of making copies of themselves, and that do so with enough reliability to be represented from generation to generation. Vehicles, by contrast, are what replicators lodge themselves in, what house one or more replicators. Replicators and vehicles (or interactors) may but need not be the very same entity, a point that Hull emphasized. Dawkins's thesis in *The Selfish Gene* is that genes are replicators, and individuals are vehicles. Thus, since replicators are what natural selection operates on, genes are the units of selection. Using this same distinction, we can say that Dawkins's thesis in *The Extended Phenotype* is that a replicator's phenotype need not be restricted to the vehicle that replicator happens to occupy.

A corollary of this view, one prompted by Dawkins's own probing questioning of the past focus on organisms in evolutionary biology, is that organisms are simply convenient ways of packaging many phenotypic characters: *their* existence is also a result of the extended reach of the gene on the world at large, since packaging biological matter in this way has proven to be mighty effective in preserving replicators across evolutionary time. Although the "convenient way of packaging" expression comports with the general view of individual organisms in *The Selfish Gene*, the final chapter of *The Extended Phenotype*, entitled "Rediscovering the Organism," treats the emergence of individuality itself more seriously, taking up suggestions in the work of John Bonner on development and phylogeny that I will return to briefly later in this chapter.

In championing the extended phenotype, Dawkins saw himself as liberating the phenotype from the bounds of the individual organism, and with it the crucial notion of phenotypic differences between organisms within a population. The idea that phenotypes can be and sometimes are *extended* in the sense that Dawkins intends seems to me both true and important, though we should not overemphasize this importance. Dawkins's own "wildest daydream ... that whole areas of biology, the study of animal communication, animal artefacts, parasitism and symbiosis, community ecology, indeed all interactions between and within organisms, will eventually be illuminated in new ways by the doctrine of the extended phenotype" (1982, p. 7) has not be realized, and the practice of what Dawkins called an "extended genetics" (1982, p. 203), which would supplement conventional genetics by following the effects of genes out into the world beyond the individual organism, has hardly developed over the last fifteen years.

I shall focus below on three ways in which the idea of the extended phenotype as Dawkins presents and defends it is significantly more controversial than what we might think of as the bare-bones extended phenotype. I will say why this is so, and in so doing propose a divorce between the bare-bones extended phenotype—the idea of the extended phenotype in itself—and that idea as Dawkins develops it.

First, Dawkins presents the extended phenotype as a natural consequence of his defense of the selfish gene. (This is one reason that what in the preface he calls the "heart of the book," articulating the idea of the extended phenotype, is to be found in three chapters that follows ten others devoted to cleaning up misunderstandings about and objections to the idea of the selfish gene.) Since genes are, to a good approximation, the only or best replicators in the evolutionary process, they are the units of selection and their differential survival is what matters in evolution. They replicate via the phenotypes they express, of course, but only traditional bias leads us to think of these as strictly *bodily* or *organismic* manifestations of the gene—thus, the extended phenotype. Those with qualms about the selfish gene view will see this defense of the extended phenotype as not much more than an interesting exercise in reasoning.

By contrast, Dawkins's most forceful arguments, in my view, for embracing the extended phenotype are parity arguments that rely only incidentally on the selfish gene view. In these arguments Dawkins uses widely accepted views of what sorts of things count as phenotypes and the relation between genes and phenotypes, arguing that since there is no relevant difference between these paradigms and phenotypes that extend beyond the boundary of the organism, such parity offers a defense of the extended phenotype. If you are prepared to accept something that grows as part of an organism as a phenotype—a shell, perhaps—why not accept something that it acquires through its interaction with the world—another shell—as a phenotypic expression of its genes? If behaviors—such as stalking in lions—can be phenotypes, as the ethologists convinced us long ago (prior to the sociobiology of the 1970s), then why not behavior that reaches into the body, and the behavioral repertories of other organisms—such as that of parasitized or otherwise manipulated hosts? Similarly, in Dawkins's own words, since "we are already accustomed to phenotypic effects being attached to their genes by long and devious chains of causal connection,... further extensions of the concept of phenotype should not overstretch our credulity" (1982, p. 197).

