). But the species of DST on which I want to concentrate here challenge this form of individualism by claiming that some (or many) developmental systems contain resources located beyond the boundary of the organism. Such versions of DST view developmental systems themselves as reaching beyond the bodily envelope of the organism. The most plausible way both to articulate

externalist versions of DST and to provide a more concrete idea of what they might be is, in my view, to begin with individualistic forms of DST and show that they lead one naturally (even if eventually) to disregard the organismic boundary as developmentally significant. This strategy has certain parallels with a strategy of defending externalism about cognition that I have deployed elsewhere (Wilson 2004a), parallels I shall note where appropriate.

Developmental systems are causally and functionally integrated chains of developmental resources, and these, individually and collectively, must play a replicable causal role in ontogeny and inheritance. This allows for developmental resources to include genes but also chromatin markers, cytoplasmic organelles, and protein gradients, all of which are parts of an organism that play a replicable causal role in ontogeny and inheritance. But to form part of a developmental system such resources must be causally and functionally integrated such that they collectively, as a whole, play that role. Isolated, incidental, or coincidental resources that are not so integrated do not form part of the relevant developmental system. Two things should be clear from this characterization.

First, there is a ready and principled way to extend the list of developmental resources from within the organismic envelope to beyond it, and so to move from individualistic to externalist DST. As with externalist psychology, here externalist developmental systems will have realizations that cross the boundary between organism and environment. In principle, parental diets, behavior patterns, population structures, and environmental modifications, such as ant nests or beaver dams, none of which are located within the organism, can all serve as part of a developmental system. But to support any particular claim about something being a developmental resource in the relevant sense it is not sufficient simply to identify its replication or reoccurrence over generational time, or its causal contribution (however minimal) to survival and reproduction. Rather, one needs to chart the causal chain linking that putative resource to a series of other so-linked resources, such that they can plausibly be said to form an integrated developmental system. This requirement imposes a severe constraint on the number and range of wide developmental systems there are.

Second, and subsequently, there is no single developmental system, any more than there is any single cognitive system, but many. Some of these will be individualistic, others externalist. Some of these will be genetic, others nuclear, cellular, organismal, or environmental. Consider four examples of developmental resources that satisfy organismic boundary individualism.

Hox genes form part of a range of such systems. Their generic function is to contribute to processes that construct gross features of bodily symmetry in animals. While Hox genes may have a high-level coding function within

those systems, to think of them primarily as “master genes” for body plans (e.g., Gehring 1998; cf. Robert 2001) would be a misleading simplification in this context. The chromatin marking system is a nuclear system containing proteins, methyl groups, and RNA complexes whose function is to facilitate the transcription of chromatin (see Jablonka and Lamb 1995, 1998, 2004). The cytoskeleton of the non-nuclear part of cells contains actin fibers, microtubules, and intermediate filaments crucial for polymerization, chemical transportation, and mechanical structure. Aphids transmit their *Buchnera* bacteria to offspring cytoplasmically, and these form part of the developing digestive system of those offspring (Griffiths and Gray 2001). Hox genes, methyl groups, actin fibers, and symbiotic bacteria all belong to distinct developmental systems that are located within the boundary of the organism they construct.

External developmental resources tend to be identified more generically, and are often shared by individuals, features that make the identification of the relevant developmental system less obvious than in the case of organismic developmental resources. Parental care is a generic developmental resource that plays a role in various developmental systems; to specify these, we need to fix on determinate instances of parental care. For example, many birds that hear their mother’s song reproduce that song, which then comes to function in species-specific mate recognition (see Marler 1984, 1991). So this form of parental care forms part of their developing mate recognition system. The play that canines engage in with their young structures many species-specific behaviors, such as those involved in hunting and dominance hierarchies (Bekoff 1995, 1998). Likewise, an ant nest or a beehive is a shared developmental resource that forms a part of the developmental system of many individual organisms in a colony of bees. That a parental behavior does not exclusively target an individual does not imply it cannot be appropriated as part of one or more developmental systems.

