#### **Evolution: Lessons from Some Cooperative Ravens**

Thom van Dooren and Vinciane Despret

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#### Introduction

Since the middle of the 1980s, the ravens of Vermont and Maine have been the recipients of some strange gifts: carcasses, some of them weighting 150kg, some of them of animals never before seen in the region, have been mysteriously appearing in the forest. If these birds took a strong interest in the matter - which they likely did - then they may have noticed that a man, the same man, was the source of all of this meat: cows, deer, moose, sheep, goats, slaughterhouse offal, rabbits, snow shoe hares, raccoons, beavers and even squirrels. This man was a scientist named Berndt Heinrich. Even at this early stage in his career, Heinrich was already well on his way to becoming one of the world's foremost experts on the behaviour of ravens. In laying carcasses out for them in the way that he did, he was acting like some primatologists do with baboons or chimpanzees: As these animals could hardly be approached and would run away each time the primatologist wanted to get closer, some researchers finally found it to be more convenient to attract them with food. Indeed, ravens were rarely seen in Maine or Vermont in the absence of baits like these. Heinrich himself reports that without his baits, on average, he saw one pair of ravens for every 5.6 hours of watching: 'to randomly accumulate 20 birds should thus require 1,120 hours of daylight, or 140 days given 8 hours of daylight per day'.<sup>1</sup> Clearly this was no way to go about assembling a reliable understanding of these birds. But Heinrich's needs were even more specific than this. He was not interested in seeing ravens doing just anything. He laid these carcasses out for them because he wanted to understand if, how and why ravens might share these miraculous 'food bonanzas' with one another. That was the point.

Heinrich was initially drawn into this research by an accidental observation. While out in the forest studying bumblebees (his initial specialisation), he happened upon a pair of ravens 'doing something solitary animals are not 'supposed' to do: They were sharing valuable food'.<sup>2</sup> These ravens did not quickly and quietly eat carcasses they found. Instead, they tended to call out loudly, seemingly advertising the find to others. As a biologist steeped in the lessons of evolution by natural selection he could not readily understand why they should act in this 'irrational way'.<sup>3</sup> How could such a generous approach to others be evolutionarily adaptive and so selected for? As Heinrich put it: 'I always look for some evolutionary, self-serving reason why animals do things ... [t]his time my mild failed to provide a clearly selfish, evolutionary cause for the apparent sharing'.<sup>4</sup>

And so he was left with a puzzle. Alongside a range of other fascinating questions, Heinrich's subsequent research and publications over roughly the next two decades has sought to provide the solution to this puzzle: to explain how this behaviour might – as it must(?) – enhance the fitness of those who engage in it, such

that it becomes possible at all in the world that Darwin (perhaps) taught us that we inhabit.

Taking these ravens and their food sharing proclivities as a starting point, this chapter explores the 'puzzle' of cooperation. We are interested in ravens and their interactions, but equally in how their biologists have made sense of, and with, them. What does it means to cooperated in an evolutionary context? How have 'self interest', or even 'selfishness', and 'evolution by natural selection' become almost interchangeable concepts for many biologists, as in the quotes from Heinrich above? How has this situation, in turn, created such a stubborn puzzle out of cooperation?

Answering these questions requires us to ask how it is that competitive self interest came to occupy a position as the assumed norm against which sharing and other similar behaviours stand out as oddities. Michael Ghiselin offered what has become a very well know example of this dominant framing of our (biological) world when he commented that:

The economy of nature is competitive from beginning to end ... What passes for cooperation turns out to be a mixture of opportunism and exploitation. The impulses that lead one animal to sacrifice himself for another turn out to have their ultimate rationale in gaining advantage over a third. ... Given a full chance to act in his own interest, nothing but expedience will restrain him from brutalizing, from maiming, from murdering – his brother, his mate, his parent or his child. Scratch an 'altruist,' and watch a 'hypocrite' bleed.<sup>5</sup>

From this perspective, one raven stealing from another is just nature; one raven giving to another is a perversion in want of an explanation – ideally an explanation to show how the giver is actually benefiting more than it costs him, and so in a sense, according to this framing at least, not really giving at all.

Figuring out who gets what from an interaction is, in many ways, the central question of biology after Darwin. From this perspective, every trait, including every behaviour – assuming that it is adaptive, which one ought not to do lightly<sup>6</sup> – must be able to produce a cost/benefit ratio in which the fitness of the individual actor/bearer (or its genes) is enhanced by its possession.<sup>7</sup>

According to contemporary evolutionary theory, cooperative behaviour should be selected against because, using the language of the game theory that is often deployed here, 'free riders' or 'cheaters' would inevitably emerge who would attract the benefits from others' cooperative behaviour while avoiding any of the costs associated with contributing (introducing a relative cost for cooperators). In this context it is usually argued that free riders would inevitably out compete others and so undermine any fragile forms of cooperation that did begin to take hold.<sup>8</sup>

From this perspective, altruism is even more puzzling. While cooperation merely requires that an individual act in a way that benefits others *as well as* self, altruism demands *self-sacrifice* of some sort and so poses what is thought of as a severe distribution problem. Importantly, in this context neither altruism nor cooperation have anything to do with the motivational state of an actor. Trees can be

altruistic or cooperative if they evolve to grow in ways that make room for each other. As Elliot Sober has succinctly put it: 'a mindless organism can be an evolutionary altruist'.<sup>9</sup> All that is relevant is the 'bottom line' of evolutionary fitness: does the behaviour sacrifice or compromise one's own fitness for that of another?<sup>10</sup>

Of course, despite all this focus on self interest, cooperative behaviour is not at all peculiar to the ravens of New England. All over the world, many different kinds of animals - but also plants, bacteria, fungi, in fact members of all the kingdoms of life - form cooperative associations with others. Amongst the broader crow family (genus *Corvus*), to which these ravens belong, there are a great many active and creative cooperators. Some crows collaborate to mob larger predators in coordinated ways; others work together in groups of all sizes to rear their young.<sup>11</sup> In the lab, rooks (Corvus frugilegus) and other species have shown their willingness to work together on difficult tasks – for example, the coordinated pulling of a string – to gain access to food rewards.<sup>12</sup> These rooks have invented new forms of cooperation in the face of a puzzle scientists have created for them. There is a double puzzle at play here, both of its facets coming from the two major traditions that have questioned animals, experimental psychology and natural history: one puzzle is constructed out of bits and pieces of string and timber in the lab, the other, larger, puzzle is one that we have made for ourselves through a history of understanding biological life as, at its foundation, driven by competitive individualism.