Dawkins's basic point is that there is nothing in the concept of a phenotype restricting it to the boundary of the organism, and this point stands independent of the selfish gene view. As he says in several places (e.g., 1982, pp. 198, 214), he is making a "logical point" about the concept of a phenotype, and as such the point has little to do with significantly more controversial views of the unit of selection. This implies, of course, that one could augment the traditional, individual-centered view of natural selection and adaptation, the idea that the individual is "the" unit of selection (or at least, in these heady pluralistic days, *a* unit of selection) with an extended conception of the phenotype. In fact, there would seem little to bar one

from incorporating the extended phenotype into a pluralistic view of the units of selection that embraced forms of group selection, such as David Sloan Wilson and Elliott Sober (1994, Sober and Wilson 1998) have recently defended.

Second, and relatedly, Dawkins often talks of the "extended phenotypic effects" (1982, p. 4) that replicators have, the "phenotypic effects of a gene" (1989, p. 238), and of phenotypes as the "bodily manifestation of a gene" (1989, p. 235). This creates the impression that Dawkins thinks of phenotypes as properties of genes (as in "the long reach of the gene"), and so obscures the point that phenotypes are, in the first instance, properties of individual organisms. Genes certainly have phenotypic effects (extended or otherwise), in the sense of playing a significant causal role in bringing about those effects, but they do not have phenotypes, that is, they are not the subjects of phenotypic predication; phenotypes do not belong to genetic replicators, but to the organismic vehicles in which they are housed. Eye color, running speed, and wing shape are all phenotypes of individual organisms; but so too are the extended phenotypes of web morphology (spiders), shell choice (hermit crabs), and dam size (beavers). If this is correct, then organisms are presupposed by the extended phenotype view, in that they are the entities to which these phenotypes are ascribed. This means that organisms are not simply the means by which genes are packaged and propagated through generations; rather, they are central to making sense of the extended phenotype. What we might call the mere vehicles view of individual organisms doesn't do justice to the overwhelmingly nonrandom distribution of the bearers of extended phenotypes, bearers who will, of course, be the subject of generalizations about the phenotypes, extended or otherwise, that they instantiate.

There is an ironic even if implicit admission of this point in the final chapter of *The Extended Phenotype* when Dawkins turns to consider the question, "Why organisms?" Given that there was nothing requiring replicators to be packaged into these nice, discrete bundles that we call (paradigmatic) organisms, why are they so packaged? Dawkins's answer is that organisms have a regular life cycle, that is, a sequence of development that "permits a new beginning, a new developmental cycle and a new organism which may be an improvement, in terms of the fundamental organization of complex structure, over its predecessor" (1982, p. 262). Organisms reproduce, rather than simply grow, and the developmental bottleneck that reproduction creates allows for the possibility of the intergenerational modifications that constitute adaptations. Here Dawkins acknowledge his debt to Bonner's *On Development*, and one irony of Dawkins's interesting discussion is that it is Bonner's student, Leo Buss, whose *The Evolution of Individuality* (1987) not only answers Dawkins's question, "Why organisms?" in more detail than any other work but also provides an insightful critique (pp. 171–197) of Dawkins's selfish gene view.

Third, Dawkins contrasts organismically bounded phenotypes with those that reach into the world at large, identifying the extended phenotype with the latter. This creates the worry that extended phenotypic effects, unlike their bodily bounded kin, will be unsuited for systematic study, since the effects of genes on the world at large are infinite in number and various in strength. Call this the *dissipative concern* about the extended phenotype: systematic study of an organism's extended phenotype is precluded, because once we move beyond the boundary of the organism the phenotypic effects such study would require dissipate into the world at large.

