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In 1902 Peter Kropotkin, the anarchist prince, former page boy to Tzar Alexander III and darling of the Russian revolution, published the book *Mutual Aid* in which he promoted a radical new perspective on evolution. Counter to the prevailing view that natural selection drove organisms toward selfishness and competition alone, Kropotkin insisted that cooperation, both with one's own and other species, also helped define the form, diversification and organization of life on earth. Kropotkin summarized his insight as follows "There is an immense amount of warfare and extermination going on amidst various species; there is, at the same time, as much, or perhaps even more, of mutual support, mutual aid, and mutual defense... Sociability is as much a law of nature as mutual struggle" (Kropotkin 1902).

Yet despite the intuitive observation that life cooperates, it took over a century for Kropotkin's ideas to be incorporated into modern evolutionary theory. Had his insight been recognized sooner, we may have avoided the deeply regrettable misapplications of evolutionary theory witnessed in the eugenics and social Darwinism movements of the 20th century. Unfortunately, cooperation fell on the wrong side of the political axis, as far as Western Capitalist society was concerned, and the misconception that evolution drives selfishness alone both persists in popular consciousness and continues to stifle the fruitful application of evolutionary theory to our understanding of human society.

In *Mutual Aid: the other law of the jungle*, Pablo Servigne and Gauthier Chappelle seek to first overturn the misconception that nature is only selfish and then equip the reader with an understanding of how the evolved mechanisms that drive and maintain the ubiquity of cooperation in non-human organisms, are also manifest in humans, our society and political institutions. Throughout, the authors' case for cooperation is built on carefully curated evidence from biological and interdisciplinary literature betraying an awareness developed through years of research and reflection. From this foundation the authors elaborate a model considering how an evolutionary approach could establish societal conditions promoting an upward spiral of cooperation, versus a defective vortex coupled to destruction of common goods. This argument is applied all the more forcefully as climate change and resource consumption necessitate new approaches to engender cooperation at the level of the global society.

Ultimately, Servigne and Chappelle amply restore Kropotkin's perspective that cooperation is a dominant force in life. Indeed, they go further still and argue that recognizing the omnipresence of cooperation and interdependence of life forms necessitates a reevaluation of the concept of self, if not its abandonment altogether. The implications for evolution, as well as the role of the individual in society are apparent and provoke ample cause for reflection.

Yet, as compelling as the evidence and arguments are, the reader is left with a niggling worry that skepticism has been neglected as the authors follow a single cooperative narrative. Does the cold water poured on natural selection at the level of the selfish gene undermine the wellspring that in fact gives rise to both cooperative and selfish behaviour? Does selfishness acquiesce to the good of the group, and does the dissolution of the self generate a healthy society? Indeed, what is the individual and on what level does the self persist in the face of a mantra that espouses cooperation above all else? To address these questions, highlight key insights into human cooperation and tease apart the authors' arguments regarding human societies, it is necessary to take a deeper dive into the book.

Evolved mechanisms govern human cooperation

Servigne and Chappelle open with an introduction to their premise: that cooperation drives life and human behaviour. Thus begins an entertaining jaunt through 3.5 billion years of evolution illustrating the ubiquity of cooperation at every level, from genes to cells to individuals to societies. For the non-biologist, this may seem exhaustive, but the breadth of material covered so quickly is impressive and builds the author's initial irrefutable argument, that life forms are interdependent and cooperative.

Of course, humans are no exception and Servigne and Chappelle elaborate on our pro-social nature emphasising that we are innately primed for cooperation. Many may balk at the word innate, which conjures the now defunct nature vs. nurture dichotomies. For clarity, the authors helpfully provide evidence of the fascinating gene-by-environment interactions that give rise to the exceptional lability of human and other organism's behavior (and morphology and physiology I might add). Indeed, they

illustrate the role that environment plays in the ontogeny of cooperation at the level of the individual and the positive, or negative, feedback that we therefore see between societies and the individuals from which they are built. Here lies one of the first insights from a biological perspective on human behavior: cooperation mechanisms beget cooperation in a society, yet the reverse spiral of selfishness may also be true.

At this point, the authors turn to the question of why, if cooperation is so ubiquitous, did evolutionary theory emphasise competition, selfish genes and the 'self-serving' human for so long? Undoubtedly, the schism in our global political world between capitalism and communism played a role, and the resulting missteps were tragic. The worst misapplications of 'selfish' evolutionary theory to human society should not be forgotten, from the spurious notion of biologically superior races, to justification of so-called instinctual behaviour thereby negating individual responsibility for unconscionable acts.

