The strategic revolution

Andy Gardner

University of St Andrews, Dyers Brae, Greenside Place, St. Andrews KY16 9TH, UK. Correspondence: andy.gardner@st-andrews.ac.uk

On the 40th anniversary of the publication of Richard Dawkins's The Selfish Gene, we explore the origins of cynical, strategic thinking in evolutionary biology, investigate how this illuminated the sexual and social lives of animals, and assess Dawkins's suggestion that evolution is best understood by taking the gene's-eye view.

Introduction

Richard Dawkins's *The Selfish Gene* (Dawkins, 1976), now entering its fifth decade, was unequivocally the most important popular book on evolutionary biology of the 20th century. It describes a revolutionary approach to animal behavior that was storming the academic community, wiping out the conceptually bankrupt ''group selectionist'' thinking that had come to dominate much of biology and opening up new vistas for exciting scientific enquiry. Unlike many works of popular science that give the impression of providing the last word on a topic, Dawkins's book reads as an entry point into a much larger discussion and encourages the reader to join the conversation. This reader did exactly that: I can point to Dawkins's book as the reason why I chose to study and pursue a career in evolutionary biology. And, as numerous conversations with school pupils, undergraduates, and PhD students have shown me, it continues to pull in new recruits to this day.

Here, I will consider three aspects of this landmark publication. First, I will explore the prehistory and context of the ''strategic revolution'' that provides the substantive core of Dawkins's book. This fastens attention on the idea of biological entities as agents employing strategies in the pursuit of conflicting agendas and emphasizes that one needs to be clear as to which entities manifest agency and what they are striving to achieve. Second, I will discuss how this revolution was changing the way we think about animal behavior, providing simple explanations for general patterns observed in the natural world and unveiling hitherto unappreciated battlegrounds and suites of fascinating adaptations. Third, I will assess Dawkins's particular suggestion that we must focus on the interests of the gene if we are to understand animal behavior, and I will investigate the relationship between selfish-gene theory and intragenomic conflicts of interest.

The Good of the Group

The core feature of life is its apparent purposefulness. Prior to Charles Darwin, this had been attributed to the work of deities, but the theory of natural selection made clear how the appearance of design could instead emerge automatically as a consequence of heritable traits having differential impact upon their bearers'

reproductive success. Strangely, in the first half of the 20th century, this central and far-reaching scientific discovery was almost completely neglected by population geneticists, who treated natural selection as just another evolutionary force without any special importance. As a result, there was little formal clarity on issues of adaptive evolution and the question of which biological entity was supposed to manifest design and for what purpose.

A key exception was R.A. Fisher, whose masterpiece *The Genetical Theory of Natural Selection* (Fisher, 1999) emphasized that it is individual organisms who become adapted, as shown by his ''fundamental theorem of natural selection.'' In the 1958 edition of his book, Fisher included a section on ''the benefit of species,'' emphasizing that any benefit of adaptation to the species as a whole is purely incidental. But the general assumption among population geneticists was that better allelic variants make for better bodies that make for better populations. They supposed that the question as to what ''better'' should mean may be of philosophical interest but of little consequence for science.

However, purpose is inescapable in biology, and many of its subdisciplines are motivated and organized according to the idea that there is a functional, adaptive rationale underpinning biological structures. Consequently, the vacuum created by the population geneticists led to the insidious establishment of a pseudoscientific ''group selectionism'' that explained away all biological traits as functioning for the good of the species. Thus, reproduction and parental care were interpreted as being for the continuation of the species, as was the industry of sterile workers in social-insect societies and the gentlemanly antler-locking rituals of stags deciding access to does. By giving the impression of providing an explanatory framework that readily accommodated such phenomena without further investigative work needing to be undertaken, group selectionism opposed the advancement of the biological sciences.

This state of affairs culminated in the 1962 publication of Vero Wynne-Edwards's book *Animal Dispersion in Relation to Social Behavior* (Wynne-Edwards, 1962). Wynne-Edwards documented various fecundity-modulating behaviors across the animal kingdom, with a particular focus on bird populations, which he interpreted as group-level adaptations for regulating population density. He regarded the individual as exercising reproductive self-restraint so as to avoid overstretching resources and hence ensure continued population survival.

