Dawkins or Lewontin or both? Review of The Gene's-Eye View of Evolution, by J. Arvid Ågren, Oxford, U.K: Oxford University Press.

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J. Arvid Ågren's expansive book appropriately starts with a simple description of the "gene's-eye view of evolution"—"natural selection is conceptualized as a struggle between genes… [or, rather] between different alleles of the same gene within a population" (p. 2)—and a brief survey of the "debate over the value" of that view (p. 2), including the "discomfort" it has caused to many (p. 3). Indeed, Ågren recounts how "a senior colleague… wondered if he really would be a suitable person to provide feedback [on the manuscript] as he disagreed with 'virtually every aspect of the field' and [had] 'trouble separating their bad science from good faith attempts to describe it'" (p. 3). The first few introductory pages of *The Gene's-Eye View of Evolution* thus reflect what seem to be the two aims of this book:

1. to flesh out the gene's-eye view as clearly and starkly as possible, including reviewing what Ågren takes to be its "empirical implications";
2. To trace the history of the origin and reception of the gene's-eye view, including identifying Richard Dawkins as the single, most vociferous and influential defender of the view.

Undoubtedly, this is a valuable book. It fulfills both these aims valiantly, and with clarity and synoptic vision. There are other contributions in the gene's-eye tradition that also fulfill these aims (among others), including Segerstråle (2000), Okasha (2006), and Godfrey-Smith (2009). But this is the first time a conceptually and historically complete book on the subject has been published. (Segerstråle's book is written from a cultural historian's perspective, whereas Okasha'a and Godfrey-Smith's books are almost exclusively technical and philosophical.) Thus,

Ågren's book is a welcome contribution that satisfies the culturally and historically hungry as well as the technical and philosophically curious.

But this book is also written from a particular perspective. Ågren claims that "Dawkins is a strong contender for the most famous evolutionary biologist alive" (p. 44). Although sadly perhaps true today, at the time of the book's publication, Richard Lewontin would clearly have been another "strong contender" (Winther 2021). Without wishing to reify this as a dualistic battle, and certainly not as a Manichean one between "good" and "evil," there is a powerful tradition opposing the gene's-eye view. This alternative tradition grew out of the population genetic work of, among others, Sewall Wright, Motoo Kimura, and Theodosius Dobzhansky, and crystallized in the creative and influential work of Lewontin.

The *Lewontinian* tradition includes Lloyd (1994, 2020), Sober and Wilson (1998), and Wade (2016). It emphasizes group and hierarchical selection; organismic agency and niche construction; and gene epistasis and developmental holism. If it has a manifesto, it is Levins and Lewontin (1985). If it has a rallying cry, it is the last sentence of Lewontin's classic *The Genetic Basis of Evolutionary Change*: "context and interaction are of the essence" (Lewontin 1974, p. 318). Although Ågren correctly lauds "Lloyd [for the] enormous job in clearing up and sharpening the debate about units and levels of selection" (p. 60) and good-naturedly describes Wade's book as a "lovely personal account" (p. 36) of the history of group selection, it is of course unsurprising that Ågren downplays many of the arguments and framing devices by the Lewontinians. He reduces Lloyd's complex "four different questions" framing of the units and levels of

selection to just one: "the gene's-eye view is based on the conviction that the beneficiary question is the most important one" (p. 61); similarly, Ågren recognizes Wade's critique—"Wade reviewed the mathematics of epistasis in light of the gene's-eye and suggested that it usually provides a too simplistic account of the underlying genetic interactions" (p. 94)—but Ågren does not make much of this important critique. Thus, with respect both the *vertical averaging* debate about which level(s) and unit(s) of selection are meaningful in evolutionary theory and the *horizontal averaging* debate about whether genes act singly or in combination, Ågren merely reiterates a gene's-eye view without providing strong and clear counter-arguments to Lloyd's and Wade's analyses. (On vertical vs. horizontal averaging, see Winther et al. 2013, cf. Winther 2021.)