To pre-empt the punch line, this chapter argues that cooperation only becomes a puzzle when we understand competition and selfishness so broadly that they consume the world; from this perspective cooperation is indeed fragile and perplexing, if not outright impossible. The reality, however, is far more interesting. As such, this chapter asks what kinds of narratives have been proposed to explain (seemingly) cooperative associations, what kind of constraints do they take for granted and thus impose on the ways that we might think evolution, and how might other narratives help us to re-open, to renew, to re-engage, to disclose, other hypotheses and so other ways of being with others?<sup>13</sup>

In taking up these questions this chapter is an effort to challenge some 'routine' biological thinking about evolution (that is, modes of thinking grounded in ossified habits that rigidly impose their own schemas). Increasingly, this routine thinking is today being rejected – but it still lives on amongst many biologists, in much of the humanities and social sciences and in popular understandings. This chapter does not take up all of the issues that animal studies scholars will likely have with evolution: ranging from biological determinism and adaptationism through to various forms of genetic reductionism. Instead, the chapter aims to grapple in a serious way with one little set of questions: what is cooperation, and what does thinking about it through the lens of evolution by natural selection have to teach us about our world?<sup>14</sup>

## Why cooperate?

Crows fascinate us, in part at least, because they have managed to captivate a group of passionate and intelligent biologists like Heinrich; biologists who have given them more chances than many other creatures have had to be 'interesting'.<sup>15</sup> These

biologists have sought out a variety of intriguing sites to document and explore cooperative associations. Called in a serious way by the puzzle of cooperation, they have been required to painstakingly create the conditions for an *observable* cooperation in the context of an enigmatic sharing of food: to build blinds, lug carcasses through the snow, spend hours crouched down in the cold watching birds, and to all the while maintain their relentless curiosity about what this all means. As Thelma Rowell has noted, animals are more interesting when they cooperate because cooperation asks them to do more things, it requests more cognitive and social competencies, such as the ability to coordinate collective actions and to learn to pay attention to others over time, to communicate in a reliable manner, to take into account what others need, or in the more specific case of ravens (or Arabian babblers<sup>16</sup>), to cultivate bravery.<sup>17</sup>

Through the exploration of these cooperative behaviours, crows have in some cases been able/enabled to fly against the predominant headwinds of biological understandings, with their focus on competition to the exclusion of all else. Even still, as we have already seen in the case of Heinrich, there is a tremendous intellectual inertia here that constrains interpretations, that constrains what it is that crows are able to do within the worlds of even generous and attentive biologists. Heinrich's analysis creates opportunities to understand these birds, this behaviour, and indeed biology more broadly, otherwise. In some places, we have been required to push Heinrich and his collaborators in directions they wouldn't necessarily want to go. This act of 'pushing' the scientists is similar in form to the way that generously imaginative scientists like Heinrich interact with the ravens or other animals that they are interested in: we address a proposal to them, a sort of 'what if...?', inviting them to contest it or to accept it. The textual material of our hypothesis is, in this case, the device – the 'what if...?' – that should be put to the test.

For Heinrich, the ravens of New England were particularly fascinating research subjects because they presented him with a puzzle within a puzzle. While there are certain kinds of answers that are now readily available within the discourses of contemporary biology for the question of how cooperation and (seeming) altruism can evolve and endure, this particular food sharing behaviour seemed not to readily submit to them. This is what struck Heinrich so profoundly in his initial encounter with these birds. When a raven finds food, she calls out in a general way. She calls out loudly. In short, she calls to anyone who can hear. As such, it seemed to Heinrich that ravens were sharing *indiscriminately*.

The two broad explanations that are now usually offered by biologists to explain altruistic and cooperative behaviours can be grouped under the general headings of kin selection and reciprocal altruism. The theory of kin selection (or 'inclusive fitness'), associated with the pioneering work of W.D. Hamilton, offers an explanation for altruistic behaviour when it occurs within groups of (relatively) closely related individuals.<sup>18</sup> In these cases, while an organism might act in a way that compromises its own self-interest, if it does so in a way that benefits closely related individuals, it is ultimately benefiting its own genetic material. Because we share much of our genetic material with close relatives, from a larger evolutionary perspective this behaviour can still be selected for because the (selectively) altruistic genes of one individual are likely to also be found in its relatives (assuming that the altruistic trait is inherited genetically). Behaviour that is disadvantageous at the level of the organism is thus advantageous at the level of the gene. Thus, biologists have suggested that the proportion of genetic material that one organism shares with another might be some guide to the degree of self-sacrifice that the individual will be willing to undergo. As Haldane is said to have once commented: 'I would lay down my life for two brothers or eight cousins'.<sup>19</sup>