The explicitness with which Wynne-Edwards framed his account within the group-selectionist mode of thinking provided a foil against which George Williams was able to launch an attack against this pseudoscientific paradigm, with his 1966 book *Adaptation and Natural Selection* (Williams, 1966). Dawkins relates Williams's key argument as to why group selectionism doesn't add up: no matter how much individual selflessness would promote the health of the population, if selfish individuals enjoy greater reproductive success, then they will be favored by natural selection, such that adaptations are not expected to promote the fitness of the population but must instead be explained in terms of individual advantage.

As highlighted by the title of his book, Dawkins descends lower in the biological hierarchy to locate adaptive agency at the level of the gene. He conceptualizes individual organisms as ''gene machines,'' built by the genes to transmit copies of themselves to future generations. However, he makes clear that this view of adaptation is philosophically rather than scientifically motivated and suggests that, whether we view the gene or the individual as the strategic agent, we will always derive the same empirical predictions. I'll return to this issue later in this essay but for now will focus on how evolutionary biology was transformed by thinking carefully about the individual's— or gene machine's—advantage.

Individual Advantage

The strategic, individualistic view of evolution provided greater illumination of a wide range of adaptive phenomena that were previously inexplicable from a group-selectionist perspective, immediately suggesting simple and direct explanations for many patterns observed in the natural world. Moreover, with the new understanding that appeals to the good of the group are untenable, there was a job to be done to explain apparently selfless behaviors that appeared to conflict with the Darwinian view of survival of the fittest. Dawkins's account of this revolutionary work is framed in his language of gene machines, but he makes clear that the researchers in question would not use or even agree with this language, preferring to think of the individual as a free agent in her own right.

One topic particularly revolutionized by the strategic view was the evolution of the sexes. Much of this understanding had been anticipated by Darwin, but these ideas were now given extra precision and predictive power. Geoff Parker and colleagues (Parker et al., 1972) developed mathematical models showing how, in ''isogamous'' populations in which all sex cells are initially of the same size, selection will simultaneously favor small, motile sex cells that selfishly exploit the resources carried by their mating partners and large, resource-laden sex cells that compensate for this exploitation, giving rise to the evolution of male versus female reproductive tactics. The very origin of the sexes was now explicable within this paradigm of cynical and selfish strategizing.

From this basic asymmetry in resource investment would spring many other sex differences. Robert Trivers (Trivers, 1972) showed how the greater investment of resources made by females should render them less willing to abandon a current offspring in order to pursue future reproductive success and hence leave them more likely to be deserted by their mates and left holding the baby. This explained the scarcity of paternal care in the natural world. Moreover, intense sexual selection experienced by males to secure as many mating partners as possible explained extravagant and costly ornaments such as the peacock's tail. Here, Dawkins discusses Fisher's (Fisher, 1999) suggestion that these are the products of a runaway process whereby, so long as an ornament is preferred by females in general, all females are favored to mate with ornamented males in order that their sons be similarly ornamented, even if it is unconducive to their survival, so that they may attract mating partners. And he contrasts this with Amotz Zahavi's (Zahavi, 1975) view that the ornament instead functions as a

signal of male quality precisely because it is so burdensome. Either way, such cumbersome ornaments highlight that selection is not simply concerned with the individual's survival but also their reproductive success and that wasteful extravagance may prevail so long as it gives a selfish, competitive advantage.

A further refinement of the notion of fitness would make clear that this is distinct from fecundity and that individuals who produce more offspring may actually have fewer descendants in the long run if this leaves them with fewer resources to invest into parental care. Here, Dawkins celebrates the work of David Lack (Lack, 1954), whose studies of clutch size in wild birds showed that, indeed, rather than more eggs always translating into more surviving chicks, there is instead an optimal number of eggs that maximizes the number of offspring surviving to adulthood. Lack also showed that, under resource scarcity, the optimal clutch size may be rather smaller than under plenitude. Accordingly, individuals may be favored to voluntarily curb their fecundity in times of dearth. Here was an explanation for the self-restraint described by Wynne-Edwards, framed entirely in terms of strategic, individual advantage.