While not all external developmental resources are shared by multiple individuals, many are. This idea of a shared developmental resource and its role in characterizing the externalist developmental systems can be elaborated, and some of the mystery surrounding it dispelled, through consideration of the parallel with the resources that constitute externalist cognitive systems. Part of the puzzle to address is how we can make sense of developmental systems that physically overlap, and what makes wide developmental systems belong to particular individuals. Consider just the first of these here (see Wilson 2004b: ch. 7 for discussion of the second).

The properties of the ambient optical array (Gibson 1979), of external storage systems (Donald 1991), or of the distributed cognitive systems involved in navigation (Hutchins 1995), can be exploited by individual

cognizers through their active, bodily engagement with these pre-existing informational structures. These are shared cognitive resources, but their incorporation into the cognitive systems of individuals does not imply that these cognitive systems themselves physically overlap, any more than does our digging at the same hole suggest that our actions physically overlap. Even though developmental resources appropriated through an organism's interactions with the world can involve the sharing of precisely the same physical body of matter, either cooperatively or competitively, the separation of organisms in space and time make such cases of physically overlapping developmental systems unlikely to be the norm. In any case, the main point here is that externalist developmental systems need not physically overlap, even if such cases of physical overlap can be accommodated within the DST view.

The key idea here is that both cognitive and developmental systems can form causal loops that extend beyond the boundary of the individual without dissipating into the world at large (and, I think, without compromising organismal agency). Even externalist developmental systems, like externalist cognitive systems, are constituted by many resources that are themselves located within the boundary of organisms. When we move to cognitive or developmental systems for which this is no longer true, or when we are focused on explanatory questions about a series of externalist resources, then the connection to individual agency is diminished.

For example, termite mounds are intricate physical structures that are built and maintained by organisms that belong to two phylogenetically distant taxa – by termites (of the genus *Macrotermes*, for example) and by the fungi that they cultivate within the mounds (see Turner 2000: ch. 11). Regulating the temperature and airflow within the mound is crucial to the survival of members of both species, and the mound is a developmental and ecological resource for each. But do termites build the mound in order to cultivate and harvest the fungus? Or has the fungus figured out an easy way to earn its keep by getting another species to build its home? There are reasons to answer both of these questions affirmatively, and further empirical details certainly reveal respects in which there is clearly termite agency, and others in which there is clearly fungus agency. Yet it is hard to shake the feeling that accepting both termite and fungal agency compromises the agency of each. Moreover, when we turn our attention to shared developmental resources themselves – for example, the termite mound itself – and the broader causal nexus that they form a part of, these can take on a certain kind of agency themselves, perhaps even a kind of *biological* agency. This is likely to complicate any acceptable view of individuals, agency, and systems.

A related complication is that developmental resources and organismic phenotypes are often intricately connected. What begins as a developmental resource, such as a tree that has rotted, may contribute to the expression of an extended phenotype, such as the dam that a beaver builds, given how a particular developmental system operates. And these extended phenotypes can, in turn, lead the organism to deploy further developmental resources, such as resultant water levels, to express further extended phenotypes, and so on. Just what an extended phenotype *is* will be as murky as (but no more murky than) the issue of what a phenotype more generally is. But conceptualizing phenotypes as parts of developmental systems at least improves the prognosis for an integrated view of development and evolution.

This should go some way to alleviating the concern, expressed by Philip Kitcher amongst others, that DST does not “offer anything that aspiring researchers can put to work” (2001: 408; cf. Griffiths, in press). But there are also at least two further independent, concrete programs of research in contemporary biology that further exemplify ways to explore developmental agency within this overarching externalist framework.

The first of these is J. Scott Turner’s (2000) *extended physiology*. Taking his cue from Dawkins’s (1982) idea of the extended phenotype, Turner argues that an organism’s physiology can extend beyond the boundary of its skin. Turner provides a range of examples where what would clearly be classed as a physiological process were it to occur inside the boundary of an organism can be found existing either between organisms (as in the carbonic acid cycles in living coral reefs) or in the environment of an organism (as in burrow construction in the mole cricket). Consider the latter of these. The male mole cricket constructs and modifies a burrow used primarily to attract females through singing. The burrow is constructed in a funnel shape and functions as an amplifier for the tiny chirps the cricket emits. In constructing it, the cricket emits short chirps before each modification, testing the intensity of the resulting sound. This process lasts about an hour before the cricket settles into the back of the burrow and sings away for several hours. Burrow excavation is a tuning process that involves a feedback loop passing through the organism’s environment, which is actively modified through that process. Because of this, as Turner says, the “only thing the cricket need carry around in its genes is the fairly simple behavioral program for burrow building and a sensory system capable of assessing the burrow’s acoustical properties and correcting its structure as needed” (Turner 2000: 178).