Reciprocal altruism, on the other hand, offers an explanation for cases in which the group of cooperators is not composed of closely related individuals (or even members of the same species). This approach also attempts to explain this behaviour in a way that allows it to be, and to remain, evolutionary advantageous for the individuals who engage in it. This approach in not a competitor to kin selection, but an alternative avenue through which cooperative behaviour might evolve. On the surface, a behaviour that is advantageous to both cooperators would not seem to need much explanation. What does require further elucidation, however, is 'the critical mechanisms stabilizing cooperation'<sup>20</sup> that prevent other individuals from taking advantage of this behaviour and out competing the cooperators, or one cooperator from defecting in a way that free rides on the other's effort. Drawing on the 'prisoners' dilemma,' biologists have argued that in a straightforward encounter between individuals it never makes sense to cooperate. This 'prisoners' dilemma' puzzle was eventually solved by Trivers and further developed by Axelrod and Hamilton.<sup>21</sup> Their modelling indicated that in an 'iterated prisoner's dilemma' - in which individuals can reasonably be assumed to meet again, and they are able to alter their behaviour in relation to their past experiences (especially if they're capable of recognising individuals and remembering specific past interactions) - the numbers shift and strategic cooperation can deliver fitness payoffs. Subsequent research has revealed a range of other scenarios and mechanisms whereby individuals might benefit from cooperation in ways that limit or prevent 'cheating'.<sup>22</sup>

But the ravens that Heinrich observed in New England weren't just sharing food with close relatives (which might – but not necessarily – enable a kind of kin selection), and nor were they just sharing with a fixed group of other birds (which might enable – still not necessarily – a more conventional pattern of reciprocal altruism). If this was the case, then how did the announcer benefit from the act of sharing?<sup>23</sup> Why didn't the lucky raven just keep the valuable find to herself, eating as much as she could now and carefully caching bits away in the snow for later (caching being widely practiced amongst ravens and some other corvids)?

But share they did. Again and again Heinrich observed the same pattern. When a raven discovered one of his carefully placed carcasses in the forest, she would cautiously check it out, perhaps over a period of a day or two. Then, without eating herself, she would loudly announce the location of the food. Heinrich observed that:

If the birds respond to each other's calls and behavior ... as well as a human can, then those in the neighborhood for several square

kilometres ... could hardly fail to be alerted, and in a minute or two they could probably determine the source and/or reason for the calls.<sup>24</sup>

Heinrich explored this call and response relationship using live birds who had discovered bait carcasses as well as the replaying of recorded raven calls from other bait sites. Ravens seemed to be well tuned to one another's calls. In almost all cases, once a carcass was announced, other ravens quickly began arriving.

But these ravens took their sharing even further than this. Heinrich observed that large groups of birds often arrived together at a carcass early in the morning, likely coming from a communal roost occupied over night. Many of those arriving had not previously seen the carcass, and so it seems that these roosts may operate as 'information centres.' According to Heinrich, the groups of ravens arriving together were not close relatives, they weren't even fixed groups: raven populations in the area are dynamic and shifting with juvenile and vagrant birds dispersing widely and moving around frequently.<sup>25</sup>

Why do ravens share if there is little chance of their actions primarily benefiting their kin (and so their genes) or themselves? Even 'group selection' explanations have trouble here, as there is no fixed group to benefit from this behaviour. In this context, in terms of evolutionary games, what is there to stop individual ravens from keeping their own finds a secret, but benefiting from the finds of others that were announced – presumably, eventually, leading to the breakdown of sharing altogether as the 'secret keepers' got the upper hand on the altruistic 'announcers'? In fact, Heinrich observed that birds that had had their fill of a carcass (and cached some away for the future) did not just sit around saving their energy – like 'good' self-interest maximising neo-Darwinian actors – but took to the sky, expending energy, to find more carcasses that they would then (presumably) share with others too. What could explain this perverse behaviour, this seeming (because it is always only 'seeming'?) refusal to conform to the dictates of natural selection?

#### Key concepts in cooperation

Before answering these questions it will be helpful to make a small detour to consider a little more closely the way in which notions of selfishness, competition, altruism and cooperation are commonly deployed in the biological literature. The first thing to note in this regard is that in an evolutionary context, selfishness and altruism are not at all concerned with motivations (as previously noted). This situation is in stark contrast to more standard ('psychological') definition of these terms which are specifically focused on motivations: 'altruism' requiring that an action be deliberately directed towards another's wellbeing (often at cost to oneself), and 'selfishness' that one deliberately act in one's own interest with little or no regard for others. As Frans de Waal has noted there is an important distinction here between 'function' and 'motivation' (often presented as a distinction between 'ultimate' and 'proximate' causes). In his words: Evolutionary biology persists in using motivational terms. Thus, an action is called 'selfish' regardless of whether or not the actor deliberately seeks benefits for itself. Similarly, an action is called 'altruistic' if it benefits a recipient at a cost to the actor regardless of whether or not the actor intended to benefit the other [or even intended to perform the act].<sup>26</sup>

We will return to this important distinction in more detail in the final section of this chapter. For now, however, we are interested primarily in another aspect of the common biological usage of these terms: namely, the way in which they tend to be taken up in a highly dualistic manner.

For evolutionary biologists, altruistic behaviours are those that have a higher cost than benefit (in the 'single currency' of (reproductive) fitness). These acts are commonly viewed as being in the interest of others, and consequently not in the actor's own self interest. But, as we have seen, it is generally accepted that such a behaviour could not be adaptive. And so, those behaviours or traits that *seem* to be altruistic must have their foundation in some self benefiting mechanism – either for the organism or its genes. As such, evolutionary altruism is, by definition, an empty category – an impossibility. In evolutionary discussions, the term is simply a placeholder in a puzzle; it names a curious facet of the world that has not yet been properly explained. In revealing the mechanisms that enable 'altruism', the biologist explains how the behaviour is not really altruistic at all.

To some extent this is all quite reasonable. Even though this is not at all what we mean, or ought to mean, by the term 'altruism' in other contexts, this is yet another piece of biological terminology 'protected by the stipulation of a technical meaning'.<sup>27</sup> This situation becomes particularly problematic, however, when everything outside of this sphere of altruism – that is, *everything* – is labelled as 'self interested' in a way that readily slips into 'selfishness.'