To redress our understanding of evolution, Servigne and Chappelle take particular aim at the selfish gene concept as the basis for natural selection, which they perceive as incompatible with cooperation (pg 35-37). However, sweeping away selfish gene theory as the basis for natural selection based on initial misapplication would be doctrinaire in its own right and I question the authors clarity on this point. While science did initially overlook the role of evolution in generating cooperation, modern evolutionary theory recognises that genes promoting selfishness or those promoting cooperation, including with unrelated individuals, will be favored where this enhances the genes own replication. The means may differ, but the outcome is the same with selfish genes promoting themselves: the essence of natural selection. The selfish gene remains central to our dynamic understanding of biological evolution which now incorporates the role of environmental feedback in shaping organismal phenotypes and consequently their genetic success (Laland 2015).

Although modern evolutionary theory incorporates cooperation, reconciling natural selection with both the self-serving and mutually beneficial actions manifest in living organisms proved to be devilishly tricky and was only satisfactorily resolved in recent decades. Ultimately, the greatest theoretical impediment was the prisoner's

dilemma. Put simply, any individual that initiates a cooperative act pays a cost while other selfish interactants will gain a benefit with no cost: selfish wins. Likewise, in a cooperative group, individuals who are selfish gain benefits that are greater than the cooperators around them. In short, selfishness should either prevent the establishment of cooperation, or cooperative societies, or bring them down from within, irrespective of whether it is in the interests of the group as a whole to cooperate. Communicating evolutionary strategies that resolve the prisoner's dilemma is perhaps the area in which this book and arguably science more generally, can make the strongest evidence-based contribution to political theory. Specifically, by identifying the mechanisms that facilitate cooperation we can illustrate how these are manifest and arguably necessary for human societies, institutions and political systems. The outcome is momentous, or at least biologists think so.

The solution, as clearly conveyed by Servigne and Chappelle, is to build from cooperation at the level of the individual forward to large human societies, comprising anonymous individuals without immediate interdependence. Between familiar individuals, cooperation is built on reciprocal altruism (I cooperate now, so you will cooperate later), and critically, individuals carry a reputation such that cooperators may exclude defectors by assessing reputation and reward cooperators with ongoing interaction. This mechanism is apparent between humans as well as other organisms. For example, cleaner wrasse are small fish that live on coral reefs and eat parasites from client fish's skin yet prefer to cheat clients and eat their skin mucus. Clients will therefore monitor cleaner wrasse interactions and will visit a different cleaner wrasse if they see another client being cheated, or attack the cleaner wrasse if they themselves are cheated (Bshary et al 2006). The reputation mechanism can take human society far, indeed, reputations can indirectly precede individuals, thereby facilitating cooperation in larger groups of unfamiliar individuals. Nevertheless, defection pays and thus the second evolved mechanism is punishment to enforce cooperation. If building a positive reputation is the carrot, then punishment is the stick, and the authors present a small portion of the growing evidence that humans will go to remarkable lengths to reward

cooperators and punish defectors, including when not directly involved in a cooperative/selfish interaction.

The next big hurdle is to accomplish cooperation between unfamiliar and unrelated individuals who have little chance of interacting more than once. Yet this is precisely what humans do in our largest societies. How then do we maintain cooperation on this scale? Here, the mechanistic solutions are intuitive, and clearly laid out, but the implications troubling and perhaps inadequately explored within the book. First, beginning in smaller societies we establish norms of conduct that dictate cooperative actions. In effect, these are predictable rules of engagement that govern behavior. Again, humans show a remarkable predisposition to acquire and enforce norms, and though evidence to this effect is still growing, it seems likely that this is another evolved mechanism for cooperation. Second, we as a society provide a mandate to enforcers of norms, effectively institutions that administer punishment despite having no familiarity with protagonists. So long as this is done to promote cooperation, the institutions maintain their mandate. Although not stated explicitly by the authors, the implication is clear; large cooperative societies, composed of unfamiliar individuals, require institutions with a mandate from the people to enforce rules of law. This structure emerges from behavioural mechanisms that have evolved to facilitate cooperation.