The second is the *niche construction* paradigm in ecology developed by John Odling-Smee and colleagues over the past 20 years, and synthetically presented in Odling-Smee, Laland, and Feldman’s *Niche Construction: The Neglected Process in Evolution* (2003; see also Laland et al. 2000).

Proponents of the niche construction paradigm build on Richard Lewontin's (1983) rejection of a view of organisms as proposing solutions to pre-existing problems posed by its environment in favor of a *constructive* view of both niches and organism-niche interactions. Niche construction is defined in terms of two ways in which organisms can act:

Niche construction occurs when an organism modifies the feature-factor relationship between itself and its environment by actively changing one or more of the factors in its environment, either by physically perturbing factors at its current location in space and time, or by relocating to a different space-time address, thereby exposing itself to different factors. (Odling-Smee et al. 2003: 41)

Common external structures found across phylogenetically distant taxa, such as nests and burrows, as well as taxa-specific structures, such as dams (beavers), webs (spiders), hives (bees), and bowers (bowerbirds) require, however, not simply an act of initial construction, but ongoing maintenance and modification that shapes up a range of the behaviors of the animals who make use of them. Animals are active shapers of their environments, but they are also active responders to the changes that they have wrought in those environments. As Odling-Smee and his colleagues suggest, this externalist perspective has broad implications for how we think of evolutionary, ecological, and developmental aspects of biological agency.

6. Cognition, sociality, and evolution

The final area of the social, behavioral, and biological sciences in which the debate between individualists and externalists has left an indelible footprint is less well-worn and perhaps less clearly delineated than that of the levels of selection and the nature of genes and organismic development. It concerns the relationship between cognition, sociality, and evolution. "Evolutionary psychology", "the evolution of cognition", and "the evolution and origin of sociality", each names a large cluster of approaches or phenomena that fall under this rubric. As these labels suggest, each is concerned primarily with the evolutionary origins and trajectory of intelligence and sociality, where both of these phenomena are taken as epitomized in our favorite species, *Homo sapiens*.

There has been a healthy interaction between much of the recent work on cognition, sociality, and evolution and that in the cognitive sciences. For example, the evolutionary psychology articulated by Leda Cosmides and John Tooby is self-consciously cast as a natural extension of Chomskyan, computational cognitive science (Cosmides and Tooby 1992, 1994; see Pinker 1997

for a popular gloss). In particular, they take Chomsky's nativism seriously, and view themselves as exploring the evolutionary conditions for the emergence of the thousands of mental modules that they think implied by this nativism. (Notoriously, neither Chomsky nor Chomsky's Bulldog on matters modular, Jerry Fodor, are all that enthusiastic about evolutionary psychology; see, e.g., Fodor 2000). In work on the evolution of cognition more generally, there has been attention to topics first explored in detail in developmental psychology, such as on the theory of mind, and cross-fertilization between this still burgeoning sub-field and more recent work in primatology (see, e.g., Tomasello and Rakoczy 2003). Perhaps the most developed paradigm for thinking about the relationship between cognition and sociality in an evolutionary framework – that of those working on the *Machiavellian intelligence hypothesis* – has drawn on the resources of evolutionary game theory, studies of primate cognition, and comparative neuroanatomy (Byrne and Whiten 1988; Whiten and Byrne 1997).

A recognition of these sorts of links between this work that is fundamentally adaptationist about cognition and sociality and that in these other fields is important in understanding how it is positioned vis-à-vis the debate between individualists and externalists. For one might expect such research programs to be resoundingly externalist on the grounds that adaptationism is one of our paradigms of an externalist research program, aiming as it does to identify the environmental parameters that drive natural selection in particular circumstances (cf. Godfrey-Smith 1996: ch. 2). But in fact much of this work seems to have inherited an orientation that is much closer to the individualistic paradigms prevalent in the cognitive sciences on which it draws. Let me make this a little more concrete, and so, I hope, perspicuous.

