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# Would Venus evolve on Mars? Bioenergetic constraints, allometric trends, and the evolution of life-history invariants

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If there is ever a time in which we must make profession of two opposite truths, it is when we are reproached for omitting one.

– Pascal, *Pensees*<sup>1</sup>

### Introduction

A famous metaphor in integrative biology refers to the relationship between environmental constraint and evolutionary change as “the ecological theater and the evolutionary play” (Hutchinson, 1965). In the forty years since the penning of that phrase, the relationship between play and stage has been a matter of vigorous and fascinating debate. The issues have profound implications, not only for our scientific account of the evolutionary process, but also for our expectation of what life might look like on other planets and, indeed, for our philosophical and theological understandings of what it might mean on this one.

The controversy involves differing conclusions about the roles of contingency and constraint in evolutionary history, including, among other things, the way in which fundamental regularities of the physicochemical environment, or “stage,” influence the unfolding of the evolutionary drama. On the one hand, many prevalent expositions of the evolutionary play suggest that the fundamental or ultimate actors are genes, not organismic (much less mental) agents (Dawkins, 1976, 1998; Dennett, 1995). The drama itself is a theater of the absurd, a plotless improvisation using whatever props are contingently provided by the environment (Gould, 1989, 1996). Contingency is held to exert determinative influence on history, and, according to Stephen Gould’s widely cited metaphor, “we would probably never arise again even if life’s tape could be replayed a thousand times” (1989, p. 234). Thus, our existence

<sup>1</sup> Pascal (1958). *Pensée* no. 865.

is “utterly unpredictable” and “entirely contingent.” Come back to the theater on another night, and one is likely to see an entirely different play. Or none.

On the other hand, some accounts of evolutionary change emphasize a scientifically explicable thematic continuity and even a plausible, perhaps inevitable, directionality (Carroll, 2001; Conway Morris, 1998, 2003; de Duve, 2002; Denton, 1998; Salthe, 1993; Szathmáry and Maynard Smith, 1995; Williams and Fraústo da Silva, 2003; but see Szathmáry, 2002). Like a good melodrama, revisit the theater and one will see variations on a recurrent theme.

There are two classes of explanation for this, both of which emphasize evolutionary constraint. One approach to this issue focuses on the preconditional fitness of the *abiotic* environment – the cosmos, earth, and/or physicochemical variables – for life. Structural design of the theater predictably constrains the plot of the play, as environmental ordering trumps or at least mitigates contingent influences on evolution. This could occur through intrinsic, prebiotic properties of the stage. Or it could occur interactively through modification of the environment by organismic agents, which directionally transform stage construction by their chemical metabolism (Williams and Fraústo da Silva, 2003). Another approach involves fundamental *biotic* constraints, emerging, of course, from underlying chemistry. These constraints operate at the internal level of bioenergetic (West *et al.*, 1999a, 2004) or developmental (Maynard Smith *et al.*, 1985) limits, or at the interactive level of selectionally optimized or invariant strategies for allocating resources across life history (Kozłowski and Weiner, 1997).

Of course, metaphor may help frame (or serve to obscure!) a question, but it will not answer it. In this chapter I hope to clarify the contingency/constraint debate and its relationship to environmental fitness and directionality by focusing on several conceptually related examples of convergent functional trends in physiological and evolutionary ecology. Although all cases of convergence or directionality entail questions of physicochemical constraint, the effects may be manifest at various levels of biotic organization, including the molecular mechanisms of replication and metabolism, structures of cellular integration, multicellular functional complexity, and even intelligence. In fact, Williams and Fraústo da Silva (2003, p. 323) recognize this organizational hierarchy itself as an “inevitable progression” driven by the sequential oxidation of the environment through living cells’ reductive organic chemistry. Various contributions to this volume address each of these levels. I wish to emphasize the “upper” end of the continuum by focusing not on the traditional apex of intelligence, but on the evolved capacity for interorganismal investment or “inter-subjective commitment” (Nesse, 2001). I will argue that, within bioenergetic constraints of metabolism and selective constraints of fitness tradeoffs in energy budgets, evolution has predictably, perhaps inevitably (although not eliminatively) converged on life history strategies with particular relational significance. These

strategies involve the capacity to recognize other individuals and make significant, protracted investments in their welfare. In life history theory, this has culminated in what has somewhat euphemistically, although not altogether facetiously, been called the transfer of benefits or “live to give” hypothesis (Lee, 2003; Wade, 2003).

Vigorous controversies notwithstanding, I must begin by acknowledging that the roles of constraint and contingency in evolutionary processes are, of course, not mutually exclusive. In fact they are mutually necessary (Carroll, 2001). Nevertheless, a significant amount of both the scientific and interdisciplinary literature on these issues has been characterized by an unnecessary dichotomization of causal explanations and a regrettable polarization of rhetoric. There are two reasons for this, both of which I hope at least to avoid, if not to redress.

First, these questions have obvious entanglements with ideological and metaphysical issues. On the one hand, philosophical precommitments influence the plausibility criteria by which theories are assessed. On the other hand, scientific conclusions have implications for the justification of theological and moral belief. We will clearly see these dynamics at work in the controversies that follow.

Understandably, extreme assertions have begotten extreme responses. The cliché exhortation here would be to disentangle the science from metaphysics; but given the nature of the issues, it is not clear that this is entirely possible, or even desirable. A more modest and potentially more constructive response would be to explore the issues in light of an explicit and nuanced recognition of the logical entailments. As I will argue below, and contrary to prominent assertions (Gould, 1989, 1996; Ruse, 1996, 2003), the dichotomized scientific accounts are not diametrically opposed in their theological implications. Either can be, and each has been, employed on behalf of both theologically hostile and hospitable arguments. This does not mean the issues are irrelevant, and in fact I will argue that the very ambiguity is theologically significant.

Second, and more specifically, two logically separate but related scientific aspects of these questions have frequently been intertwined, if not conflated. However, they have quite different evolutionary foci and interdisciplinary ramifications. These involve questions of what might be considered the *necessary* versus *sufficient* conditions for the evolution of life. The first question involves the issue of which features of the abiotic environment are requisite to the origin and manifest diversification of life. This has been the traditional domain of “fine-tuning” arguments. A less metaphysically laden and more historically consistent way to speak of it would be in terms of “the fitness of the environment,” as emphasized nearly a century ago by Lawrence J. Henderson (1913). Darwinian theory typically addresses the fitness of organisms to the environment. A complimentary question – which at face value is *a priori* to the question of natural selection – is the fitness of the environment to life, or the preconditional requirements of the “theater,” to support an evolutionary drama.