At this point, it is worth noting the irony of our changing understanding of the evolution of cooperation; contrary to Kropotkin's anarchism, theory leans toward laws and punishment coupled to centralized institutions as the most effective means of scaling up to large cooperative societies. Taken to an extreme, the self is subjugated to the interests of the group and free to do any action, or norm, that promotes group interest, but nothing else. Is that what humanity wants? Concerningly, animal societies closest to this model, bees, ants, wasps and termites, display strict caste systems where individuals are specialized to different and unequal castes valued only for their utility. Why the authors do not comment on this potentiality driven by their arguments, nor on the role of selfishness in disrupting this outcome, is puzzling. Perhaps this does not work with a narrative developed around cooperation as driving natural selection and

societies, in spite of selfishness, rather than societies as emergent from natural selection and shaped by cooperation and selfishness.

Intriguingly, when discussing evolved mechanisms to support cooperation, Servigne and Chappelle continue their 'selfish-blindness' by making no reference to the role of cooperation as a means of signaling an individual's own quality to potential partners, often termed 'prestige' (Roberts et al 2021). Prestige works where individuals increase their relative social value, and therefore their own access to resources, by 'showing off' through apparently selfless cooperative acts. Ask yourself this question: would you be more likely to donate money to a charitable funding drive (the group), if the representative was an attractive person of your preferred gender? Turns out that we do and will even compete to make the biggest donation when perceived competitors are present (Raihani and Smith 2015). Coupled to broader reputation benefits, this has further implications for politics and society where the intentions behind highly visible and apparently magnanimous acts can be reinterpreted. One might exploit this mechanism by promoting opportunities for prestige to better engender cooperation; every politician likes a signing ceremony. More generally, self-oriented prestige likely plays a key role in cooperation alongside reciprocal altruism, yet its failure to fit the purely 'cooperative' narrative perhaps resulted in its exclusion from this book's narrative? Either way, we discern once more that the evolution of cooperation is driven by self-interest at a fundamental level.

To return to large-scale human societies and their institutions, Servigne and Chappelle are of course not naïve and recognize that neither the path to large societies, nor their persistence, is typified by institutions that retain the public mandate. They do allude to the issue of self-serving institutions, but in fact miss a trick here with respect to our understanding of the selfish behavior of groups within groups. Indeed, the vanguard of research on the evolution of human behaviour and society once more has more to offer (Grief *et al* 2017; Muthukrishna 2017; Raihani 2021). To summarize briefly, any sub-group of individuals that act cooperatively for their own good, but not that of the larger group, can prosper by doing so. If those groups have hijacked the institution responsible for enforcement of norms, they may work the institution for their own

cooperative benefit and other's cost. Here, I would digress and discuss the consequent importance of mechanisms to enforce accountable governance thereby ensuring the institution maintains its mandate. Similarly, we might follow this tangent to explore how power accumulated by a sub-group can enable domination of the broader society. However, the authors do not and nor has evolutionary theory expanded into this domain at present. Instead, we must consider the implications of group competition for cooperation.

Group-group competition is a thorny issue, and worth unpacking, both when considering the consequences for promotion of one's own group identity and aversion to others, as well as how groups may cooperate with one another. With respect to the former, Servigne and Chappelle present the evidence that humans generate collective group identities, feverishly so under some circumstances. This can extend to a negation of self-interest, potentially as a result of mechanisms that pay on average but can go awry, even resulting in individuals putting their own life at stake for the good of the group. Research on the role of prestige in such behaviour is yet to be undertaken, but one would anticipate that those with the most to gain from image scoring and who are at the lowest risk, would put themselves in harm's way. The authors also illustrate the role of hormones, specifically oxytocin, in driving pro-group behavior, yet also in 'othering' non-group members. Here lies the issue: humans are primed for generation of 'in' and 'out' groups. Worse still, where groups have divergent interests conflict can beget conflict in a process termed negative reciprocity, which exaggerates competition. Thus, our cooperative grouping mechanisms in fact make cooperation between groups particularly challenging and we return to consider the negative implications of group-level competition later.

A model for cooperative societies

Departing from their prior empiricism and linear narrative on the emergence of cooperation, the authors adopt a more free-associative, normative, approach when presenting a model of the conditions that promote cooperative societies. They boil cooperative conditions down to three words: security, equality and trust, a three-word motif which though convenient is only one way of rotating the factors that affect

cooperation around simplified themes. Nevertheless, and despite my misgivings, the model is clear: security provides a 'membrane' around the group, with shared interests consequently aligned; equality reflects all individuals' perception that others are cooperating within the group; and trust illustrates the predictability of interactions under group norms to facilitate interaction. Promoting these three axes promotes cooperation. Notably, there is no mention of freedom, which is perhaps of note given its perceived importance at this point in history. Freedom might better be considered an emergent property from a society that achieves security, equality and trust as envisaged by the authors, balancing both self-interest and group interest.