Val Plumwood taught us to see the destructive and highly political nature of this kind of dualistic notion of altruism. Her focus was not on evolutionary but rather ethical frames. She noted that within Liberal political philosophies 'egoism and self-denying altruism are presented as an exhaustive set of alternatives'. This 'polarised division of the world creates a false dichotomy' in which altruism (in its 'pure' form) is easily viewed as unachievable and even undesirable.<sup>28</sup> And so the rationality of egoism – which quickly slips into its 'pure' form – becomes commonsensical. For Plumwood, however, ethical forms of life take place in the grey spaces between these simplistic categories which can only lead to 'inappropriate strategies and forms of rationality that aim to maximize the share of the 'isolated' self and neglect the need to promote mutual flourishing'.<sup>29</sup>

Similarly, in an evolutionary context, a whole range of fascinating encounters and relationships happen in the grey spaces between those acts that solely benefit others and those that solely benefit the self (indeed, within complex ecologies these black and white spaces don't actually exist). This grey space is a terrain of complex mutualisms and commensalisms, of shared benefits and becomings, that is at present often conceptually reduced to a space of 'selfishness' because the actor *also* benefits in some way – because they are not 'genuinely altruistic.' While adaptive traits cannot cut against an organism's own self interest, this in no way implies that they must be competitive or selfish (in any meaningful sense of these terms). Given the right conditions – conditions that we see all around us in countless different contexts – self interest is perfectly compatible with enhancing the interests of self *and others* in cooperative relationship. 'Selfishness' and 'self interest' are in no way equivalent concepts. Treating them as such covers over a range of important differences, a diverse range of strategies for life, and so a range of fascinating *questions* that might be drawn out in more theoretical and empirical detail.

This broad notion of 'selfishness' is closely linked to a similarly broad notion of 'competition'. Evelyn Fox Keller provides insight into the historical and conceptual foundations of this situation.<sup>30</sup> She argues that biologists have tended to assume that in a finite world resources are scarce and scarcity necessarily gives rise to competition.<sup>31</sup> In such a world, two organisms needn't ever encounter each other, simply by virtue of overlapping resource demands they are competitors. As Keller notes, this 'technical' understanding of competition means that it incorporates a wide range of interactions that are not at all hostile or aggressive.<sup>32</sup> If, for example, one group of crows develops a more empathetic response to their young than another (meaning that they produce a higher number of healthy offspring), and this response is hereditary, and as a result this trait eventually replaces the less empathetic one within the larger population (through interbreeding), the conventional logic requires us to read this as a 'competitive' interaction.

It is in this way that selfishness and competition have come to be treated as substantially equivalent to natural selection.<sup>33</sup> Both terms have effectively become synonyms for 'successful' or 'effective'<sup>34</sup>: with all adaptive traits and behaviours – whatever outward form they take – being labelled as 'competitive' and understood to maximise the individual's wellbeing (the impact on others is usually either treated as negative or irrelevant).

But in using terms like 'selfishness' and 'competition' in this broad way, they are rendered entirely meaningless; they tell us nothing at all about the specific interactions in question. If, however, we make a distinction between a more conventional understanding of competition (in the sense of contest) and cooperation, a range of new and interesting questions become visible.<sup>35</sup> For example, we can begin to ask: *how* is a behaviour or other trait successful? At what cost or benefit to self *and* others? As Joan Roughgarden notes:

It's an open empirical question whether effective cooperation ... versus effective competition ... underlies most evolutionary progress[?]. But to stipulate that evolutionary success equals selfishness means we can't ask the question of which, cooperation or competition, is the more common route to evolutionary success.<sup>36</sup>

In short, while differential survival and reproduction may be the name of the game in natural selection, the routes to this kind of 'success' are complex and diverse and can't be assumed to be 'competitive' or 'selfish' (in any meaningful sense of these terms) at the outset.

## Selfish ravens?

The ravens of New England offer an ideal example of the complex grey space that opens up when a distinction is drawn between 'selfishness' and 'self interest' and 'competition' is no longer treated as a synonym for success. Food sharing is a behaviour that has been well documented amongst many species of mammals and birds<sup>37</sup>, but Heinrich's analysis of this behaviour is particularly rich and developed, paying serious attention to the ecological and social context. For him, the key to understanding food sharing in this case is 'the great advantage of reciprocity given the birds' specialization on ephemeral and scarce food bonanzas in fall and winter'.<sup>38</sup> In other words, carcasses are infrequent resources that are unevenly distributed in the landscape. They also often contain more food than any individual raven can reasonably consume. Heinrich argues that this specific ecological context creates a relatively low threshold for sharing to evolve: as mammalian carnivores are the main consumers of carcasses in the area, a bird that shares with others likely gives up little (that wouldn't have been lost anyway when a mammalian predator discovered the carcass); likewise, 'cheating' (in the form of not sharing with others) is unlikely to produce much of a benefit in this ecological context.

But this is not the full story according to Heinrich. Across his broader body of work, he considers a range of other factors that might contribute to this food sharing dynamic, from the improved predator vigilance of groups to their capacity to better keep a carcass from being covered by snowfall. Ultimately, however, two hypotheses emerge from his discussion as central: what Mesterton-Gibbons and Dugatkin have referred to as the 'status-enhancement' and 'posse' hypotheses.<sup>39</sup> The first of these hypotheses centres on the idea that calling other ravens to a carcass may play a role in enhancing the status of a bird, helping to secure desirable mates, etc, in the future. The second hypothesis relates to the fact that young ravens are often chased away from carcasses by resident breeding pairs who have set up a territory – and don't announce and actively share carcasses that they find. In this context, Heinrich hypothesises that being part of a loose posse – formed by the act of announcing a carcass – may enable juvenile and subadult birds to gain or maintain access to food in the presence of dominant adults.<sup>40</sup>

And so, neither kin selection nor reciprocal altruism (in a narrow sense, at least) can explain this behaviour for Heinrich. Instead, the key factors that cement this behaviour are not cooperative at all, and certainly aren't altruistic, basically amounting to improving one's own social status and necessary collaboration to overpower a third party (breeding adults).