But could the strategic view of individual advantage explain cooperation? Dawkins discusses the work of Trivers, John Maynard Smith, and George Price, showing that cooperative behavior can be favored when individuals react against each other. Trivers (Trivers, 1971) developed the theory of reciprocity (or ''if you scratch my back, I'll scratch yours'') to show how a cooperative act may be costly in the short term but may nevertheless improve the individual's lifetime reproductive success if it elicits extra cooperation from her social partners. Maynard Smith and Price (Maynard Smith and Price, 1973), developing the economic ''theory of games'' for application to behavioral ecology, showed that frequency-dependent selection could maintain cooperation, even if cheats enjoy a fitness advantage when rare, and emphasized ''retaliator'' strategies whereby otherwise cooperative individuals meet aggression with aggression in a manner reminiscent of Trivers's reciprocators. This reveals that cooperation can indeed result from strategic self-interest.

What about altruism, whereby a behavior actually reduces the actor's lifetime reproductive success? Dawkins shows that this, too, can be framed in terms of individual self-interest, provided that we rethink what it is the individual wants. Hamilton's (Hamilton, 1964) theory of ''inclusive fitness'' is based on the idea that an individual may transmit her heritable traits to future generations not only through personal reproduction, but also by promoting the reproductive success of her relatives, with whom she shares heritable traits in common. This insight revealed that altruistic behavior that reduces the actor's direct fitness may be favored by natural selection so long as it provides a sufficiently large benefit to individuals who are sufficiently related to the altruist. This is altruism, though of a cynical, nepotistic flavor. Hamilton's theory provides no basis for thinking organisms will ever behave for the good of the species as a whole.

The precision of strategic agenda becomes particularly important in the context of interaction between relatives, where there is scope for nepotistic altruism but also the possibility of conflict. Trivers (Trivers, 1974) investigated a particularly

striking instance of such tension, between parent and offspring whom, despite sharing half of their heritable constitution in common, may nevertheless be embroiled in extreme conflicts of interests. For instance, a mother may have some optimal amount of her reproductive resources that she will want to invest into her son, holding back the remainder for her future reproduction. But her son values his own future reproductive success more than he does his mother's and, accordingly, is favored to extract more investment from her. Dawkins discusses manipulative begging and other postnatal behaviors, but such parent-offspring conflict may occur even before birth, with the fetus engaging in physiological warfare to drain his mother's blood stream of nutrients for his own use. The hardships of pregnancy and the battle of wills that is the daily reality of parents of young children are placed in a new, evolutionary light.

The Gene's Eye View

This revolutionary science was framed by these researchers in terms of individual advantage. However, Williams and Hamilton did also toy with the idea of seeing the gene, rather than the individual, as the strategic agent. In 1972, Hamilton (Hamilton, 1972) took a short diversion from an account of inclusive fitness to imagine an intelligent gene deliberating as to which alternative behaviors of its carrier would lead to more of its copies being transmitted to future generations. Dawkins elaborates this idea so that it comes to underpin his entire book, with the strategic revolution being couched in explicitly gene-centric language. But why does he do this, and is the approach successful?

Dawkins gives two main reasons for identifying the gene as the strategic agent. First is the idea that, although the individual has only a fleeting existence over timescales appropriate to evolutionary change, the gene is potentially immortal. Second, he regards as axiomatic the idea that natural selection inevitably favors selfishness, such that altruistic behavior of individuals must be considered illusory and driven instead by more fundamental, selfish agendas.