For example, the science of extended *genetics* that Dawkins dreams of will remain merely a dream. If the reach of the gene were viewed as extending into the world beyond the organism, then the organism's phenotype would include all sorts of greater and lesser effects that those genes have. Conventional population genetics is largely concerned with phenotypic variance within a population, particularly that portion due to genetic variance, and the organism serves as a clear boundary for individuating (and so measuring) phenotypic characters of study. But in an extended genetics with dissipative genetic effects this presupposition is absent, and so what variation is to range over becomes unclear. Similar problems would arise in other areas of systematic study that seem to presuppose a circumscribed conception of the phenotype, such as evolutionary taxonomy or developmental genetics.

The problem here stems, I think, from Dawkins's own dichotomy between organismically bounded phenotypes and phenotypes that reach into the world at large. This dichotomy is not exhaustive, and so the forced choice it presents is a misleading one. For we can see extended phenotypes as bounded by systems *larger than the individual organism*, and so as *not* dissipating into the world at large. That is, by recognizing systems, even individuals, that include individual organisms as proper parts, as the units at which extended phenotypes end, we can extend the phenotype beyond the boundary of the organism without losing the focus on a bundle of phenotypic effects that could be subject to systematic study. We can make this suggestion clearer, perhaps, by considering a range of Dawkins's own examples.

In *every* example that Dawkins provides—caddis fly house shape, spider web morphology, beaver dams, termite mounds, fluke parasitism in snails (and parasitism in general)—the phenotypic effects are part of some well-defined and bounded system: caddis fly + house, spider + web, beaver + dam, termite(s) + mounds, parasite + host. Thus, although phenotypes are extended in the sense of extending beyond the boundary of the individual organism to which they belong, they are not to be identified, in general, as "all the effects that [a gene] has on the world" (1989, p. 238). Rather, extended phenotypes are circumscribed by individual entities larger than (and that contain) the organisms to which they belong. This addresses the dissipative

concern expressed above by identifying an organism-like unit within which one can locate (and so taxonomize and quantify) extended phenotypes.

In making this point, I have restricted myself to considering Dawkins's own examples. In all of these examples, the extra-individualistic or what I have called elsewhere (Wilson 1994, 1995) wide systems are exhaustively composed of an individual organism, an organismic artifact (such as a shell, a dam, a mound), and the relations between them. In doing so I do not mean to prejudge the forms that wide systems can take, or to suggest a tidy formulaic account of when they should be invoked in science. In fact, since the wide *cognitive* systems that we and other animals have are not made up of individual organisms plus individual artifacts in those organism's environments (see Wilson 1999 and below), and thus differ from the above examples in significant ways, theorizing formulaically about the full range of wide systems available to one in rethinking the relevant sciences in nonindividualistic terms would seem premature.

I have thus far suggested thinking of these extra-individualistic systems as providing a boundary for the corresponding extended phenotypes as a way of addressing what I am calling the dissipative concern. On this view, the individual organism remains the bearer of the extended phenotype, as I noted it should in making the previous point. But might we go further and posit these *wide* systems themselves as the bearers of extended phenotypes? After all, to return to the language of replicators and vehicles, such wide systems—individual organisms plus their environmental appendages—are no less vehicles for the delivery of replicators than are individual organisms themselves. On this view, phenotypes would extend beyond the body of individual organisms, but they would fall inside the boundary of these wide systems and so *not* be extended with respect to them.

To accept this view would require a more far-reaching revision of our conception of the individual in biology than the relatively modest revisions I have been suggesting so far. In effect, these larger systems of which organisms are a part would *replace* organisms in biological theory. This would imply, given the traditional view of the unit of selection, that *these* systems were the units of selection; alternatively, given genic selectionism, it would be these systems that were the vehicles via which genes were selected. It would be these systems, not organisms per se, that have their various places in the Linnaean hierarchy, and these wide systems that underwent life cycles, formed ecological communities, and had innate behavioral repertoires. Moreover, at least in the case of systems that include multiple organisms—host-parasite systems, predator-prey systems, mutualistic and symbiotic systems—talk of manipulation, deception, and cooperation would seem less appropriate, since we would now be characterizing the relationships that held between two parts of one

overall system, not one organism and something that *it* acted on in some way. I pass no judgment on the plausibility of this shift in perspective, but simply point to some of its implications.