A broader concern is whether the three factors identified are in fact themselves emergent properties that arise from more fundamental mechanisms. Specifically, security emerges from cooperation when self-interest is aligned with shared interest, and can be applied at all levels, from genes, to cells, to individuals, to societies. Meanwhile, equality and trust are the outcome of reputation, group norms and punishment mechanisms. Thus, simply aligning interests and facilitating fundamental mechanisms enables cooperation. Despite these misgivings, security, equality and trust sound considerably more appealing, and less paranoia inducing, than reputation, norms and punishment. Further, Servigne and Chappelle's model is generative in its own right. Security illustrates that humans need to have a group interest and a perceived group with whom they are aligned; equality is essential otherwise individuals self-serve, indeed, high-profile acts of selfishness have tremendous capacity to promote defection by others. Furthermore, individuals whose unequal wealth and power accumulation leaves them with little interdependence on others, actually reduce their relative cooperative input to society. Inequality therefore ferments reduced cooperation providing a strong argument for a progressive taxation system. Finally, trust speaks to fair interactions, predictability and a perception of legitimacy in society, or between societies. Security, equality and trust are evident in effective cooperative societies, or undermine them when not present.

Servigne and Chappelle introduce their model in part to preface their consideration of how humans can tackle collective action problems, specifically climate

change. Of course, they are not the first to do so and a major thrust of research on the evolution of human behaviour in regard to resource use has been the 'tragedy of the commons' (Hardin 1968). A purely selfish perspective suggests the impossibility of separate individuals cooperating, resulting in human's overuse and ultimate exhaustion of common pool resources for short-term personal gain. Once more, our old political dichotomy rears its head; the first solutions proposed were either collectivization, or privatization. In both cases, we see centralized control by a single entity whose self-interest is tied to sustainable resource use. However, an alternate solution has been demonstrated by the work of Nobel laureate Elinor Ostrom (1990), who showed that independent individuals can self-organize and sustainably manage a resource. The conditions broadly overlap with those of a society featuring Servigne and Chappell's model of security, equality and trust; no coincidence one suspects.

At this point, we may be tempted to raise a toast to our collective salvation as we anticipate the ongoing integration of our different global societies to promote mutual aid, resolve climate change and foster sustainable resource use in perpetuity. Yet Servigne and Chappelle argue quite the contrary; the conditions required for cooperation between societies will be challenging if not impossible to achieve given our current state. Our societies share overlapping interests, but differ on many fronts, promoting group-group competition and the resulting negative reciprocity discussed earlier. We have huge inequality and the missed-opportunity costs of cooperation are highest for those in developed societies, which also have the least to gain from cooperating. Finally, we do not share a common framework of norms, nor a capacity to enforce them to ensure adequate trust. A pessimistic outlook for sure, though the authors do at least indicate that all is not lost if we can better communicate the existential threat that aligns our shared interest, while organizing to decrease inequality at the global scale.

Given the difficulty in achieving this goal, it is perhaps unsurprising that Servigne and Chappelle build their final chapters to argue that all societies, nay civilizations, gradually develop through cooperation, but then enter a trajectory of increasing inequality, break-down of security and loss of trust in institutions resulting in inevitable implosion. Curiously, they look upon the post-collapse rejuvenation of human societies,

through cooperation, in a somewhat rosy light. Perhaps the confirmation of their theoretical propositions will ameliorate the toll of death and suffering to some extent. I do not share the authors' fatalist perspective, since we are aware of our imperiled state and still have the capacity to act; history continues to rewrite its own rulebook. I therefore find it surprising that they end their tome on cooperation by resolving that cooperation ultimately fails at the level of the global society, albeit that cooperation will rise again like a phoenix from the flames of civilizations' collective failure.

Dissolution of the self

Throughout their book, Servigne and Chappelle have one overarching theme, that life evolves to cooperate, and the self dissolves to favor groups. This appears broadly true when we consider genes that cooperate to form individuals in which they have a shared fate. Further, individuals cooperate with others of the same species, and even of different species, such that their survival becomes interdependent. Take for example your own self, a multicellular assemblage born with an inoculation of mutualistic bacterial cells essential for your function. In fact, more of the cells in and on your physical body are bacterial cells (albeit very small), than are 'human' cells. You were born into an environment primed for interaction with other organisms, mutualists and food species and simultaneously joined a society of cooperative humans upon which you rely. Your prosocial nature can even drive you to ecstasies of group integration within a mob or crowds, a fused existence of organisms with united interest.