This question may be asked at the level of the physical constants of the cosmos, the life-sustaining features of our planet, or the unique aspects of chemistry that are fundamental to life. If, on empirical grounds, those preconditions appear to be highly specific or biophilically constant, it raises the teleological question of the environment's fitness not just *to* life, but *for* life.<sup>2</sup> Furthermore, if – on non-empirical but some would argue rationally justifiable grounds – the specificity seems to be highly unlikely (a complicated and perhaps intractable question; see Barrow, 2002; Manson, 2000), it raises the metaphysical question of fine-tuning or divine design. It is possible to affirm the former without affirming the latter (Henderson, 1913; Denton, 1998).

In contrast to the question of necessity, which entails the characteristics of the environment (E), required for life (L) to evolve, given what we know of life ( $L \rightarrow E$ ), the question of sufficiency entails the characteristics of life that must have come to pass, given what we know of the environment ( $E \rightarrow L$ ). This involves precisely the question of inevitability in playing the tape over and getting the same results. However the environment came about, and however finely tuned its properties are or are not, does the environment that exists so constrain biochemistry that the origin of life and the direction of its evolution were highly probable, if not certain? Is evolutionary “unfolding” in any way predictable *before* the fact of history? (Freeland, Chapter 14, this volume). The idea that the world is so constructed as to guide the historical unfolding of life in a way that is open to, if not suggestive of, developmental or teleological interpretation has attracted vigorous theological interest. However, although these issues are theologically significant, there is no theistically “right” answer here. One can answer this fascinating question affirmatively, without advocating theistic precommitments or conclusions (de Duve, 2002; Denton, 1998; Wright, 2000), or negatively, while accepting them (Behe, 1996; Behe *et al.*, 2000; Dembski, 2001, 2002).

The two different issues of sufficiency and necessity – if, and only if – are alluded to in the subtitle of Simon Conway Morris's (2003) book, *Life's Solution: Inevitable Humans in a Lonely Universe*, and involve, respectively, determinative or requisite constraints in evolution. This chapter will focus on the question of sufficient or determinative constraint. The question of whether the environment is suited or fit to ensure the arisal of complex, socially affiliative life is both scientifically and theologically significant. I will argue that directional and convergent trends in the evolution of life history strategies reflect an inherent tilt toward increased

<sup>2</sup> Lest the “to” versus “for” distinction seem obscure, let me illustrate by pointing to the differing implications of saying the heart is fit *to* pump blood and the heart is *for* pumping blood. Or a Stradivarius may be fit *to* burn but is not *for* kindling. Although teleology in terms of Final Causes has been extruded quite legitimately and fruitfully from science, there is significant debate about whether teleological explanations remain helpful, perhaps essential, in organismic or evolutionary biology (Fodor, 1998; Bekoff and Allen, 1998). Henderson posited such a teleology without supernatural metaphysical entailments.

interorganismal investment. In so doing, I will make some general comments about inferences of directional trends and constraint, survey three major and interacting domains of evolutionary trend, assess current debates over their possible relationship to intrinsic constraints, and conclude with some theological comments on how these scientific issues relate to questions of cosmic purpose, or “plot” in the evolutionary play.

### **Of trends and *telos***

The issue of evolutionary directionality as it reflects finely tuned constraints involves three levels of disagreement.

### ***Trends or no trends?***

The first issue is whether there even *are* meaningful evolutionary trends suggestive of constrained directionality rather than contingent variability. Of course, evolutionary history exhibits directional change: we have life now and did not have it four billion years ago. And since the origin of life, organisms have become, among other things, larger, multicellularly complex, taxonomically diverse, and energetically intensive (Bonner, 1988; Maynard Smith and Szathmáry, 1995; McShea, 2001b; McShea and Changizi, 2003; Szathmáry and Maynard Smith, 1995; Williams and Fraústo da Silva, 2003). The question here is whether this represents the merely contingent directionality of a few “major evolutionary transitions” (Janis, 1993) precipitated by unpredictable geo- or climatological cataclysms or whether directional change representative of consistent evolutionary trends, involving, in Eldredge and Gould’s terms, “biostratigraphic character gradients” (1988, p. 211)? If so, and most important, does this reflect the fact that “life was in a physical chemical tunnel and there was only one way to go” (Williams and Fraústo da Silva, 2003, p. 335)?

Although I will assess evidence for the latter, the question has been complicated by theological entanglements. The twin issues of evolutionary progress and directional inevitability have been invested with substantial significance in the wake of natural theology’s displacement by Darwinian naturalism. Once organismic *products* could no longer be construed as evidence of intervention by a designing deity, the evolutionary *process* was argued to represent the historical drama of a divine playwright (Ruse, 1996). Thus, debates over progress and inevitability are frequently represented as disputes between theism-friendly and theism-hostile versions of evolution (Gould, 1989, 1996, 2002; Ruse, 1996, 2005). But this is not necessarily the case on either count. With respect to progress, although there has been a flourishing of evolutionary eschatologies since Chardin (Schloss, 2002), no intrinsic theological warrant exists for believing that historical change must

naturally incline toward improvement. In fact, some thoughtful traditions reject a ruddy optimism gleaned from extrapolation of progressive trends in favor of theological hope for redemption of a fundamentally ambiguous creation (Barth, 2000; Kierkegaard, 1995; Pascal, 1958). Perhaps it is even tilted toward chaos, or at least vulnerable to demise (Polkinghorne and Welker, 2000; Russell, 2002; Schloss, 2002; Watts, 2000). With respect to inevitability, it has almost become a shibboleth to say that contingency is irreconcilable with providence. In his seminal and oft-quoted *The Meaning of Evolution*, George Gaylord Simpson maintained that “a purposeless and materialistic process that did not have man in mind . . . [means] he was not planned” (Simpson, 1967, p. 344). Similarly, Stephen Gould concludes that seeing another drama on replaying the tapes is incommensurate with notions of Providence (Gould, 1996). But this is uncritically to infer metaphysical from historical contingency. It also conflates the lack of intentionality in a mechanistic cause (or process) with the lack of a final cause or divine purpose. Ironically, these are precisely the errors that are justifiably criticized in creationists’ rejection of evolution.

Moreover, if contingency is not necessarily the foe of providence, inevitability is surely not the friend (Gingerich, 2005). With the rise of seventeenth century mechanism, this very issue was the focus of debate between Descartes and Gassendi, whose views were rooted in the even more ancient differences of Tomists and nominalists (Osler, 1994). Indeed, with no contingency at all, there is no room for final cause or purposeful agency. Einstein’s aphorism reflects longstanding theological questions of causal necessity: “I want to know whether God had any choice in creating the universe.” These same issues are still unresolved between two very different (and equivalently over-simplistic) contemporary approaches to natural theology. One argues that the inevitability of life’s origin and evolutionary history is testimony of divine purpose, and another infers divine design precisely from the wildly contingent improbability of obtaining what we have (Behe, 1996; Dembski, 1998, 2001; Ross, 2001). My point is that the contingency/constraint debate is not a dispute between science and religion, but is a fundamental issue of ambiguity existing within both theological and scientific interpretations of nature.