Since discussion of these three points has been somewhat lengthy, let me bring them together by way of an interim summary of the chapter so far. What I am suggesting is a version of the extended phenotype that (a) is divorced from its association with the selfish gene, (b) explicitly acknowledges the centrality of individual organisms, and (c) facilitates the prospects for a systematic study of extended phenotypes by recognizing the reality of individual entities larger than organisms.

By no small coincidence, these three suggestions parallel claims that I have defended about computationalism in contemporary cognitive science (Wilson 1994, 1995 [ch. 3], 1999). In reverse order, they are: (c') a call for the exploration of *wide* computational systems, systems of computational, cognitive states that extend beyond the boundary of the individual; (b') an acknowledgement of the place of the individual (or parts of that individual) as the subject of those states; and (a') a general plea for the divorce of the computational theory of mind from the individualistic company that it often keeps. In the next section I turn to some of the metaphysics that lies beneath the surface and the metaphors that bubble up to the surface of the individualistic views of biology and psychology to which I am opposed.

# 2 Causal Powers and Encoding

There is an illusive cluster of views of the scientific exploration of the mind that involve an appeal to the notions of causal powers and encoding whose discussion sheds some light on corresponding views in the biological sciences.

As I have said, individualism in psychology is the view that psychological states should be individuated or taxonomized so as to supervene on the intrinsic, physical properties of the individuals who have those states, and since it implies that physically identical individuals must have the same psychological states, it is often taken to be a *minimal* materialist constraint on psychology or cognitive science. Individualism is sometimes glossed as the view that psychological kinds are demarcated "by causal powers," meaning that psychological states with the same causal powers must belong to the same kind. So glossed, it has been claimed (e.g., by Fodor 1987, ch. 2) to gain support from a general thesis about scientific kinds, namely, that they are taxonomized by causal powers. This view articulates the intuitions that psychology stops at the skin—really, at the skull—and that environmental variables are relevant to psychology only insofar as they impinge on the internal, physical states of indi-

viduals. The name "individualism" is used, in part, to suggest the idea that individuals serve as the uppermost boundaries for the entities that are relevant to do psychology.

This view of the role of causal powers in psychology provides support for a familiar view of mental representation: that it involves *encoding* information about objects, properties, events, or states of affairs. A well-known version of the encoding view is the picture or copy theory of mind, according to which to have a mental representation of m is to have a mental picture or image of m in your head, where the picture is "of m" just because it looks like m. A version of the encoding view prevalent in cognitive science is the language of thought hypothesis, according to which to have a mental representation of m is to have a token in your language of thought, m, that stands for or refers to m. Unlike the copy theory of mental representation, on this view there need be no resemblance between the representation and the represented. On either view, because mental representations encode information about the world, cognitive scientists can (and should) explore *these* properties rather than the relationships that exist between organisms and environments.

I have argued at length elsewhere (e.g., Wilson 1995, 1999) that both of these views are false, but that is not my plaint here. At the end of my introduction I characterized causal powers and encoding as metaphors, and it is viewing them as such that allows us to make a connection back to the biological sciences. In calling them metaphors, I mean to suggest both their literal falsity and that they create a certain overall conception of what sorts of things mental states are: they are encapsulated in individuals, located in the brain, buried away from direct impingement from the world. Thus they can be investigated as self-contained entities causally insulated from—yet reflective of—the world beyond the organism. This sort of metaphor should be familiar to biologists, since it is the dominant metaphor governing the conception of genes. In genetics, this metaphor has its root in Morgan's school in the 1920s and was developed through the incorporation of the informational language of codes, templates, instructions, and programs in the 1940s and '50s (see Fox Keller 1995). But I think that a variation on the metaphor that places less emphasis on the idea of encoding per se also structures contemporary thought about cells, organs, and even organisms themselves, with influential historical antecedents in Schwann's doctrine of the cell as the unit of living systems in his physiological investigations of the 1830s, and the development of theories of cellular respiration in the 1920s (see Bechtel and Richardson 1993, esp. chs. 3–4).