Consider evolutionary psychology's search for "Darwinian algorithms" in an organism's cognitive architecture, algorithms that underlie species-specific cognitive adaptations. These algorithms are located in the heads of individuals, and they are invoked not simply to explain individual behaviors but, ultimately, "the generation of culture" (see Barkow et al. 1992). As algorithms, these cognitive structures are to be individuated computationally, and given the widespread assumption that computational individuation is individualistic, there are clear senses in which at least this brand of evolutionary psychology is individualistic. The cognitive machinery is organism bounded, and the properties of organisms important for the evolution of both cognition and culture supervene on what is inside those organisms.

Likewise, despite the central role given to social structures in the evolution of cognition under the Machiavellian intelligence hypothesis, much of this work is more individualistic than one might have expected. The Machiavellian intelligence hypothesis claims that the sophisticated cluster of abilities

that we know under the heading “intelligence” were driven by facts about the social evolution of hominids and their primate ancestors. More specifically, it is the view that “the advanced cognitive processes of primates are primarily adaptations to *the special complexities of their social lives*” (Whiten 1999: 495). Again, as a species of adaptationism, work under the banner of the Machiavellian intelligence hypothesis is driven to examine the world beyond the boundary of the organism in order to make sense of changes within that boundary. But the conception of cognition itself, of the distinctive organismic contribution to cognitive evolution, is typically expressed as a form of both organism boundary and supervenience individualism. My claim is that in both this case and in the case of evolutionary psychology, this is due to a reliance on views within the cognitive sciences that are predominantly individualistic.

One might ask – indeed, one might ask in despair if one is working in either of these paradigms – just what an acceptably robust externalist approach to cognition, sociality, and evolution would look like. In the abstract, such an approach should strive to satisfy at least two constraints. First, it should treat sociality not primarily as an external triggering or structuring cause (*sensu* Dretske 1988) for cognition, but as a part of cognition itself. Second, it should be open to the prospect of there being central explanatory posits that themselves cannot be identified with or reduced to the intrinsic properties of individuals.

Analogues of each of these constraints have played at least an implicit role in the development of plausible externalist programs in the other two areas of the biological sciences that we have looked at in this review, that of the levels of selection, and genetics and developmental biology. For group selection to represent a genuine alternative to individualistic models of natural selection, groups themselves must, in some sense, be causal agents; they cannot simply be understood as the “context” in which organismic or genic selection takes place, and so parameterized away to the periphery of the theory of natural selection. Likewise, for developmental systems theory to provide the basis for an externalist research program in developmental biology and the theory of inheritance, developmental systems themselves, systems that in some cases cross the organism-environment boundary, need to be taken seriously. They are not reducible to or replaceable by developmental resources, such as genes, that lie entirely within the organism. External resources are not simply detected by organisms or encoded by their genes, but are developmental resources in their own right. Parallel morals could be drawn, I would suggest, from a more detailed examination of the other two examples that I mentioned at the end of the previous section, those of an extended physiology and of niche construction.

What might this mean more concretely? Consider what I have elsewhere (Wilson 2001, 2004a: ch. 11) called the social *manifestation thesis*:

some psychological states and structures are manifested only when the individuals who have them form part of a social group of a certain type.

The social manifestation thesis was originally introduced as a sort of middle-ground between individualistic views of cognition and the recent renewal of interest, in both the biological and social sciences, in the idea that groups have minds (see D.S. Wilson 1997, 2002; Douglas 1986). But if we give a strong reading to the social manifestation thesis, one that in effect replaces “are manifested” with “exist”, then we have a thesis both that links sociality to cognition in more than an instrumental way or as cause to effect, and that posits cognition itself as irreducibly social, and so not as supervenient on the intrinsic properties of individuals.

On this view, cognition remains a property of individuals, yet it is externalist in all three senses that I articulated earlier. Cognition extends the organismic boundary in that it involves cognitive systems that, like developmental systems, cross that boundary. We might reconceptualize a range of cognitive capacities in this vein; those of particular relevance to thinking about cognition, sociality, and evolution include our folk psychological system (rather than simply an internal “theory of mind”) and the various cognitive abilities on which our explanatory forays depend (see Wilson and Keil 2000). Likewise, both forms of supervenience individualism must be rejected for socially manifested cognitive states and structures, for they are in part individuated relationally, where some of the relata lie beyond the boundary of the organism.