I find neither of these arguments particularly persuasive. With respect to time-scales, the central feature of Darwin's theory is that it explains adaptive design, and this adaptive design is manifested in the here and now and is packaged into units that we recognize as individual organisms. It is the individual organism that we actually see striving to maximize inclusive fitness, so it seems natural to seek adaptive explanations from this perspective. And with respect to the axiom of selfishness, I cannot see why selfishness should take conceptual precedence over altruism. Ironically, Dawkins's argument is analogous to that of the group selectionists whom he was railing against. While they sought to explain individual-level altruism by appealing to group-level selfishness, he seeks to explain it by appealing to gene-level selfishness. More generally, the altruistic individual and the selfish gene are metaphors that can only be judged according to their empirical usefulness, and if, as Dawkins suggests, they always yield the very same testable predictions, then neither can be regarded as being ''more correct.''

I also find Dawkins's discussion of selfish genes somewhat inconsistent and often vague. When most focused on the biology, he speaks of genes as if they are physical scraps of DNA residing in the bodies of living organisms. But when being more philosophical, he emphasizes that this is not what he means and that the gene is instead a distributed agent that simultaneously encompasses all identical copies in the population. That is, the hero of Dawkins's book is actually the selfish *allele*. The allele's-eye view is necessary in order for Dawkins to maintain his focus on selfishness: whereas the physical scrap of DNA—like a miniature organism—is favored to maximize its inclusive fitness (Gardner and Welch, 2011), for example, by providing altruistic aid to other scraps of DNA with whom it has some probability of sharing identity by descent, the allele is locked in a zero-sum game of gene-pool frequencies that ensures success is synonymous with selfishness. But I don't think this is the most useful way of thinking about evolu- tion, and indeed, I believe it has actually obscured some interesting biology.

In particular, the big disappointment of *The Selfish Gene* is that Dawkins doesn't use this concept to explore intragenomic conflict. The genome is a battlefield of conflicting interests that simply cannot be understood in terms of individual advantage and must be interpreted from the gene's-eye view (Burt and Trivers, 2006). Dawkins would have been aware of several examples of such intragenomic conflict, including meiotic drivers and sex-ratio-distorting sex chromosomes, and many more have subsequently come to light following his book's publication. I find it strange that such phenomena are overlooked in a book that is ostensibly about selfish genes. (Some measures are taken to address this in later editions.)

In several places in his book, Dawkins comes tantalizingly close to identifying situations in which intragenomic conflicts may arise, but he does not truly embrace the gene's-eye view and instead continues with standard, individual-level ''gene machine'' thinking. For instance, in explicating the (now largely discredited) ''haplodiploidy hypothesis'' for insect eusociality, he points out that female hymenopterans are more related to their full sisters via their paternal-origin genes than via their maternal-origin genes, on account of their father having only one haploid genome to pass on to his daughters. Explicit consideration of the gene's interests would therefore suggest that, if a female's genes had information regarding their parent of origin, her paternal-origin genes would place more value upon her sisters and would be more inclined to have the female enact altruism toward them, whereas her maternal-origin genes would place a lower relatedness valuation upon her sisters and would be less inclined to altruism.

Such intralocus parent-of-origin conflict is the basis for David Haig's ''kinship theory of genomic imprinting'' (Haig, 2002), which may explain why some genes are consistently silenced when inherited from one parent but not the other. Had Dawkins really had his eye on the gene's interests, he might have anticipated this exciting development in the theory of inclusive fitness—and the explosion of interest in intragenomic conflicts more generally. Was this simply a lack of imagination on his part? No. I think Dawkins's focus on the selfish allele may

have been a barrier to him noticing this potential conflict. While physical scraps of DNA of maternal origin may come into conflict with physical scraps of DNA of paternal origin, owing to differences in relatedness, it is difficult to frame such conflict in terms of the divergent interests of competing alleles, as the allele does not have a parent of origin.

Conclusions

Dawkins's *The Selfish Gene* has captured the imagination of generations of budding evolutionary biologists, as well as the general public. Even if some details do not seem to stand up to scrutiny, its overall message remains both insightful and timeless. Its enduring appeal lies in the way that it overturns folk wisdom on the harmony of nature, exposing the cynical tensions, all-out warfare, and occasional glimmers of true altruism in the sexual and social lives of animals in a way that is both shocking and yet also profoundly resonant with everyday human experience.

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