With this conception comes a certain view of these self-contained entities as *loci of action*: since they are the things in which the relevant causal powers are located, their investigation is central to understanding the corresponding phenomena. In cognitive

science, this plays out in the fantasy of being able to read the language of thought off of the brain; in genetics, it is manifest in the rhetoric of DNA as the "code of codes" and the exclusive concentration on the gene as "the" mechanism mediating inheritance, embryogenesis, and more generally, development. In both cases, environments are relevant only insofar as they are encoded by the corresponding entities—neural states or genes—and more complicated systems, such as neural circuits and developmental pathways, are conceived of as spatial aggregates of neutrons or temporal aggregates of genes.

Despite the reluctance of practicing scientists to view themselves as engaging in metaphysics (Hey, that's for *philosophers!*), there is a general metaphysics in the background of this conception that is perhaps worth identifying more explicitly. The general metaphysics here is a twentieth-century update of seventeenth-century corpuscularianism, a view that we might call *smallism*, discrimination in favor of the small and so against the not-so-small. Small things and their properties are seen to be ontologically prior to the larger things that they constitute, and this metaphysics drives both explanatory ideal and methodological perspective; the explanatory ideal is to discover the basic causal powers of particular small things, and the methodological perspective is that of reductionism. In the days of Locke and Boyle, corpuscles were the very small things and the properties they had were referred to as *primary qualities*, these being taken to inhere in the corpuscles themselves, and derivatively in the things they compose.

The problem with smallism as a general metaphysics is that many of the kinds of things that there are in the world—modules, organisms, species, for example—are relationally individuated, and thus what they are cannot be understood solely in terms of what they are constituted by. Moreover, regardless of how the entities themselves are individuated, many of their most salient properties—their functionality, their fitness, their adaptedness, for example—are relational properties, which, since they don't inhere in the entities that have them, can't be discovered by focusing exclusively on what falls inside the boundaries of those entities.

To illustrate what this objection is getting at, let us return to the extended phenotype. If the phenotype literally extends beyond the body of the organism that has it, then what that phenotype is can't be explored and understood solely by examining an organism's causal powers or its intrinsic, physical properties. Rather, one needs to shift one's focus to the relations between the organism and its environment, to the extra-organismic *system* of which the extended phenotype is a part. This is not to imply that an individual's intrinsic causal powers are not relevant to what extended phenotypes it has, but to point out that the object of study contains individuals as proper parts, not boundaries beyond which one may not venture.

One might look to defend smallism from this objection by moving to a larger individual that, effectively, makes these relations intrinsic properties of this larger individual, a view what I entertained at the end of my discussion of the extended phenotype. The idea of this reply is perhaps best illustrated with another example. Consider Ernst Mayr's biological species concept: "a species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature" (1982, p. 273). Since the property of being a member of a reproductive community (conspecifics) is not an intrinsic property of an individual organism (I<sub>1</sub>)—for it could be lost in a given case simply by changing those conspecifics being a member of a particular species appears to be neither individualistic nor intelligible in smallist terms. But we can now move to consider the larger "individual," the whole breeding population or even species (I<sub>2</sub>) itself, to revive both a sort of individualism and smallism. By shifting up to a larger individual, we convert a relational property of I<sub>1</sub> to an intrinsic property concerning the relations between parts of I<sub>2</sub>. And we can understand I<sub>2</sub> in terms of its parts and their relations to one another. Smallism is thus defended.

Briefly, there are two problems with this strategy for defending smallism. First, this response simply supposes that one is able to "convert" relational properties into intrinsic properties in this way in general, but there is a range of examples (being highly specialized, being a spandrel, being a face-recognizer) for which this seems a little too reminiscent of reconstructive philosophy of science in the name of saving a general philosophical thesis. It *may* be that one is able to defend smallism in this way, but that is something that one will known only after one has explored the range of individuals that there *are* across the various sciences. (One can't simply make up what counts as an individual.)