### ***Biased vs. driven trends***

Even if one tentatively grants the existence of significant and constrained evolutionary trends (Bonner, 1988; Gould, 1988a,b; Knoll and Bambach, 2000; Maynard Smith, 1970; McShea, 1998, 2001a; McShea and Changizi, 2003; Stanley, 1973; Szathmáry and Maynard Smith, 1995; Wagner, 1996), differing understandings remain about (a) the nature of this directionality and (b) the factors that constrain it. One involves debate over whether the trends involve passive or driven evolutionary

change (McShea, 1994, 1998; Wang, 2001), the other over whether factors constraining major trends are primarily internal or external (Carroll, 2001).

Driven change would involve biased replacement or movement away from one pole and toward another pole of a character gradient, mediated by consistent selective advantages and/or fundamental biomechanical–developmental constraints. Conversely, a passive trend would involve no evolutionary bias at all, but rather random diffusion away from a minimum functional threshold of size, complexity, or other quality (Bonner, 1988; Gould, 1988b; Knoll and Bambach, 2000; McShea, 1994, 1998; Stanley, 1973). In fact, in the absence of such a minimum, there would be no directional trend at all, but simply an adirectional increase in phenotypic variance (Gould, 1988b).

As above, this debate has involved both ideological and theological issues. Ideological implications include the concern that claims of a strong evolutionary or “natural” bias toward particular biological characteristics have been used to justify, and have also often reflected, an ideologically based social vision (Gould, 1981, 1988a; Ruse, 1996). This is regrettably true in historic cases such as Social Darwinism, eugenics, Marxist genetics, and some theories of gender and social stratification (Gould, 1981; Kaye, 1986; Larson, 1995; Lewontin *et al.*, 1984; Sahlins, 1976; Sayers, 1982). For this reason, Stephen Gould has been a strong proponent both of largely contingent evolutionary history and, in clear cases of constrained trends, of passive rather than driven change. His powerful metaphor for this is a drunk’s random stumbling down a street with a wall on one side. This strong rejection of progress or any kind of directional bias in evolution contrasts with earlier views, congenial to the argument presented here, that posited a life history trend toward higher and more selective investment in other organisms (Gould, 1977). His position appears to have emerged while writing his 1981 treatise on biological racism, *The Mismeasure of Man* (Ruse, 1996).

It is indeed important to avoid using a theory of how things are as a justification for how things should be – the naturalistic fallacy (Moore, 1903). But it is equally important not to reject an idea on the basis of its implications if misused – the consequentialist fallacy. In fact, there is a long (though controversial) history, from Thomas Huxley (1894) to Richard Dawkins (1976) and George Williams (1993), of recognizing the morally ambiguous, even objectionable, nature of the evolutionary process and many of its products. Far from rejecting the underlying science on this basis, these writers have argued that it can be used to inform and exhort a human morality founded on selectively resisting, rather than uncritically endorsing, all aspects of nature.

Theologically, the image of a drunk stumbling down the road is certainly evocative, and the metaphor of passive diffusion rather than driven change is less connotative of evolutionary *telos* or inevitability. Connotations notwithstanding, I should

point out that although differences between passive and driven trends have important implications for understanding the specific causes of directional change in the evolution of various characters, each view harbors completely equivalent implications for the issue of inevitability. A diffusional process is entirely non-contingent, and although I will argue that the following trends reflect strong biases, they would be no less certain if they entailed passive, diffusional increase in maxima. “Passive trends towards increases in organismal size, complexity, and diversity from some initial minima are certain to prevail in any system” (Carroll, 2001, p. 1108). Moreover, the metaphor of diffusion (and metaphor it is) functions merely as a description of pattern, but not an explanation of cause (McShea, 1994). Even if trends are passive, we still need to examine the reasons for constrained minima and inevitable movement away from this boundary (McShea, 1998).

### *Internal vs. external constraints*

There is increasing discussion over whether major evolutionary trends, particularly patterns in life history evolution, reflect constraints that are primarily internal or external in nature. “Internal” constraints are taken to be inherent to the physicochemical, metabolic, or developmental limits of the organism and in some cases are posited to entail universal first principles underlying all organisms. “External” constraints are understood in terms of what will reproductively flourish or “work” in any given environment. They involve selectional tradeoffs between solutions to a variety of challenges imposed by different abiotic and biotic environmental factors. Many of these factors, such as dispersals of predators and competitors, or geological and climatological cataclysms, may be contingent.

Like the above two controversies, discussions of this issue have become somewhat intellectually dichotomized and rhetorically polarized.<sup>3</sup> Although advocates of the positions seem to represent differences not so much in ideological as in disciplinary commitments, the arguments reflect profoundly contrasting ways of understanding the history and, indeed, perhaps the nature of life. On the one hand, the impressive and rapidly growing literature on internal constraint, involving significant contributions by physicists and chemists, strongly maintains that physicochemical principles are sufficient to determine major evolutionary patterns. They entail provocative proposals for a universal or master equation of metabolism (Gillooly *et al.*, 2001; Savage *et al.*, 2004) or an oxidatively driven “inevitable progression” from prokaryotes to metazoan nervous systems to human beings (Williams and Fraústo da Silva, 2003). On the other hand, the notion of external constraints,

<sup>3</sup> For an excellent representation of the arguments in one recent and particularly fascinating instantiation of this debate, see the theme issue of *Functional Ecology* (2004, **18**, 2) dedicated to internalist and externalist understandings of allometric trends in metabolic rate.

emphasized by many comparative physiologists and evolutionary ecologists, acknowledges far less clarity and inevitability in evolutionary history. It views directional patterns as being underdetermined by physical necessity and reflecting the stochastic outcomes negotiated by natural selection (Bokma, 2004; Charnov, 1993; Hochachka and Somero, 2002; Kozłowski and Konarzewski, 2004; Kozłowski and Weiner, 1997; Stearns, 1992).

This issue is significant for two reasons. First, providing an account for any set of generalized patterns that goes beyond statistical description to causal explanation in terms of first principles, would represent a revolutionary contribution to the biological sciences. This is especially true for ecology and evolutionary biology, which have been markedly recalcitrant to such approaches (Whitfield, 2001). This question is germane to the themes of this volume, because it is central to the concept of biochemical fine-tuning or the Hendersonian notion of environmental fitness: it is physicochemical first principles that would constitute sufficient constraints, i.e. the suitability of the prebiotic cosmos to predictably generate the kind of life we observe.