It was interesting to me to see Ågren use the category of "reification" in the book's conclusion:

> A little bit of familiarity [with the gene's-eye view] may also help avoid the issue known as reification. This fallacy occurs when metaphors or abstract constructions are treated as if they were real physical things: 'a map is not the territory' as Korzybski ([1994 (1933)], p. 58) put it. Throughout this book, I have described several instances where critics of the gene's-eye commit this fallacy. (p. 187)

I have written a book on reification, maps, and philosophy of science, where pernicious reification is analyzed as a combination of ontologizing, universalizing, and narrowing a particular paradigm, theory, or model (Winther 2020a; cf. Winther 2020b). Unfortunately, Ågren neither clarifies nor uses the concept of reification elsewhere in his book, leaving readers to wonder *where* "critics" have committed "this fallacy."

Permit me to be blunter. As a counterpoint to Ågren's adulation of Dawkins, here is a Lewontinian rereading of Dawkins' gene's-eye view. With *The Selfish Gene*, a powerful theoretical map of evolution was unleashed upon the world. In this influential popular science book, Dawkins articulated the gene's-eye view by integrating (1) the behavioral ecology of his PhD advisor Nikolaas Tinbergen and David Lack, (2) the game theory of John Maynard Smith, (3) the inclusive fitness or kin selection theory of William Hamilton, (4) the anti-group selection gene-focus of George C. Williams, and (5) the population genetics of "Sir Ronald Fisher, the greatest biologist of the twentieth century" (Dawkins 2006 [1976], p. 124). *The Selfish Gene* abstracts from multiple disciplines to formulate an explanatory theory or map of the potentialities of its postulated central figure, the selfish gene. Admittedly, Ågren provides elegant historical discussion for exactly how Dawkins integrated these many voices and framings.

Now, given the specific explanatory contexts and epistemic concessions within these bodies of work influencing Dawkins, a successful integration must be done carefully and pluralistically. Unfortunately, however, Dawkins' ambitious but simplistic integration resulted in a reductive theory, treating genes merely *as if* they were agents duking it out on the evolutionary stage, each with the goal of leaving as many copies of itself as possible in the next generation. In this play, kin matters, in a particular way. After all, your sister or, to a lesser extent, your cousin has a higher chance of carrying the same gene (more precisely: allele) than a random member of your species. Moreover, cost-benefit analyses of each possible behavioral strategy must be calculated by genes and selection, in agential conjunction. One is tempted to say that Dawkins reifies genes, which are his prime example of replicators, *as performative agents making game-theoretic decision analyses weighted by coefficients of relatedness*. Indeed, such an "agential view" can be celebrated: "the gene's-eye view… brings to the forefront evolutionary biologists' peculiar habit of speaking of biological entities as having intentions, deploying strategies, and pursuing goals" (p. 3; cf. pp. 86−89). This is not the place to trace the history of an agential view or agential habit, which reaches back philosophically to Aristotle, Immanuel Kant, and William James, although they explicitly framed *organisms* as the owner of agency (e.g., Guyer 2014; Walsh 2015; McGranahan 2017; cf. Sultan et al. 2021). There are many good reasons to be skeptical of an agential view vis-à-vis genes, alternative metaphors for genes are on offer, and it remains unclear how beneficial the use of metaphor in this context is.

I suspect the debate surrounding the gene's-eye view will continue, probably without end. One interlocutor's truth claim is another's pernicious reification. Potentially, the mathematics are inconclusive and Dawkinsian formulations (e.g., of inclusive fitness, cf. chapter 4) can be rewritten or rethought formally in Lewontinian language, metaphor, and mathematics. Analogously, the empirical data and implications are so theory dependent that it is hard to even understand what "selfish genetic element" (chapter 5) means, independently of the gene's-eye paradigm. Thus, neither formalism nor empiricism will help us—or *has helped us*—decide between a gene's-eye view and a group selectionist and/or developmental holist view. There is a beautiful and irreducible pluralism (Longino 2002; Winther 2006, 2020a,b) of views here that seem destined to be repeated and reiterated. (Indeed, I hope that there is a PhD student or two somewhere writing a conceptual history of the Lewontinian view.) Ågren's book is the most recent, and a rather complete, analysis and history of the Dawkinsian gene's-eye view. It definitely merits reading and careful study by anyone interested in grand questions of evolutionary theory.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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