Over the years Heinrich has written about raven food sharing in several sole authored works, journal articles and books, and in collaboration with John Marzluff, another eminent crow biologist.<sup>41</sup> This broad body of work is grounded in the notion that, as Heinrich and Marzluff succinctly put it: 'self-sacrificing behavior, or helping, buys delayed or hidden benefits. In other words, selfishness lies behind seemingly selfless behavior'.<sup>42</sup> From this perspective it makes sense to argue that: 'Attraction of a crowd [at a carcass by calling] can yield a great variety of different costs and benefits. But the balance must be positive for attraction signals to evolve'.<sup>43</sup>

Much is revealed in this final, simple, sentence. The balance must be positive. But positive for whom? Again and again in this work, the puzzle of sharing is reduced to one of explaining the benefit to the caller: 'the challenging task at hand is to determine how helping behavior can evolve in terms of individual fitness'.<sup>44</sup> But, cooperation is, by definition, much more complex than this. What distinguishes cooperation from competition is that it cannot be brought into the world and maintained simply by maximising one individual's fitness. A different kind of 'balance' is at work here: not the individual's costs versus benefits, but the balancing of multiple organisms' wellbeing.

In keeping the focus on a single bird – the caller, the (seeming) altruist – Heinrich and Marzluff's account too readily lends itself to individualistic and competitive analyses. When a raven calls, other ravens do not simply come like mindless automata to a stimulus. In fact, more recent work by Thomas Bugnyar and colleagues on the same species of ravens in Austria has revealed a varied and nuanced landscape of response in which listener birds likely understand much about *who* is calling and *what* is being called about and presumably make decisions about whether or not to attend on this basis.<sup>45</sup> However this happens, the key point is that the behaviour of calling can only be selected for within a specific social context in which (some) other birds respond, and it also benefits them to do so. As Barlow and Rowell note: 'because communication must involve both a sender and a receiver, it must be a coevolved system. The sender is part of the environment to which the receiver must adapt, and vice versa'.<sup>46</sup> And so, the relevant behaviour is not signalling in isolation, but rather the entangled practices of signalling, responding and sharing. Costs and benefits of signalling mean nothing outside of this context.<sup>47</sup>

In short, this is a *cooperative* behaviour: it only 'works' (in the sense of cost benefit analyses) for the caller because it also works for the receivers; because it is *mutually* advantageous. Of course, it is mutually beneficial in unequal ways. Interestingly, in this case the caller is not necessarily, perhaps *usually* not, the primary beneficiary: according to Georgine Szipl, Bugnyar and colleagues' research, birds respond more readily to calls from subordinates who often get less food in a crowd than the more dominant responders.<sup>48</sup> It is these entangled sets of interrelated costs and benefits – of give and take, of compromise – that make this a fundamentally *cooperative* behaviour that no single calculus can adequately account for.

For Heinrich, however, starting from a framework of assumed individual self interest, the only behaviour that is a puzzle is the calling. The responding and consuming of meat – the taking – requires no explanation. It is perhaps for this reason – in addition to the obvious practical challenges – that in his large body of work in the area Heinrich has not studied *which* birds respond (unlike Bugnyar and colleagues). As a result, the story that he and Marzluff tell is one in which a behaviour that 'had at first sight seemed to be a mutually beneficial reciprocal altruism ... was more likely to be a device for gaining access to otherwise unavailable food [and status enhancement]'.<sup>49</sup>

But why are these mutually exclusive possibilities, such that the discovery of a benefit to the caller somehow undermines or replaces the possibility of a mutualism? Why can't it be a 'mutually beneficial altruism' *and* a means of gaining access to food and other goods (prestige, relations, possible alliances...)? Indeed, our position is that in order for it to be the latter – in the meaningful long term way that it seems to be – it *must* also be the former. Fascinatingly, recent work by Bugnyar and colleagues also reopens this question, indicating that ravens recognise who is calling and respond accordingly: joining social allies and avoiding dominant birds.<sup>50</sup> If this is the case, social relationships may enable calling to primarily benefit kin and allies, and so throw kin selection and reciprocal altruism back into the mix as at least partial explanations for the evolution of this behaviour.

In contrast, it only makes sense to describe this behaviour as one in which 'selfishness lies behind seemingly selfless behavior'<sup>51</sup> if we are operating within the context of the aforementioned black and white framework in which anything but 'pure' altruism is deemed to be selfish (and pure altruism is by definition impossible to sustain in the context of natural selection). But, perhaps this criticism of Heinrich and Marzluff is unfair. It is difficult to tell because the language that they use does not tease out the relevant nuances. Perhaps they simply mean that selfishness is *also* part of this behaviour, not that it is selfish *instead of* being selfless. Indeed, at points in their work they do seem to be saying something like this, for example when they call carcass sharing a unique 'combination of self interest and common good'.<sup>52</sup> Also, perhaps when they say that 'selfishness lies behind seeming selfless behaviour' they don't mean 'is more fundamental' or is 'the reality', but rather just that it is less obvious, hidden from view, but *also* present as a relevant factor.

These differences make a difference. We suspect that Heinrich and Marzluff know this, but their language doesn't always hold open this complexity – and in the context of what have become reductive and routine descriptions in biology, their account is very likely to be read in this unhelpful way. This situation is compounded by the fact that the most simplistic statements of their position have tended to be those produced for 'popular' audiences.<sup>53</sup> In using terms like 'selfishness' in such a broad way we lose the capacity to describe dynamic interplays of *balanced* costs and benefits that are, by definition adaptive and responsive to the needs of a diverse range of participants. Interwoven forms of balanced cooperation and competition, self interest and altruism, produces this *successful* form of life (which is anything but straightforwardly 'selfish').