Second, because internal constraint would presumably influence evolutionary unfolding in a way less vulnerable to contingent variation than selection-mediated tradeoffs in solutions to independent environmental challenges (Clarke, 2004; Clarke and Fraser, 2004; West and Brown, 2004; West *et al.*, 2004), it has implications for the theologically charged question of inevitable evolutionary directionality or divine *telos*. That is undoubtedly one reason for the interdisciplinary nature of this volume. However, I have already argued that inevitability is theologically ambiguous. In what follows, I will also argue that the vigorous and fascinating debate over internal and external constraint – prominent in each of the following issues – entails but does not reduce to necessitarian versus contingent views of evolutionary history.

### Bioenergetic trends

Two of the most significant trends in evolutionary history – and perhaps two of the most notable generalizations in all the biological sciences – entail evolutionary increases in body size (Cope's Rule) and energetic intensiveness across and within the major taxa. Although the former relates to the latter in several ways, I want to discuss two manifestations of energetic trends across evolutionary history that have significant implications for life history strategy. First, energy flow through biota and individual organisms has generally escalated. Biomass density, gross primary productivity, production efficiency, and secondary productivity have all increased. More significantly, energy utilization per organism has increased with increasing body mass, and mass-specific metabolic rate has increased from unicellular organisms, to ectothermic metazoans, to endothermic metazoans.

These trends represent a fascinating and well established instance of necessary conditions having been progressively generated by the action of life itself upon the environment (see, for example, Williams and Fraústo da Silva, 2003). Life-generated prerequisites to these trends include increases in atmospheric free oxygen, biomass density, and biomineralization over evolutionary time. But what drives utilization of these substrates in the direction of increased energetic intensity? Approaches to this involve internal and external constraints. Vermeij proposes a coevolutionary arms race, in which defensive armaments and attendant counter-measures result in a continuing “evolutionary escalation” (1987, 1994). Selection favors energetically intensive adaptations such as locomotor performance, toxicity, armor, high growth rates, and metabolically demanding increases in information gathering and processing. This involves intrinsic directionality, perhaps spiked by episodic and contingent environmental increases in nutrient availability (Vermeij, 1987). Alternatively, Stanley Salthe (1993) has an elegant proposal for an intrinsic increase of energy utilization in developing systems, followed by a decrease during senescence. These developmental changes occur with concomitant changes in information and organizational complexity and apply to developmental processes at organismal, ecological, and evolutionary scales (Salthe, 1993). The above approaches and others involving external and internal constraints need not be mutually exclusive, and may even be nested. Importantly, all posit intrinsic and sufficient conditions for evolutionary increase in energetic intensiveness.

The second and more specific bioenergetic trend involves thermoregulation. Beyond the fact that its very emergence represents a historic vector (primitive organisms are thermal conformers), there are two fascinating and sometimes conflated aspects of a trend toward thermoregulatory escalation. First is the increase in body temperature, or differentials between organismal and ambient temperature (Hamilton, 1973). This consistent progression is evident along an extensive phyletic continuum that includes invertebrates, amphibians, reptiles, monotremes, marsupials, eutherian mammals, passerines, and non-passerine birds. It is a dramatic example of a consistent directional trend across major taxa, but even within taxa it is tempting to describe temperature relations as reflecting a drive toward maximization or “maxithermy” (Hamilton, 1973). The preferred temperatures and thermal performance curves of most organisms are not normal but skewed left, with temperature optima that approach the highest sustainable in a given environment (Hamilton, 1973) and that are often quite close to upper-critical and even lethal temperatures (Huey and Bennett, 1987).

Why is this the case? Numerous studies provide evidence for the selective advantage of increased body temperature for food capture, prey avoidance, assimilation efficiency, and growth rates (Avery, 1984; Avery *et al.*, 1982; Christian and Tracy, 1981; Greenwald, 1974). Locomotor performance in a wide variety of species is

optimized at temperatures higher than ambient, and compensation for the depressing effects of decreased temperature does not appear to be effective: “in regards to locomotion, warmer appears to be better” (Bennett, 1987, p. 422). This appears to entail a driven directional and convergent trend across major evolutionary transitions, that involves the direct physicochemical effects of temperature.

A question that is related to but separate from the issue temperature of increase is that of convergence: why does body temperature in independent endotherms approximate 36–38 °C? Paul (1986) argued that the body temperatures of most endotherms approximate the 36 °C temperature at which the specific heat of water is lowest, and hence the temperature at which the least heat would be lost to the environment. However, the problem with this proposal is that the actual rate of heat loss, and hence the behavioral or metabolic costs of heat replacement, is entirely independent of specific heat. Thermal flux is determined by the driving force or the temperature differential between organism and environment, and elevating the temperature of endotherms to 36 °C actually results in greater heat loss. An alternative physicochemical proposal, based on this observation, is that raising the organism–environment temperature differential, and hence the driving force, facilitates the dissipation of excess metabolic heat in birds and mammals, by conduction, convection, and radiation, rather than by costly evaporative loss of water (Calder, 1986). A complimentary proposal posits the optimization of water’s viscosity, which decreases with temperature, and the solubility of hydrophobic molecules, which increases with temperature. The intersection of these curves occurs at approximately 36 °C (Duntee and Benner, 1986).

The significant bottom line is that fundamental physical and chemical properties of the abiotic environment appear to have resulted in both an increase and a convergence of body temperatures. But how do organisms maintain these temperatures? The second aspect of thermoregulatory trends involves escalation, not of the set-point, but of the modes of temperature regulation, which have become increasingly metabolically and behaviorally costly. One aspect of this involves the maintenance of body temperature by internal (metabolic) rather than external means, the progressive employment of endo- versus ectothermy, which convergently arises across vertebrate, invertebrate, and even plant taxa. Another aspect involves increasing precision of temperature regulation, the transition from poikilo- to homeothermy, entailing higher peak performance and narrower thermal performance breadth. These strategies represent not dichotomies but continua, which have increased and been coupled over evolutionary history.<sup>4</sup>

<sup>4</sup> Although some primitive organisms inhabiting thermally stable environments have been referred to as nominal homeotherms, this is a misnomer as such organisms are not thermal regulators at all, much less precise ones. Some dinosaurs may have been inertial homeotherms, relying on their large thermal mass (McNab, 2002).