Second, this will be smallism defended only if there are no further explanatory important properties of  $I_2$  that are relational, for, if there are, then we need to move to some larger individual still,  $I_3$ , that includes  $I_2$  (and hence  $I_1$ ) as a proper part. If relational properties of *any* individual are significant properties of that individual, then there will always remain something that the smallist view leaves out. My hunch now is that the antecedent of this conditional is true, but at the moment it is not much more than a crude guess at what we will find when we examine the relevant sciences. It is a hypothesis to be confirmed or falsified like any other.

### 3 Individuality, Complexity, and the Locus of Control

In his short book *The Individual in the Animal Kingdom*, Julian Huxley suggested three minimal conditions of biological individuality: heterogeneous parts whose

significance derive from the whole individual to which they belong; self-maintenance and continuity, either of its self or of its progeny; and some level of independence of merely inorganic nature (1912, p. 28). Huxley also suggests that there has been an increase in these qualities, a heightening of individuality, over evolutionary time and through the process of evolution by natural selection. It is this latter idea, and the idea of environmental independence, that I want to discuss here, returning first to the case of psychology.

The idea that cognition affords creatures some measure of autonomy from the immediate worldly envelope in which they find themselves seems uncontroversial enough. As cognitive creatures, we are not bound by the here and now, by mere stimulus and response. Belief and memory allow the past and the distant to influence what we feel and do, and desire and expectation do the same for the future and distant. And although we are sometimes compelled to act and feel as we do by such cognitive states, there is always an internal complexity mediating emotion and action that would seem at least typically to create a space for choice and decision, independent of the particular environmental details impinging on one at that time. I would like to explore the move from this view to a more substantive and interesting thesis about cognition and environmental autonomy that parallels Huxley's evolutionary thesis about individuality, complexity, and environmental independence.

Consider in particular the idea that heightened cognitive complexity brings with it increased environmental autonomy, culminating ultimately in symbolic capacities that can be (and should be) construed individualistically. We might express this claim in terms of a correlation between increasingly sophisticated cognitive abilities and the independence from the environment of what we might think of as one's cognitive *locus of control*, a claim that I shall make more vivid in the rest of this paragraph. Lest what follows be confused with a serious attempt to explore real-life cognitive evolution, the real history of the mind (where the determiner serves to pick out *human* minds), let me put this in terms of an entirely *imaginary* evolutionary move: that from *reactive* through *enactive* to purely *symbolic* cognitive systems. The claim that I want to consider is that in the move from reactive to enactive to symbolic cognition the locus of control shifts from the environment through the body to the mind. Table 17.1 expresses this claim more succinctly and explicitly than I could with more sentences.

With this much (or this little) said about the psychological case, return now to the case of biological complexity. We might see much the same sort of correlation between biological complexity and environmental independence: as we move from biologically simple to biologically complicated creatures, we see organisms that increase their biological autonomy from their environment. Prokaryotes and micro-

**Table 17.1** 

Locus of Control	Type of organism/ representational system	Example in humans
environmental	reactive	reflexes
bodily	enactive	mimetic skills
cranial	symbolic	beliefs, desires

organismic eukaryotes react to the world beyond their boundaries; "higher animals," in François Jacob's words, "literally live within themselves" (1970, p. 188), since they have evolved the internal machinery to enable themselves to delay brute reaction and so gain relative autonomy from their environments. The description of other complicated biological entities—genes come to mind—as "literally living within themselves" would also seem natural on what, in light of the previous section, we might call an *encodingist* conception of them.

Here I believe that the psychological case is instructive for the biological case. For there it is relatively clear that the internal locus of control that characterizes symbolic capacities is compatible with a rejection of individualism. That is, organisms that clearly have an internal, cranial locus of control for the core of their mental life may also possess what we might think of as a cognitive loop extending into the world beyond its own boundaries. In fact, I think the point can be strengthened modally: not only can symbolic representational systems with an internal locus of control be wide rather than narrow cognitive systems, but in some cases they must be wide. These are cases in which organisms have developed strategies of shifting the representational load from inside their heads to their external, symbol-laden environments through the development of what Merlin Donald (1991) calls external storage systems, such as writing systems, conventional symbols, and gestures. In short, creatures like us who posses cognitive systems with an internal locus of control can instantiate internal, bodily, and world-involving cognitive capacities. Table 17.2 puts this graphically in terms of what physically realizes these various capacities.