Whether there are or have been any socially manifested cognitive states and structures is ultimately an empirical matter, one that I suspect we are some way from confirming or falsifying. But *prima facie* candidates for such cognitive states and structures include various metarepresentational capacities, emotions such as fear and anger that often take other cognitive agents as their objects, and the aspects of consciousness that are associated with processes of awareness (rather than mere phenomenology), such as introspection and attention. They are plausible candidates for socially manifested states and structures not now, but in our evolutionary past, precisely because their starting points are likely irreducibly social. This is not simply in the sense that they are organismic responses to particular social situations, but in that they arise themselves as social abilities, as ways of negotiating aspects of the social world. They evolve not only in a given social domain but as interpersonal relations that are then, over evolutionary time, incorporated into the cognitive repertoires of the individuals they relate.

One model for this kind of externalism about cognition and sociality and their evolution might be provided by a way of conceptualizing problem-solving in novel artifactual domains. Consider the children's game of Rush Hour, in which one tries to move a pre-arranged set of cars on a board so as to allow a designated car escape, through a set of simple, rule-constrained moves, from the gridlock represented by that initial arrangement. To solve a given Rush Hour problem we must interact with the board – perceptually, tactilely, through imagined action plans and chains of moves. Now we bring a lot of internal cognitive sophistication to this task, even when it is somewhat new to us: we can understand rules, goals, and engage in means-ends reasoning, for example. In that respect it is a misleading model for the evolution of socially manifested cognitive capacities, for what I have in mind is this sort of mind-world interaction in the absence of this pre-existing cognitive sophistication.

The idea is this. We solve a problem in our interactions in some interpersonal domain – sharing and caring, as well as competing and beating. Those interactions constitute the cognitive capacity, which can then, at some point, be detached or generalized from those very circumstances. The same is likely true for a range of cognitive capacities we have, and they too should be reconceptualized as interpersonal, social abilities. Evolutionary behaviorism, perhaps, but when the goal is to explain the origin and evolution of cognition, interpersonal behavior seems a good place to start.

References

- Adams, F. and Azawai, K.: 2001, 'The Bounds of Cognition', *Philosophical Psychology* **14**, 43–64.
- Baltimore, D.: 2001, 'Our Genome Unveiled', *Nature* **409**, 814–816.
- Barkow, J., Cosmides, L. and Tooby, J. (eds): 1992, *The Adapted Mind: Evolutionary Psychology and Generation of Culture*, Oxford University Press, New York.
- Bekoff, M.: 1995, 'Play Signals as Punctuation: The Structure of Social Play in Canids', *Behaviour* **132**, 419–429.
- Bekoff, M.: 1998, 'Playing with Play: What Can We Learn About Evolution and Cognition', in D. Cummins and C. Allen (eds), *The Evolution of Mind*, Oxford University Press, New York.
- Beurton, P.J., Falk, R. and Rheinberger, H.-J. (eds): 2000, *The Concept of the Gene in Development and Evolution: Historical and Epistemological Perspectives*, Cambridge University Press, New York.
- Bourke, A.F.G. and Franks, N.R.: 1995, *Social Evolution in Ants*, Princeton University Press, Princeton, NJ.
- Byrne, R.W. and Whiten, A. (eds): 1988, *Machiavellian Intelligence*, Cambridge University Press, New York.