Three classic explanations for the evolution of endothermic homeothermy all entail bioenergetic constraint: increased stability of body temperature enabling refinement of optimal performance, increased spatial and temporal independence of body temperature enabling expanded domains of activity, and increased metabolic scope enabling higher and more sustained peak performance (McNab, 2002). Because these advantages obviously entail tradeoffs between costs and benefits, the directional trend they are proposed to explain is not eliminative: although there is an increase in maximal thermoregulatory investment, there are still plenty of ectotherms and thermal conformers. Crucial to our focus, though, the trend is very strongly driven to converge with other life history traits, particularly parental care. The higher energetic requirements of this thermal strategy demand substantially greater parental input into young, especially because the surface area: volume ratio of juveniles involves high heat loss. Thus, while natural selection has produced and sustained a variety of thermoregulatory strategies, there has been a directional increase and convergent arisal of maxithermy, endothermy, and homeothermy – which are associated with one another and have driven concomitant increases in parental care.<sup>5</sup> If this account is correct, thermodynamics entails parental investment.

Three fundamental affirmations are relevant at this point. First, there are clear directional and convergent trends of increase in energetic and thermoregulatory intensity within and across lineages. These trends appear to have both passive and driven components, but in both cases increased maxima reflect evolutionary inevitabilities. Second, debated explanations of these trends employ internal and external constraints, but little theoretical or empirical warrant exists for considering them mutually exclusive, nor is there any credible account that is wholly contingent. Third, both energetic and size increases harbor significant implications – separately and in their interaction – for parental care and, as we shall see, other major life history trends.

### **Allometry: of mice and men**

Although trends in body size and energy utilization are significant in themselves, the scaling relation between mass and metabolism represents a crucial, some argue universal (Savage *et al.*, 2004; West and Brown, 2004), convergent evolutionary pattern. Not only is it one of the most fundamental and widely discussed regularities

<sup>5</sup> A recent revisionist theory has suggested that instead of the selective advantages of endothermy driving the evolution of parental care, the reverse was the case. High parental attentiveness drove the evolution of endothermy by the requirements of a stable temperature during development and sustained performance levels for postnatal parental provisioning (Farmer, 2000; Watanabe, 2005). These approaches may not be mutually exclusive, as it is possible to have autocatalytic effects. But while the fascinating question of the evolution of endothermy remains unresolved, the undisputed and for our purposes crucial point is the tight linkage with parental care.

in the biological sciences, but also it relates – empirically if not causally – to the important life history characteristics under discussion here.

Bergmann (1847) first noted that metabolic rate in mammals appeared to scale to a  $2/3$  power. Rubner (1883) observed that heat production appeared to be more closely correlated with surface area than mass, positing the widely cited Rubner's rule or "surface law." Huxley (1932) advocated fitting metabolic rate to a power function of mass, and based on the most extensive empirical analysis to date, Kleiber (1932) concluded that the exponent was  $3/4$ . By mid-century we had the " $3/4$  rule." Surface area explanations of metabolic scaling were abandoned. For one thing, they required a  $2/3$  exponent (representing the linear dimension squared) that did not fit the data. In addition, metabolic rate scaled to body mass by a similar power function in ectotherms, for which the metabolic replacement of surface-mediated heat loss was not relevant.

In spite of the general acceptance of the  $3/4$  rule, which has become a prominent "textbook example" of scaling, discussion has continued about whether this value for the exponent is reliable. The debate has been renewed over whether the exponent is  $2/3$  (Heusner, 1982a,b) or  $3/4$  (MacMahon, 1973, 1975; Feldman and MacMahon, 1983). There has also been concern about whether the interspecific slope reflects experimental or statistical artifact (Elgar and Harvey, 1987; Heusner, 1991; McNab, 1986, 1988). An adequate mathematical understanding of these relations has been described as "the central question in comparative physiology" (Heusner, 1991, p. 34). Indeed, until recently we have lacked not only a consensus description of how metabolism and mass scale, but also, and more importantly, a coherent mechanistic proposal for why they do so (Bennett, 1988).

That has changed dramatically over the past several years, with the groundbreaking work of West and co-workers (West *et al.*, 1997, 1999a,b, 2003; West and Brown, 2004; see also Brown *et al.*, 1993; Enquist *et al.*, 1998, 1999; Savage *et al.*, 2004). In two seminal papers, West *et al.* (1997, 1999a) accept that the  $3/4$  law is empirically warranted, and assume that natural selection maximizes resource exchange and minimizes time and energy for resource transport. They develop a model that describes resource transport through a branched, fractal-like network of circulatory tubes (1997) or, more generally, a space-filling distributional surface area (1999a), corresponding to every level of biotic exchange from digestive cavities or plant leaves to transport vessels to cell surfaces, mitochondria, and even molecules. Unlike external surface area, which scales as the square of the linear dimension, an internal, space-filling surface area scales to the cube. Energy utilization will scale as a function of  $D/(D + 1)$ , where  $D$  = the number of dimensions. The adaptations to provisioning an internal, "three-dimensional" surface area effectively endow living systems with an additional, "fourth" dimension.

The authors conclude that these geometric and physical constraints so limit the possibility space on which selection can act, that all organisms reflect quarter-power scaling laws –  $3/4$  for metabolic rate,  $1/4$  for internal time and distance – that are as universal as biochemical pathways or the genetic code. However, unlike the latter two cases, which may reflect the retention of an underdetermined initial character that arose but once, adaptations that effectively contribute a fourth dimension – lungs, gills, guts, kidneys, organelles, as well as branching whole-organism morphologies – have convergently arisen at numerous times in evolutionary history.

This proposal both points out and explains the convergent scaling of numerous physiological adaptations, and it also has been extended in an impressively ambitious and promising attempt to explain a wide range of previously disparate relations in population and community ecology. This includes: proposals for universal temperature dependence of life; scaling relations in plant morphology, productivity, and life history; energy flux, carbon turnover, and biomass density in plant populations; a general allometric model for growth and development; energy flux in ecosystems and across food webs; rates of mutation and carcinogenesis; and patterns in global biodiversity (Allen *et al.*, 2002; Brown and Gillooly, 2003; Enquist, 2002; Enquist *et al.*, 1998, 1999, 2003; Gillooly *et al.*, 2001, 2002; Niklas and Enquist, 2001; West *et al.*, 1999b, 2001, 2004). It is the first attempt to provide an account of a wide array of biological and ecological generalizations on the basis of first principles.

The formulation of inherent biophysical constraints represents an emphatic alternative to radical contingency: “Does some fixed point or deep basin of attraction in the dynamics of natural selection ensure that all life is organized by a few fundamental principles and that energy is a prime determinant of biological structure and dynamics among all possible variables?” (West and Brown, 2004, p. 42). The proposal for fundamental internal constraints is one of the most broadly unifying and mechanistically based explanations advanced in evolutionary ecology. It has been widely lauded – “if it holds up, it’s going to rewrite our evolutionary biology” (Klarreich, 2005) – and also severely criticized.