From this perspective, Servigne and Chappelle argue that we are simply a part of a broader 'holobiont' formed from many levels of cooperation between organisms. Taking this to the extreme, they propose that the broader biome is a single cooperative existence of inextricable interdependent components. Yet, are we missing the trees for the forest, are all these entities collaborating as one, or are we mistaking an emergent outcome as 'intentional' when in fact it reflects a tangled mass of conflicting and cooperating self-interested organisms?

From a biological perspective, all is not cooperation, nor are all organisms aligned. The biological concept of the individual remains intact; that cluster of DNA

comprising the genes for the individual that are necessarily inherited together and whose interests are entirely aligned. Natural selection will always favor what is good for the collective passage of that material. Take for example a symbiotic bacteria and its host; they may benefit by supporting one another, since neither lives without the other, but will be under separate selection to take just a bit more for themselves than the other might wish, so long as the benefit to them outweighed the costs of losing a little of their symbiont. An uneasy alliance where mutual distrust generates an emergent compromise appearing as near perfect cooperation. Likewise, organisms that interact do not all cooperate, many eat one another, and selection favors those that evade this fate. The apparent coordination between consumers and their prey is simply emergent from the arms race between them. Likewise within cooperative relationships.

Reflect for a moment on the structure of your being, a multicellular somatic cluster enslaved to pass replicates as gametes (sperm and egg) to the next generation. Ponder why it is that gamete cells that replicate the individual are isolated from the other genetically identical somatic cells at the earliest stages of development? What would happen if a portion of your soma's genetics diverged and they pursued their own replicative interests? The breakdown of cooperation would occur and all would suffer, a phenomenon we recognize as cancer. In some organisms less reliant on a unified functional system, genetic divergence across the whole organism can indeed lead to separate reproduction of the regions, schism of the individual. This is observed in colonial slime molds where cells may take on a supportive non-reproductive role or generate reproductive spores. Less genetically related cell lineages favor adopting the reproductive role (Gilford et al 2007). Similarly rebellious and self-oriented body regions are hypothesized for plants, fungi algae and diverse animals that reproduce by 'budding' off parts of the body that develop to form new individuals (Howe et al 2022). Clearly, we do not always work as one, only where self-interest is perfectly aligned with shared interest of the group may cooperation prosper perfectly.

Ironically, arguing that individuals are each genetically independent as a counter to cooperation between organisms resulting in the dissolution of the self, in fact generates the same conclusion; namely that the self is an artifice of alignment between

a cooperative cluster of self-interested replicating units, in other words, our genes. Yet the strength of alignment, and historical association is such that we recognize our own individuality. We have opportunities to gain from acting in our own interests, for the good of the group, or not. Indeed, the agency to make this decision is largely at the heart of what it is to be an individual human being.

From a cognitive perspective, our perceived experience is an emergent property of the many interactions between our neurons and the sensory information derived from the world around. This includes input from interactions, cooperative or otherwise, with many other organisms, and we may share experiences collectively. We do arise from an organism built on interactions with other organisms, but this does not undermine the independence of our own intentions. An argument might be made that when we are no longer able to express our agency independently, the self may dissolve. As pro-social as we may be, we retain a simultaneous drive for independent self-oriented behaviour. Fulfilling both these needs is central to the human experience.

Whether an evolutionary approach will further inform our understanding of the individual, our cooperative and selfish interactions and the resulting nature of our societies remains to be seen. However, by balancing the cooperative narrative of Servigne and Chappelle with a recognition of selfish mechanisms, we may reconcile ourselves to the inevitability of components of our societal structures, but also modify them to optimize both within and between group cooperation such that we can address the resource use problems we face, as well as addressing social justice and equality.

To conclude, Servigne and Chappelle's narrative is on point: for too long we have ignored the enormity of cooperation in generating the diversity of living systems. This has colored our perception of what is 'natural', and it is necessary to reinvigorate Kropotkin's insight and thereby change human perception of their role. Impressively, and contrary to many agenda-driven books, the authors do not build their argument on a house of cards with each point tottering on a prior assumption. Instead, they collate scientific evidence and convey to the reader the insights we may gain from evolution. They write authoritatively with a collaborative, almost conspiratorial air, inviting the reader to share their journey. However, I fear that by embracing cooperation, they

exclude selfishness excessively, and in so doing miss a critical aspect of human societies and the consequent balance that permits individuals to fulfill their own selfish goals, while doing so in a fashion that does not harm the group. Facilitating this relationship is to my mind at the heart of both evolution and the mechanisms that drive our cooperative societies.

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