It is also important to note that in places Heinrich's analysis clearly refuses to lock down any singular 'explanation' for this behaviour and attempts to tease out some of the multiple interwoven factors, multiple kinds of costs and benefits for different individuals involved.<sup>54</sup> In focusing on two key factors – status enhancement and posse formation – and situating them within a specific ecological environment of scarcity and mammalian competitors, Heinrich pushes us towards narratives and explanations that complicate instead of simplifying or purifying. But in other places in his work it is clear that there is a hierarchy of causes at play. Other possible mechanisms – like the way in which many ravens working together might keep a carcass free of snow, or the way in which more birds might lead to improved vigilance for predators – are pushed to the side, a little or a lot, as not being 'prime factors' or 'main reasons'.<sup>55</sup> Like so many biologists, Heinrich is – a fair bit of the time at least – working with an epistemological framework of competition: he presents multiple possible causes and has them compete with each other for dominance (an 'either/or' model).

In contrast we're most interested in the places in his work that are characterised by a 'cooperative' relationship between hypotheses, highlighting the *many reasons* that ravens might do the things they do in particular contexts (at a functional, not to mention a motivational, level). This is a logic of multiplication, of cooperation: 'and, and, and'. To put it simply, the same explanation might not hold at all times; just because a factor isn't the whole of the story doesn't mean that it isn't part of it. There is, of course, nothing wrong with searching for something like 'key mechanisms' in the evolution of this behaviour, but multiplicity needs to be kept in the frame: the fact that there might be a variety of ultimate causes, with differing significances at different times, and that the benefits to the caller will only ever be one part of a much more complex biosocial field of interactions. Amongst other reasons, this multiplicity matters because the more we narrow, the more we rank relevant causes and make them compete with each other, the easier it becomes for complex behaviours with their complex forms of compromise, balancing and mutualism, to look like simple, singular, winner-takes-all competition.<sup>56</sup>

And so, much of Heinrich's analysis, like that of so many other biologists, takes place underneath a general assumption that (or at least readily lends itself to a reading in which), if we dig deep enough, if we look hard enough, in all cases we will find that self interest is *the* ultimate cause of the observed behaviour. Like a law of physics, maximising self interest has become the law of evolutionary biology.

In this context, our suggestion is simply that we do away with the rhetorical framing that simplifies a complex context away, reducing the explanation to one of ultimate self interest – which, in this 'ultimate' form renders the fitness of the self somehow evolutionarily more significant, prior to, the fitness of others.

We might also note that Heinrich's own intervention reproduces this complexity. To solve the puzzle of their cooperation he had to (re)create the situations in which ravens may choose to call others. In doing so he was himself 'calling' out to the ravens, offering to share food with them. Of course, he did not 'call' like ravens do – although in some situations he did, attracting ravens to his baits with the use of their previously recorded calls – but even in other cases the baits he generously offered could be understood as 'calls' in their own way. Was Heinrich selfish here in his own act of sharing? In some sense the answer is surely yes: he shared food in order to gain something – his own satisfaction and understanding. But his action was not only for himself, it was also for multiple others: for the ravens who were fed during a long winter, for the interested people (like ourselves) who get to know them a little better as a result, and so perhaps also 'for' the ravens again, through the complex possibilities of enhanced protection and care that sometimes – but definitively not always – travel along with being deemed to be interesting.<sup>57</sup>

Ultimately, what we learn here is that species do not only emerge and endure in the world by virtue of their capacity to cut others down, to out run and out compete them. They also endure and are shaped by their capacity to cooperate, to achieve mutual advantage (in both inter- and intra- species relationships). This second possibly is ignored within a worldview in which all interactions are ultimately zero-sum games. As Keller notes, drawing on the work of Richard Lewontin, 'payoff matrices are necessarily more complex than those described by a zero-sum dynamic'.<sup>58</sup> Through various cooperative approaches, organisms generate new resources (perhaps through increasing efficiency, reducing absolute requirements or opening up access to new environments).

In the forests of New England, cooperative strategies likely played a role in making possible year-round inhabitation for ravens where it otherwise would not be (by dealing with winter food shortages). Whatever the mechanism that stabilise this highly successful behaviour turn out to be, it didn't arise through one raven taking another's resources in a straightforward act of zero-sum competition, but rather through a shifting population of ravens – sometimes engaged in cooperative projects of shared (even if unequal) advancement, sometimes in competitive interactions – opening up a new environment, with new resources. This complexity cannot be reduced to simple competition or self interest. At the very least, we need also to pay attention to the fact that cooperation doesn't just reshuffle resources within a fixed world. It is also world forming, opening up new evolutionary trajectories, new collective and behavioural forms, but also new biological forms *that simply would not be possible in its absence*. And so, whatever the genesis of raven food sharing, a distinct form of social life emerged here in which cooperation has profoundly shaped what it means to be a raven in this place.<sup>59</sup>

## Multiplying raven motivations

There is a further aspect of the notion that what evolution teaches us is that life is, at some fundamental level, selfish and competitive, that demands attention. All too often, black and white, accounts of the ultimate causes of a behaviour have been allowed to shape the range of possible explanations for the proximate or motivational causes. In this way, simplistic evolutionary mechanisms become simplistic organisms in terms of their cognitive and emotional competencies. The only options available to account for the motivations of ravens present them as either mindlessly playing out the 'cost-benefit calculus of [their] genes,' or alternatively, as mindful entities who are nonetheless required by the imperatives of survival to engage in the cold and calculated exploitation of their fellow creatures.<sup>60</sup> At the heart of these accounts, however, is a confusion between functional and motivational factors. As we have seen, at a functional level selfishness (and altruism for that matter) does not in any way imply a correlating motivational orientation (or even the capacity to have motivations at all).