- Cosmides, L. and Tooby, J.: 1992, 'Cognitive Adaptations for Social Exchange', in J. Barkow, L. Cosmides and J. Tooby (eds), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford University Press, New York.
- Cosmides, L. and Tooby, J.: 1994, 'Origins of Domain Specificity: The Evolution of Functional Organization', in L. Hirschfeld and S. Gelman (eds), *Mapping the Mind: Domain Specificity in Cognition and Culture*, Cambridge University Press, New York.
- Crick, F.: 1958, 'On Protein Synthesis', *Symposium of the Society for Experimental Biology* **12**, 138–163.
- Crozier, R.H. and Pamilo, P.: 1996, *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*, Oxford University Press, New York.
- Dawkins, R.: 1982, *The Extended Phenotype*, Oxford University Press, Oxford.
- Dawkins, R.: 1989, *The Selfish Gene*, 2nd ed. Oxford University Press, New York. 1st edition, 1976.
- Donald, M.: 1991, *The Origins of the Modern Mind*, Harvard University Press, Cambridge, MA.
- Douglas, M.: 1986, *How Institutions Think*, Syracuse University Press, Syracuse, NY.
- Dretske, F.I.: 1988, *Explaining Behavior: Reasons in a World of Causes*, MIT Press, Cambridge, MA.
- Dugatkin, L.A.: 2002, 'Will Peace Follow?', *Biology and Philosophy* **17**, 519–522.
- Dugatkin, L.A. and Reeve, H.K.: 1994, 'Behavioral Ecology and Levels of Selection: Dissolving the Group Selection Controversy', in P.J.B. Slater et al. (eds), *Advances in the Study of Behavior*, vol. 23, Academic Press, New York.
- Fodor, J.A.: 1987, *Psychosemantics: The Problem of Meaning in the Philosophy of Mind*, MIT Press, Cambridge, MA.
- Fodor, J.A.: 2000, *The Mind Doesn't Work That Way*, MIT Press, Cambridge, MA.
- Frank, S.A.: 1998, *Foundations of Social Evolution*, Princeton University Press, Princeton, NJ.
- Gehring, W.E.: 1998, *Master Control Genes in Development and Evolution: The Homeobox Story*, Yale University Press, New Haven, CT.
- Gibson, J.J.: 1979, *The Ecological Approach to Visual Perception*, Houghton-Mifflin, Boston, MA.
- Godfrey-Smith, P.: 1996, *Complexity and the Function of Mind in Nature*, Cambridge University Press, New York.
- Godfrey-Smith, P.: 2000, 'Information, Arbitrariness, and Selection: Comments on Maynard Smith', *Philosophy of Science* **67**, 202–207.
- Gould, S.J.: 2002, *The Structure of Evolutionary Theory*, Harvard University Press, Cambridge, MA.
- Griffiths, P.E.: 2001, 'Genetic Information: A Metaphor in Search of a Theory', *Philosophy of Science* **68**, 394–412.
- Griffiths, P.E.: in press, 'The Fearless Vampire Conservator: Philip Kitcher, Genetic Determinism and the Informational Gene', in C. Rehmann-Sutter and E.M. Neumann-Held (eds), *Genes in Development*, Duke University Press, Durham, NC.
- Griffiths, P.E. and Gray, R.D.: 2001, 'Darwinism and Developmental Systems', in S. Oyama, P.E. Griffiths and R.D. Gray (eds), *Cycles of Contingency: Developmental Systems and Evolution*, MIT Press, Cambridge, MA.
- Grush, R.: 2003, 'In Defense of Some Cartesian Assumptions Concerning the Brain and its Operation', *Biology and Philosophy* **18**, 53–93.
- Hutchins, E.: 1995, *Cognition in the Wild*, MIT Press, Cambridge, MA.