The disagreement falls into three main classes. First, some researchers still dispute the  $3/4$  characterization of metabolic scaling (Bokma, 2004; Dodds *et al.*, 2001; White and Seymour, 2003). However, in an analysis of what is arguably the most extensive and rigorously selected data set to date, the West team confirmed  $3/4$  scaling across mammals and a variety of other taxa (Savage *et al.*, 2004). Moreover, they point out that deviations from  $3/4$  scaling, found in smaller mammals by other studies, are actually predicted by their initial model on the basis of dominance of Poiseuille rather than pulsatile flow in smaller-diameter, originating vessels.

Second, some workers affirm the  $3/4$  rule and posit an explanation for it that involves intrinsic constraints, but disagree with West and co-workers’ proposal. Banavar *et al.* (1999, 2002) advocate an account that is amenable to but more general

than West's, rejecting the notion of an effective fourth dimension to life. Instead, allometric scaling is intrinsic to all systems with directed flow and circulation times that are proportional to length but not size. However, a problem with this is that it does not provide a conciliatory explanation for all the other organismal characteristics that scale allometrically.

Darveau *et al.* (2002, 2003) propose that the relationship between body mass and metabolic rate reflects the contribution of multiple factors – ATP-utilization processes in parallel, supply processes in series – that each have different power functions. This hierarchical layering results in an “allometric cascade” that has different scaling implications for different measures of metabolism. They contend that only a multiple-factor account, and not West's (or any) single-cause account, can explain the scaling difference between basal and maximum metabolic rate (Bishop, 1999). However, the mathematical formulation of their model has been severely criticized (Banavar *et al.*, 2003; West *et al.*, 2003), and in any case it does not provide an account of why individual processes scale as a power function of mass or why the causal cascade results in a whole-organism metabolism that approximates the 3/4 rule (Bokma, 2004; West *et al.*, 2003; West and Brown, 2004).

Third, dispute exists over whether there even is a universal scaling relation and whether ostensible patterns reflect internal biophysical constraints of any kind (Clarke, 2004; Clarke and Fraser, 2004; Kozlowski, 1996; Kozlowski and Weiner, 1997; Kozlowski and Konarzewski, 2004). This is asserted for two reasons. For one thing, it is claimed that the data do not support the model. This is because the 3/4 rule itself is an artifact of an interspecific regression that traverses heterogeneous intraspecific regressions with independent slopes and intercepts and also because functionalist explanations do not adequately account for the extremely large and highly correlated residual variation (Kozlowski and Weiner, 1997).<sup>6</sup>

For another thing, it is maintained on theoretical grounds that metabolic and life history variables interact with one another in the ecological context of each species, rather than being deterministically related to body mass for all species. The balance between these factors, and their relationship to body mass, reflects the ecological conditions unique to each species and, in principle, no meaningful interspecific generalization can be formulated. Several models of evolutionary tradeoffs have been proposed to explain the same data used by West and coworkers (Kozlowski and Weiner, 1997; Clarke, 2004). However, like the above multiple factor internalist accounts, what the approach of viewing allometric trends as by-products does not do is to explain why metabolic rate scales to body mass – even within species – as a power function to begin with. Nor does it explain the generalized patterns

<sup>6</sup> For any given mass, variation in metabolic rate may span an order of magnitude, and the same metabolic rate may be found in organisms with 20–30-fold differences in mass. More importantly, the residual variation itself is not random, and many life history parameters are still highly correlated even after being adjusted for mass (Kozlowski and Weiner, 1997; Kozlowski and Konarzewski, 2004).

across taxa, i.e. why certain proportions are more likely than others (Kozlowski and Weiner, 1997) and what constrains the distribution of possibilities on which selection can act.

So what can we conclude? The proposal for internal constraints represents a path-breaking attempt to explain long-observed patterns in biology, on the basis of physical first principles. And it not only fits the basic, coarse-grained allometric data, but it has fruitfully generated new hypotheses and has been used to explain a wide array of other observations as well. None of the alternative proposals accomplishes this. However, it does not explain fine-grained patterns and significant deviations from predictions, which appear not to represent mere noise but residual variation explainable by other – most likely external – factors.

To some extent, a disciplinary divide is at work here, as “probabilistic models derived from population biology and selection theory differ fundamentally from engineering models, which depend on . . . the surface area of isometric bodies, or the structure of branching networks” (McNab, 2002, p. 35). This divide entails not only differences in analytic approach, but also in evaluative criteria that have both polarized the dispute and made it difficult to resolve empirically. However, my point is that these tensions do not require a forced choice between explanatory accounts, which are not intrinsically irreconcilable. Internal constraints may fix the allometric baseline, which selection may modify under certain circumstances. One of the postulates of West and co-workers’ model is that “organisms evolve toward an optimal state in which the energy required for resource distribution is minimized” (West and Brown, 2004, p. 38). “Toward” is the key word here, and the extent to which evolution attains any particular optimality target often reflects compromise with other selective demands: physical first principles may constrain what is optimal, but do not always determine what is actual.

Therefore, we can summarize with three conclusions that are analogous to what was affirmed in the previous section. First, there are clear allometric trends that represent convergence of scaling relations across a wide range of both taxa (bacteria, plants, invertebrates and vertebrates) and organizational levels (organelles, cells, bodies, and ecosystems). Second, although the relative contribution of “internal” (biophysical) and “external” (selection) constraints is debated, no account of these trends – which include invariant relationships – interprets them as products of primarily contingent causes or passive radiation. And third, allometric trends are strongly related to, and to some extent constitutive of, important life history trends to which we now turn our attention.

### **Life history across life’s history**

“Life history” refers to the timing and allocation of resources for growth, maintenance, and reproduction over an organism’s lifetime. The size and number of

offspring; investment in parental care; ovi- and viviparity; growth rate and adult body size; and ages of reproductive maturity, reproductive cessation, and death are presumably all under control of selection to optimize reproduction. These variables do not evolve independently of one another. Some are related by invariant ratios, and most occur in strategic constellations that represent significant directional and convergent evolutionary trends.

What I want to focus on is the capacity for selective interorganismal investment. This is represented by high degrees of parental care and social reciprocity, which are positively associated with body size and lifespan and negatively associated with specific metabolic rate and lifetime fecundity. A clear trend of investment increase over evolutionary time has been observed, although it involves an increase in maximum and not mean investment. It represents a classic example of non-eliminative, passive – although apparently inevitable – diffusion away from a minimum. On the other hand, its coupling with other parameters is a driven or strongly constrained trend.