In some cases animals may well choose to help one another in part or in full because of an obvious benefit to themselves. But, as de Waal notes, in a broad range of other cases something else must motivate this behaviour. For example, it seems highly unlikely that even birds as intelligent as ravens are aware of the complex long-term 'inclusive fitness' advantages associated with nest helping and some other cooperative acts.<sup>61</sup> In the absence of a raven-Darwin, how could they be? If they have psychological motivations at all, complex behaviours like these, behaviours without rewards that would make sense to the actor, must be motivated in some other way. De Waal argues that it seems likely that 'empathy evolved in animals as the main proximate mechanism for directed altruism'.<sup>62</sup> So, while an act may be evolutionarily advantageous to the actor (its ultimate cause or functional explanation lying in the complex fitness advantages of kin selection), at a proximate level it may well be motivated by feelings of care and concern, perhaps love, for another. Of course, this isn't the case with all cooperative behaviours, but we cannot afford to assume that we know which are which.

The key point is that 'selfishness' is a highly unhelpful concept in this context too. Sadly, however, these kinds of simplistic understandings have been actively promoted by some biologists. Perhaps most famously Richard Dawkins has argued for the 'selfishness' of genes as a fundamental evolutionary driver. In his words: 'I shall argue that a predominant quality to be expected in a successful gene is ruthless selfishness'.<sup>63</sup> While Dawkins has claimed that selfish genes do not equal selfish organisms, his own rhetoric frequently makes this connection. As he goes on to note: 'This gene selfishness will usually give rise to selfishness in individual behavior.' And in other places he has commented: 'Let us try to teach generosity and altruism, because we are born selfish' (2) and 'Blindness to suffering is an inherent consequence of natural selection ... Nature is neither kind nor cruel but indifferent'.<sup>64</sup>

A broad range of animals respond to the suffering of others in a range of different ways - they are not 'blind'. 'Nature' doesn't exist as an abstract entity capable or orienting itself in any way - be it kindly, cruelly or indifferently. Rather, 'nature' - in so far as this term means anything at all - is a composition of living (and non-living) beings of diverse species, most of whom are very far from being indifferent about a whole range of things – including their own lives and deaths, and for many species, also the fates of their close social companions. There are very good explanations for how these kinds of responsiveness towards others, grounded in a broad range of emotional and intellectual competencies, might have arisen not in spite of, but as a direct result of, natural selection (as de Waal has argued in relation to empathy). Of course, many other organisms are not involved in recognisably empathic behaviour. What is needed is attention to ecological, social and evolutionary specificity, rather than the assumption that statements can be made about 'nature' or 'life' in general - which, as decades of feminist and post-colonial theory have taught us, is usually just part of an effort to ignore specificity and read one's own biases onto the world.65

But Dawkins' statements here are equally concerning because they are grounded in a pervasive slippage between ultimate and proximate causes that allows 'selfishness' at the former level to colour, and in some cases completely subsume, our understanding of the latter. Keller drew our attention to this tendency decades ago. She noted that the use of colloquial language as technical terminology in biology – 'competition' and 'selfishness' were among her examples – 'permits the simultaneous transfer and denial of ... colloquial connotations'.<sup>66</sup>

In *Images of Animals*, Eileen Crist offers an insightful account of the many ways that the emotional, intellectual and experiential lives of animals have often

been ignored and denied within the biological sciences. She notes that within evolutionary biology:

Economic terminology is so pervasively deployed that it simply takes over animal life ... The impact of the economic idiom on the domain of experience and lived action involves the erasure of an animal lifeworld – an everyday experience of activity and leisure, pleasure and pain, abundance and hardship, exhilaration and fear, rivalry and affection.<sup>67</sup>

And so, animals' motivational states tend to be either ignored (not part of the 'big picture' of ultimate causes) or they are read as echoing these ultimate causes in a way that leaves animals working to maximise their self-interest as best they can. 'Whether run by selfish genes, wary bodies, or crafty minds, animal life exudes an atmosphere of unrelenting coldness ... [which ultimately] creates a picture of essential isolation'.<sup>68</sup>

While, in their broader bodies of work, Heinrich and Marzluff offer some of the best examples of biologists who are passionate about exploring the thick complexity of corvid lifeworlds, in their discussion of food sharing they don't do as much to escape these routine positions as they do elsewhere. In one key article on this topic they note that 'juvenile ravens possess immediately selfish reasons for this apparently altruistic act'69 and that 'our data show that carcass sharing behaviour did not evolve because of altruism, acting through intelligence and foresight, or generosity ... Surprisingly, harnessing the most selfish of motivations in an extremely aggressive species creates amazing cooperation for the common good'.<sup>70</sup> These claims are presumably grounded in some earlier research in which Heinrich and Marzluff argued that the proximate cause (motivation) for calling to announce food is likely not a deliberate effort to establish a crowd (or posse), but rather an effort to advertise one's status.<sup>71</sup> This work explicitly points to a strong difference between ultimate and proximate factors.<sup>72</sup> Even though attracting others may be a key ultimate cause for this behaviour, Heinrich and Marzluff argue that it is not relevant at a proximate level – pointing to the fact that if it were we would expect to see more calling in the presence of adults (and this isn't the case) and wouldn't expect dominants to inhibit the calls of others (rather, they should encourage them if they were trying to establish a posse).<sup>73</sup> For our purposes, what is most interesting about Heinrich and Marzluff's account is the way in which, even while explicitly acknowledging the divide between ultimate and proximate causes, when they turn to exploring the proximate domain they begin with, and focus on, the same selfinterested mechanisms that they have identified as ultimate causes. Why not start with the desire to share food (a desire that is in some cases perhaps supressed by dominants)? Or perhaps even the desire to be seen sharing food; to be seen to be an efficient and generous sharer? There is no reason why - at a proximate level - this explanation should be any less likely than a competitive one. And yet, biologists tend to start here with competitive individualism too because all of our biological thinking has been coloured by a simplistic notion that evolution teaches us the ultimately selfish foundations of all interactions.