- Jablonka, E. and Lamb, M.: 1995, *Epigenetic Inheritance and Evolution: the Lamarckian Dimension*, Oxford University Press, New York.
- Jablonka, E. and Lamb, M.: 1998, 'Epigenetic Inheritance in Evolution', *Journal of Evolutionary Biology* **11**, 159–183.
- Jablonka, E. and Lamb, M.: 2004, *Evolution in Four Dimensions*, MIT Press, Cambridge, MA.
- Jacob, F.: 1973, *The Logic of Life*, Princeton University Press, Princeton, NJ.
- Keller, E.F.: 2001, 'Beyond the Gene but Beneath the Skin', in S. Oyama, P.E. Griffiths and R.D. Gray (eds), *Cycles of Contingency: Developmental Systems and Evolution*, MIT Press, Cambridge, MA, pp. 299–312.
- Kerr, B. and Godfrey-Smith, P.: 2002, 'Individualist and Multi-Level Perspectives on Selection in Structured Populations', *Biology and Philosophy* **17**, 477–517.
- Kincaid, H.: 1997, *Individualism and the Unity of Science: Essays on Reduction, Explanation, and the Special Sciences*, Rowman and Littlefield, Lanham, MD.
- Kitcher, P.: 2001, 'Battling the Undead: How (and How Not) to Resist Genetic Determinism', in R.S. Singh, C.B. Krimbas, D.B. Paul and J. Beatty (eds), *Thinking About Evolution: Historical, Philosophy, and Political Perspectives*, Cambridge University Press, New York.
- Laland, K.N., F.J. Odling-Smee and M.W. Feldman: 2000, 'Niche Construction, Biological Evolution, and Cultural Change', *Behavioral and Brain Sciences* **23**, 131–175.
- Lewontin, R.: 1983, 'Gene, Organism, and Environment', in D.S. Bendall (ed.), *Evolution from Molecules to Men*, Cambridge University Press, Cambridge, pp. 273–285.
- Little, D.: 1991, *Varieties of Social Explanation: An Introduction to the Philosophy of Social Science*, Westview Press, Boulder, CO.
- Lloyd, E.A.: 2001, 'Units and Levels of Selection: An Anatomy of the Units of Selection Debates', in R.S. Singh, C.B. Krimbas, D.B. Paul and J. Beatty (eds), *Thinking About Evolution: Historical, Philosophy, and Political Perspectives*, Cambridge University Press, New York.
- Marler, P.: 1984, 'Song Learning: Innate Species Differences in the Learning Process', in P. Marler and H.S. Terrace (eds), *The Biology of Learning*, Springer, Berlin.
- Marler, P.: 1991, 'Differences in Behavioural Development in Closely Related Species: Bird-song', in P. Bateson (ed.), *The Development and Integration of Behaviour*, Cambridge University Press, Cambridge.
- Maynard Smith, J.: 2000, 'The Concept of Information in Biology', *Philosophy of Science* **67**, 177–194.
- Maynard Smith, J.: 2002, 'Commentary on Kerr and Godfrey-Smith', *Biology and Philosophy* **17**, 523–527.
- Michod, R.: 1999, *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*, Princeton University Press, Princeton, NJ.
- Moss, L.: 2003, *What Genes Can't Do*, MIT Press, Cambridge.
- Odling-Smee, F.J., Laland, K.N. and Feldman, M.W.: 2003, *Niche Construction: The Neglected Process in Evolution*, Princeton University Press, Princeton, NJ.
- Okasha, S.: 2001, 'Why Won't the Group Selection Controversy Go Away?', *British Journal for the Philosophy of Science* **52**, 25–50.
- Okasha, S.: 2003a, 'Recent Work on the Levels of Selection Problem', *Human Nature Review* **3**, 349–356.
- Okasha, S.: 2003b, 'Does the Concept of 'Clade Selection' Make Sense?', *Philosophy of Science* **70**, 739–751.
- Oyama, S., Griffiths, P.E. and Gray, R.D. (eds): 2001, *Cycles of Contingency: Developmental Systems and Evolution*, MIT Press, Cambridge, MA.