As with the trends previously mentioned, proposals have been promulgated for internal and external constraints. At first pass, it is tempting to account for relations between life history variables almost purely on the basis of fundamental allometric constraints. Metabolic rate, lifespan, fecundity, age at maturity, and maternal investment all vary with body mass as power functions. In fact, relations are invariant between some of these variables. For example, lifespan scales with body mass by a  $1/4$  power, and heart rate (or the rate of ATP synthesis) scales with body mass by a  $-1/4$  power. The product yields an approximately constant number of “metabolic events” in mammal species, independent of body mass or lifespan. Age at maturity / lifespan, and annual maternal investment / lifespan (for indeterminate growers) are also invariant ratios (Charnov, 1993; Charnov *et al.*, 2001; Stearns, 1992). West and Brown (2004) point out that invariant ratios, and universal quarter-power allometric trends in general, suggest underlying physical first principles. They employ their model to explain these life history relations (Enquist *et al.*, 1999; Niklas and Enquist, 2001; West *et al.*, 2001).

However, the two types of criticism leveled (I have argued unconvincingly) at their application of physical principles to scaling of metabolic rate are more telling against this being an adequate *single-cause* account of all these variables' relations to body size and one another. First, selection theory argues against an inflexible coupling of life history variables to mass (Calder, 1984; Charnov, 1993; Charnov *et al.* 2001; Kozlowski, 1996; Kozlowski and Weiner, 1997; Kozlowski and Konarzewski, 2004; Stearns, 1992). This has recently been empirically confirmed by an elegant analysis that related life history traits in mammalian carnivores to body sizes of extant species and their direct ancestors (Webster *et al.*, 2004). In those species that have recently undergone size change, life history variables were more

closely correlated with ancestral than present size; for example, phyletic giants have smaller offspring, in larger, earlier, and more frequent litters than similarly sized species that have not recently become large. Therefore, life history variables, which do scale to body mass, may be coupled loosely by selection rather than rigidly by biophysics.

Second, and perhaps more importantly, both phyletic differences and residual analysis of general relations have important stories to tell. For example, although age at maturity scales directly with average adult lifespan, the ratio decreases across vertebrate classes (fish, reptiles, mammals, birds), reflecting a gross trend toward iteroparity, or increased proportion of lifetime over which reproduction occurs. Regarding residuals, although length of maternal investment and annual fecundity scale with body mass (and hence each other), the residuals also scale with one another. That is, a strong negative relation exists between size-adjusted or relative fecundity and relative maternal investment (Stearns, 1992). This is a crucial life history trend in its own right, having an allometric but also an entirely size-independent component. Bats and primates are at the upper end of the regression and also occupy similar positions in residual analysis of lifespan and body mass. There is an evolutionary trend toward protracted lifespans, reduced fertility, and increased parental investment beyond what predicted by first principles, and a linking of these features in a fashion that is not allometrically mediated.

Here again the literature has become highly polarized, though it is not only possible but also necessary to avoid a false dichotomy. It is precisely the contribution of both internal and external constraints that is most noteworthy in these trends. The important conclusion is that natural selection has found a way of both employing and “amplifying” allometrically mediated relations between life history variables to generate organisms that invest more resources, with more selectivity, over greater timescales. Physical first principles underlie but do not wholly determine this.

A salient example of interaction between internal and external constraints in life history trends involves the issue of lifespan or the timing of senescence and death, which also turns out to have newly posited implications for investment. On the one hand, lifespan has been interpreted as reflecting fundamental allometric constraints (West *et al.*, 2001; West and Brown, 2004). Larger organisms have lower specific metabolic rates and tend to live longer. This is consistent with the quarter power account of biological time (West and Brown, 2004) and concords with metabolic damage (e.g. telomere damage, free-radical accumulation) or “rate of living” theories of aging (Finch, 1990; Rose, 1991).

On the other hand, evolutionary theories of aging posit that the timing of senescence is not mechanistically determined by metabolically induced damage, but rather, by selection’s response to *external* mortality factors. In fact, there should be no senescence at all in the absence of external causes of death. The extent to

which an organism invests in repairing damage will reflect the externally mediated likelihood that an investment in maintenance at any given point in the lifespan will result in sufficient additional reproductive opportunities to pay the investment back in future progeny. More generally, selection will allow the accumulation of deleterious mutations that are expressed late in life, when an organism's reproductive potential is low (Medawar, 1952; Hamilton, 1966). And it will actually promote, through antagonistic pleiotropy, traits that increase reproduction early in life at the expense of dysfunction later in life (Kirkwood, 1977; Williams, 1957). Various experimental (Rose, 1984, 1991; Tyner *et al.*, 2002) and observational (Keller and Genoud, 1997; Sherman and Jarvis, 2002) studies support this, which are not made sense of by first-principle, rate of living accounts.

As before, both internal and external constraints – entailed in this case by rate of living and evolutionary theories of aging – can operate simultaneously, indeed interactively. But neither has done a good job of explaining certain unexpected mortality patterns that some highly social species exhibit at the beginning and end of life. Although both approaches predict that mortality rates will increase with age across the lifespan, in some species with high parental care infant mortality actually decreases as juveniles mature, and these species also exhibit protracted post-reproductive longevity. Enter the first theory to incorporate parental care – or “transfer of benefits” as opposed to brute fertility – as the major determinant of mortality, and of life history under some circumstances (Lee, 2003). In demographic conditions where intensive parental care is essential to survival of progeny, selection may more effectively eliminate deleterious traits in offspring that have already incurred high parental investment (hence the declining juvenile mortality with age). This approach also explains how selection can operate against antagonistic pleiotropy or accumulation of mutations that are expressed later in life. Anticipated by the notion of a “grandmother effect,” in which post-reproductive individuals can still very significantly enhance fitness by caring for progeny or their kin (Williams, 1957), Lee formalizes this in a model that integrates economic exchange, demography, and population genetics. Because it provides a unified account for mortality patterns across the entire lifespan, it has been referred to as “the most comprehensive evolutionary theory of aging that we have seen to date” (Rogers, 2003, p. 9115).

In fact, under certain circumstances, the ability to “transfer benefits” to progeny or kin, rather than the maximization of lifetime fertility, becomes the primary controlling parameter for other life history characters. An organism's entire life history strategy may be optimized for this. In addition to providing a unified explanation for patterns that previously appeared anomalous, this life history theory is significant in that it explicitly posits a driven, directional trend. It entails “a positive feedback loop that selects for reduced fertility, higher consumption, greater investments in juveniles, and longer life. This describes the evolution of primates and other kinds

of species with low fertility, heavy investment in offspring, and long adult life” (Lee, 2003, p. 9640). In contrast to some representations of the debate over internal/external constraints, this feedback loop involves an inevitable convergence that is driven not just by internal biophysical, but by external selective constraints.