Granted that cognitive complexity, as epitomized in the sorts of symbolic capacities that adorn our own cognitive architecture, does provide for an internal locus of control for mentation and behavior, symbolic capacities themselves can be world-involving (and so world-dependent) in that they can require more than a mere brain to be realized. As with the case of the extended phenotype, here there is the suggestion of looking at the larger system of which the individual cognizer is a part; the individual's intrinsic causal powers (and what physically realizes them) are only part of the story to be told.

**Table 17.2** 

Cognitive Capacities in Symbol-Using Creatures	Realization of the Capacity	
purely internal	internal cognitive arrangement of the brain	
bodily	cerebral + bodily configuration	
world-involving	$cerebral\ arrangement + external\ symbol\ tokens$	

Table 17.2 should also indicate what is problematic about the encoding view of mental representation, for in neither the case of enactive, bodily skills nor that of world-involving capacities do parts of the brain encode for the other constituents of the realization of that capacity. Rather, in both cases what is inside the head and what is outside of it are related as parts of an integrated whole, with information flowing between those parts.

I want to suggest that the inference from the presence of internal loci of control to individualism in biology is likewise problematic, and that there are ways in which biological sophistication actually brings with it a *deeper* reliance of the individuals of interest on their environments. Population structures emerge, ecological dependencies are established, and the individual organism can no longer be viewed as a self-contained cluster of causal powers. The relations between individuals, and between individuals and their environments, emerge as significant.

I shall close with two brief (and very different) examples of the sort of shift in perspective that I have in mind in suggesting the abandonment of the metaphors and metaphysics of individualism and its biological equivalent, and what this shift implies in terms of more concrete research programs. Here I consider contemporary work on morphological development (beyond the gene but within the individual) and a snapshot of the history of ecology.

## 4 Concluding Examples and Remarks

In the study of morphogenesis—clearly a process that happens within the boundaries of an individual—Webster and Goodwin (1996) have recently argued for a return to rational morphology, advocating a shift in focus from genes and the notion of "gene action" to that of morphogenetic fields as complex dynamic systems. They argue that rather than concentrating exclusively on genes and their encoding powers, those interested in the development of biological form (e.g., tetrapod limbs, to take a classic case) should explore the relational principles that govern and constrain the construction of biological form, where these are not properties encoded in the genome.

As in the psychological case, it is not that genes and their powers are ignored or deemed irrelevant; rather, they are not viewed as the exclusive or even necessarily the primary locus for morphogenetic processes. The project here involves going beyond the causal powers of the gene to examine the broader principles governing development. To make this more concrete, consider an example that Goodwin discusses in chapter 5 of his *How the Leopard Changed Its Spots: The Evolution of Complexity*, that of leaf formation, particularly the positioning of leaves on a stem (phyllotaxis).

Although there are diverse shapes that leaves can and do take, there are only three ways in which leaves are arranged on the stem of a plant: in a spiral form, in a decussate form, and in a distichous form. Since one finds plants (such as those in the *Bromeliad* family) with more than one of these three ways instantiated by its various parts, and whose leaves shift from one to another form as development proceeds, it is plausible to think that there is an overall mechanism governing phyllotaxis across different species of plants that can operate in any one of three modes. Goodwin argues, following Green (1987, 1989), that this mechanism takes the form of a morphogenetic field located in the meristem, the tip of the developing plant, a field itself that is not determined solely by the information in the genes of the plant. Goodwin suggest that such a field is governed by physical forces shared by the biological and nonbiological world, forces that lead to the emergence of only some forms and not others.