- Pinker, S.: 1997, *How the Minds Works*, Norton, New York.
- Reeve, H.K.: 2000, 'Multi-Level Selection and Human Cooperation', *Evolution and Human Behavior* **21**, 65–72 [Review of Sober and Wilson 1998].
- Reeve, H.K. and Keller, L.: 1999, 'Levels of Selection: Burying the Units-of-Selection Debate and Unearthing the Crucial New Issues', in L. Keller (ed.), *Levels of Selection in Evolution*, Princeton University Press, Princeton, NJ.
- Robert, J.: 2001, 'Interpreting the Homeobox: Metaphors of Gene Action and Activation in Development and Evolution', *Evolution and Development* **3**, 287–295.
- Sarkar, S.: 2000, 'Information in Genetics and Developmental Biology: Comments on Maynard Smith', *Philosophy of Science* **67**, 208–213.
- Schrödinger, E.: 1944, *What is Life?* Cambridge University Press, Cambridge.
- Smith, R.: 1997, *The Norton History of the Human Sciences*, Norton, New York.
- Sober, E. and Wilson, D.S.: 1998, *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Harvard University Press, Cambridge, MA.
- Sober, E. and Wilson, D.S.: 2002, 'Perspectives and Parameterizations: Commentary on Benjamin Kerr and Peter Godfrey-Smith's "Individualist and Multi-Level Perspectives on Selection in Structured Populations"', *Biology and Philosophy* **17**, 529–537.
- Sterelny, K.: 1996, 'The Return of the Group', *Philosophy of Science* **63**, 562–584.
- Sterelny, K.: 2000, 'The "Genetic Program" Program: A Commentary on Maynard Smith on Information in Biology', *Philosophy of Science* **67**, 195–201.
- Sterelny, K. and Kitcher, P.: 1988, 'The Return of the Gene', *Journal of Philosophy* **85**, 339–361.
- Stich, S.: 1983, *From Folk Psychology to Cognitive Science: The Case Against Belief*, MIT Press, Cambridge, MA.
- Tomasello, M.: 1999, *The Cultural Origins of Human Cognition*, Harvard University Press, Cambridge, MA.
- Tomasello, M. and Rakoczy, H.: 'What Makes Human Cognition Unique? From Individual to Shared to Collective Intentionality', *Mind and Language* **18**, 121–147.
- Turner, J.S.: 2000, *The Extended Organism: The Physiology of Animal-Built Structures*, Harvard University Press, Cambridge, MA.
- Walsh, D.M.: 1999, 'Alternative Individualism', *Philosophy of Science* **66**, 628–648.
- Whiten, A.: 1999, 'Machiavellian Intelligence Hypothesis', in R.A. Wilson and F.C. Keil (eds), *The MIT Encyclopedia of the Cognitive Sciences*, MIT Press, Cambridge, MA.
- Whiten, A. and Byrne, R.W. (eds): 1997, *Machiavellian Intelligence II: Extensions and Evaluations*, Cambridge University Press, New York.
- Williams, G.C.: 1992, *Natural Selection: Domains, Levels and Challenges*, Oxford University Press, New York.
- Wilson, D.S.: 1975, 'A Theory of Group Selection', *Proceedings of the National Academy of Sciences USA* **72**, 143–146.
- Wilson, D.S.: 1997, 'Incorporating Group Selection into the Adaptationist Program: A Case Study Involving Human Decision Making', in J. Simpson and D. Kendrick (eds), *Evolutionary Social Psychology*, Erlbaum, Hillsdale, NJ.
- Wilson, D.S.: 2002, *Darwin's Cathedral: Evolution, Religion, and the Nature of Society*, University of Chicago Press, Chicago.
- Wilson, D.S. and Sober, E.: 1994, 'Reintroducing Group Selection to the Human Behavioral Sciences', *Behavioral and Brain Sciences* **17**, 585–654.
- Wilson, R.A.: 1995, *Cartesian Psychology and Physical Minds: Individualism and the Sciences of the Mind*, Cambridge University Press, New York.

- Wilson, R.A.: 2000, 'Some Problems for 'Alternative Individualism''', *Philosophy of Science* **67**, 671–679.
- Wilson, R.A.: 2001, 'Group-Level Cognition', *Philosophy of Science* **68**, S262–S273.
- Wilson, R.A.: 2003a, 'Individualism', in Stephen P. Stich and Ted A. Warfield (eds), *The Blackwell Guide to Philosophy of Mind*, Blackwell Publishers, Oxford, pp. 256–287.
- Wilson, R.A.: 2003b, 'Pluralism, Entwinement, and the Levels of Selection', *Philosophy of Science* **70**, 531–552.
- Wilson, R.A.: 2004a, *Boundaries of the Mind: The Individual in the Fragile Sciences: Cognition*, Cambridge University Press, New York.
- Wilson, R.A.: 2004b, *Genes and the Agents of Life: The Individual in the Fragile Sciences: Biology*, Cambridge University Press, New York.
- Wilson, R.A.: 2004c, 'Test Cases, Resolvability, and Group Selection: A Critical Examination of the Myxoma Case', *Philosophy of Science* **71**.
- Wilson, R.A. and Keil, F.C.: 2000, 'The Shadows and Shallows of Explanation', *Minds and Machines* **8** (1998), 137–159. Modified version reprinted in F.C. Keil and R.A. Wilson (eds), *Explanation and Cognition*, MIT Press, Cambridge, MA.