A distinctive, and I will suggest a beautiful, implication of the theory is its emphasis on not only the phylogenetic, but also on the ontogenetic intensification of investment or resource transfer. The progressive transition from receiving to giving benefits is itself a life history parameter that changes developmentally over the lifespan, a notion Lee considered calling the “live to give” theory (Wade, 2003). Is there, in this theory, a ground for rehabilitating Alfred Tennyson’s dashed hope in “love Creation’s final law”? Although that affirmation of Romanticism may be a bit too saccharine in light of evolutionary ambiguity, a profound and escalating other-orientation does appear to constitute a fundamental biotic constraint.

### **Conclusion: trends, progress, and purpose in evolution**

I began this chapter by observing, and lamenting, the fact that discussions of evolutionary trends have frequently been polarized by divergent theological or philosophical precommitments. However, seeking to avoid metaphysical biases need not mean refusing to reflect on theological implications. I want to conclude with some brief comments on the significance of these issues. To do so, I distinguish between evolutionary trends (change in a given direction), progress (change in a valued direction; Ayala, 1988), and purpose (regulated change in a targeted direction).

First, fashionable pronouncements of disteleology notwithstanding, there is little room to doubt the existence of significant life history trends in evolutionary history. This entails the convergent arisal, biased retention, and directional elaboration of fundamental organic structures and functional strategies that increase selective investment. Such increases appear to be the inevitable result of both fundamental biophysical and selective constraints. Moreover, these trends involve a genuinely interesting story, or to return to our initial metaphor, an evolutionary play whose plot involves increasing size, energy, complexity, diversity, longevity, and affiliative investment. This is, in a real sense, increasingly abundant *life* (Jonas, 1966).

As I mentioned at the beginning of the chapter, it is possible, even tempting, to reflect on this in a couple of ways. First, one may marvel at the stage and calculate the odds of its having been designed without input from the playwright. This is the domain of environmental fitness or fine-tuning arguments, emphasizing what I have called “necessary preconditions.” Second, one may marvel at the way the stage supports this *particular* drama and wonder whether it could have turned out differently in this theater. This is the domain of inevitability arguments entailing sufficient constraints or preconditions, which I have been emphasizing. Both of these enterprises are legitimate, and each is interesting. But both may fail to focus

on the message of the play itself. Like some forms of biblical fundamentalism that seem to place more emphasis on the method of textual inspiration than on the larger meaning of scriptural revelation, one may be so caught up in the architecture of the physicochemical stage that one does not adequately engage the drama of the evolutionary play.

Second, what then can be said about the “message” of the script itself? Here again I want to question the *Zeitgeist* and maintain that, by any reasonable sense of the word “progress,” evolutionary drama is filled with it, by virtue of an ongoing, serial intensification of the wondrous qualities of life itself. Theologian John Haught, who contributed a chapter to this volume, maintains that “Surely, by any objective standard of measurement, something momentous has been going on here . . . an overarching inclination . . . toward the heightening of beauty” (Haught, 2005, p. 520). Philosopher Hans Jonas (1966) refers to the evolutionary epic as the “the ascent of soul.” In response to qualms that such a judgment is parochially anthropomorphic, he contends it is appropriately *zoomorphic*. I would suggest that each of the major trends discussed in this paper build on one another to constitute a suite of biotic capacities that are jointly necessary for what we would call “love” or “relational commitment.” This surely constitutes progress, a change in a valued direction.

However, I want to point out two profound ambiguities in this “progress.” First, as indicated earlier, none of these trends is eliminative. Even if they constitute progress, the “world” is not getting better, in terms of either a modal increase in beneficence or an attenuation of natural evil. Second, these capacities for affiliative investment that underlie love and commitment are necessary, but by no means sufficient. For one reason, other capacities are required that lie beyond the scope of this paper (and may or may not be outside the domains of existing biological theory; (Schloss, 2004)). For another and more important reason, these capacities are just that – capacities, and not deterministic inclinations – to act in certain ways. In fact, behavioral plasticity increases along with the strategic assemblage of these capacities (Changizi, 2003). Thus, the cognitive and affective capacities, and life history and social contexts, that give rise to attachment, altruism, or moral commitment, may also facilitate manipulation, spite, or deceptive moral posturing. Ultimately, evolutionary “progress” is morally ambiguous. Like the biblical story of creation, it involves the origin of potentiality for, but not inevitability of, creaturely goodness, and the increase of this biological capacity is also coupled with an increased capacity for suffering (Schloss, 2002).

Finally, does it make sense to speak of evolutionary purpose? At one level, the answer to this question is easy. Like all mechanistic processes, evolution is non-purposive. In fact, natural selection is explicitly formulated as a non-teleological alternative to explanatory accounts invoking purposeful design. But supernatural metaphysics aside, there is a naturalistic context in which it could make scientific

sense to speak of evolutionary purpose in a way analogous to the teleonomic, goal-oriented, or purposive behavior of living organisms. Living systems exhibit “regulated change in a targeted direction.” Evolutionary change could be construed as purposive if: (a) its directionality were targeted or specified (perhaps by pre-existing or emergent environmental information) and (b) the process were adjusted by regulatory feedback loops (perhaps involving ecosystem- or biospheric-level interactions, e.g. Gaia). Although notions of environmental fitness or biochemical fine-tuning could and probably do contribute to the first requirement, the second, although it is fully naturalistic in principle, lies outside our current ability to assess empirically. Lee (2003) and Demetrius (1997, 2000) do provide conceptual proposals for how such directional feedback might occur in selection.

But the question of evolutionary purpose has another meaning, which involves not so much the purposes *of* evolution, but the possible purposes *behind* evolution. Can evolution, particularly the trends discussed here, be reasonably viewed as reflecting, even instantiating, purposes that transcend the process itself? Here again the spirit of the age is far from shy. A virulent natural atheology (Lustig, 2004) asserts that ascribing divine purpose to evolution is not only methodologically illegitimate, but also rationally incoherent (Dawkins, 2003; Gould, 1989, 1996; Rachels, 1990; Williams, 1993). Evolutionary history is represented as involving such great waste and suffering, resulting in such little if any directional progress, it is asserted that one who wishes to believe in a God behind evolution should be prepared to believe in “a monster” (Williams, 1993). Sadly, many traditional theists have either uncritically accepted or actively promoted the same view. I want to close by maintaining that the emerging understandings of evolutionary constraint described in this chapter, and in other chapters in this volume, are consistent with, even suggestive of, divine purpose. But they are by no means demonstrative of or even simplistically concordant with it. This very ambiguity is itself quite important for science and theology, both of which suffer when science is distorted to promote a false nihilism or co-opted to bolster a mechanistic optimism about the fate of the cosmos. As Pascal maintained centuries before evolutionary theory, the natural world affords enough light to allow, but enough shadow to require, theological hope rather than religious or nihilistic certainty.

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