There are more radical and less radical versions of the research program that emphasizes the role of morphogenetic fields and the principles that govern them over self-contained genes and their role in natural selection. The more radial version sketches these two views as alternatives to one another, such that the former might replace the latter as a general approach to understanding heritability and development. The less radical version—which I take Goodwin to advocate in *How the Leopard Changed Its Spots*—presupposes that the two views can be seen to supplement each other, since it claims more particularly that the morphogenetic field approach can explain phenomena that are simply assumed or ignored by the genecentered conception of natural selection.

Consider my second example, one from the history of ecology. Although "ecology" was coined by Ernst Haeckel in 1866, then term gained a foothold only in the 1890s to designate a sort of "outdoor physiology" (to use Cittadino's 1980 term) involving the measurement of the responses of individual plants and animals to particular environmental variables. This early conception of ecology was compatible with an individualistic conception of the discipline, as it was still concerned with the causal powers of individual organisms. As ecology turned not only to incorporate a study of units larger than the individual—the population, the community, the

predator-prey system—but also to introduce ways of talking about individual organisms that presupposed their location in a broader environment—as competitors, as niche-occupiers, as coevolvers—it became more difficult to conceptualize the science in terms of self-contained individuals that encode aspects of their environments. A closer examination of the concept of a *niche* will perhaps locate some debates within the history of ecology (see Griesemer 1993; Schoener 1989) within the framework of the current discussion.

When Grinnell introduced the concept of an ecological niche in the 1910s, he used it to refer to a place or space preexisting in an environment that actual or possible organisms could be slotted into. Elton's more extensive treatment of the ecological niche in his Animal Ecology shares this conception of a niche with Grinnell, although Elton emphasizes both the relation between an animal's niche and "what it is doing and not merely what it looks like" (1927, p. 64) as well as the availability of a niche across species, even across higher taxa. On the Grinnell-Elton conception, niches can be empty, characterized as they are independently of the intrinsic properties of particular organisms. By contrast, consider the concept of a niche as it features in the so-called niche theory of MacArthur and Levins in the 1960s, with its roots in Hutchinson's (1957) "formalization of the niche." On this theory, niches are utility distributions, being defined for particular populations or species. Basically, on this conception, a species' niche is the way in which that species uses the resources in its environment, and it defines a species' niche in terms of the role of the species in the overall community of organisms. Two points about the shift in the meaning of "niche" are noteworthy.

First, there is a shift from a conception of the niche as a space or "recess" in a habitat that an organism or species could fill to that of a niche as a (highly complex) property of that organism or species. This shift brought with it a focus on the measurement of things that organisms did and could do with their environments, rather than a concentration on the character of the habitats that organisms lived in. Second, in niche theory there is the potential to reduce what we might think of as population-level concepts (such as the niche itself, or the ecosystem) and phenomena (such as niche-overlap or ecosystem balance) to properties of individual organisms or species and their relations. This is because such concepts are already defined in terms of individual organisms and species, and the phenomena can thus be conceived in terms of relations between these. For example, niche-overlap can be conceived in terms of competition between individuals or species, and ecosystem balance in terms of niche occupation. In community ecology more generally, this fits with the sort of view that Gleason advocated in botany in the 1920s, one whereby entities larger than individual organisms, such as symbiotic pairs, communities, and ecosystems, are viewed as

relatively transient entities whose dynamics are to be understood exhaustively in terms of those of the individual organisms that constitute them (Taylor 1993).

My point in ending the chapter briskly with these examples is certainly *not* to try and argue that the views that I am presenting as nonindividualistic in character are a priori preferable over those that are individualistic, or even to pretend to have the relevant, missing empirically driven arguments in support of that preference. Rather, it is to gesture at two distinct areas of biology proper where one can see the contrast between something like individualistic and nonindividualistic perspectives on the subject matter exemplified in alternative research programs. I suspect that the same will be true of many areas of biological inquiry, and that considerations that have been raised for or against individualism in psychology will be relevant to many of these areas. But they remain suspicions to be substantiated elsewhere.

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