It may well be the case that individual ravens are cognizant of, and motivated by, the status enhancement (or access opportunity) that comes with sharing food. It may also be the case that they are not, or that they are *also* motivated by other factors: a desire to share with others, some of whom they care for; a desire to contribute to the collective good; a desire to reciprocate for past gifts from others. Perhaps good old self interest is a more likely motivator for this behaviour, but this question needs to be asked. Motivations cannot be assumed on the basis of supposedly 'selfish' ultimate causes.

As with the discussion of ultimate causes above, we propose that a tendency towards singular explanations resulting from competing causes, might instead be opened out into a shifting field of motivations. In this context, the gift of a carcass cannot provide insight into ravens' real motivations for sharing (that can then be generalised to all situations) – is it 'this or that' that motivates them – but can only add one more 'and' to the list: revealing only whether or not a raven is interested in sharing in a given situation. Each 'gift' that Heinirch made to the ravens created a unique site. Following Stengers we would suggest that, like all experimental devices, these gifts do not have the power to *reveal* anything; rather they *create*, crafting new possibilities for animals to respond to each proposal.<sup>74</sup> As such, raven responses even over innumerable instances - cannot provide a complete, or even an 'in general', picture of what is possible. Any time that they are interested in a carcass, or in making or responding to the calls of other ravens, we may find new motivations, according to the manner in which the situation was constructed by and for them. As Rowell notes, animals live with 'different agendas' - even for doing one and the same thing.<sup>75</sup> Complicated creatures – and ravens are certainly that, a fact that Heinrich has been instrumental in teaching us - demand more sophisticated explanations than the standard 'either/or'; they demand a kind of science for which the very truth of one hypothesis may only emerge in dynamic interaction with the truth of the others.

# Conclusion

We hope to have offered another way into the puzzle of corvid cooperation, and in doing so to have challenged some basic but unhelpful assumptions about evolution. Our key suggestion is that we ought not to rush to solve this puzzle on the terms in which it is ordinarily posed, but rather to ask why it is a puzzle at all. Doing so requires us to acknowledge that there is no fundamental level at which nature, or evolution, or natural selection, can be deemed to be *anything*, whether selfish, cooperative, altruistic or even 'indifferent'. Instead, we inhabit a world of richly diverse living beings, each exploring and taking up their own ways of being with others. There is no essence here, just creation, invention and multiplicity. The only way that all of this can be boiled down to narratives of fundamental selfishness and competitive individualism is through adopting expansive definitions of these terms that are simply wrong at a motivational/proximate level and meaningless at a functional/ultimate level. What's more, these accounts walk a dangerous line: frequently painting pictures of animal life (including sometimes human life) as slave to 'higher' processes beyond our control. This might be part of the picture, part of the

time, but it certainly doesn't yield a complete understanding and isn't at all a valid *starting point* for scientific enquiry.

While we have focused on cooperations *amongst* ravens, the same points might, of course, also be made about inter-species cooperation; about how different species strike up mutualisms of all kinds to produce new ways of life, like the ravens that lead wolves and others to carcasses and the Torresian crows (*Corvus orru*) who seem to have very quickly learnt to remove ticks from introduced banteng in Australia.<sup>76</sup> These cooperative tendencies, perhaps originally developed through interactions with other corvids, now spill out into the world creating all manner of new opportunities for living together.

Ultimately, terms like 'cooperation' and 'competition' are themselves too vague and simplistic for this complex grey space of interactions. But they are a first step towards an opening out into a world that is not, at least not necessarily, 'red in tooth and claw.' Rather, ours is a world that is put together by diverse living beings over immense periods of time. Most of these living beings are, of course, unaware of this larger picture – at least in an explicit, conscious, manner. But many of them *are* intimately aware of their daily worlds and make *decisions* that have consequences. In this way, evolution is not something that just 'happens to us.' All of us, to a greater or lesser extent, craft evolutionary futures.<sup>77</sup> Amongst their many other flaws, the dominant evolutionary stories that we now tell strip this kind of agency out of the world; in many contexts even enabling crude forms of 'justification' for human selfishness and competitiveness of all kinds. And so, paying attention to cooperative ravens should also remind us that, however limited our powers, however partial and incomplete our knowledge, we are always already shaping worlds. The question then, of course, is: how might we shape better evolutionary futures with others?

#### **Bibliography**

- Ackerman, Jennifer. *Chance in the House of Fate: A Natural History of Heredity* (Houghton Mifflin Harcourt, 2002).
- Axelrod, Robert, and William D Hamilton. "The Evolution of Cooperation." *Science*, 211. 4489 1981: 1390-96.
- Baglione, Vittorio, JosÉ M. Marcos, Daniela Canestrari, Michael Griesser, Guido Andreotti, Cristiana Bardini, and Giuseppe Bogliani. "Does Year-Round Territoriality Rather Than Habitat Saturation Explain Delayed Natal Dispersal and Cooperative Breeding in the Carrion Crow?". *Journal of Animal Ecology*, 74. 5 2005: 842-51.
- Barlow, George W, and Thelma E Rowell. "The Contribution of Game Theory to Animal Behavior." *Behavioral and Brain Sciences*, 7. 01 1984: 101-03.
- Bradshaw, Corey J. A., and Warren W. White. "Rapid Development of Cleaning Behaviour by Torresian Crows *Corvus Orru* on Non-Native Banteng *Bos Javanicus* in Northern Australia." *Journal of Avian Biology*, 37. 4 2006: 409-11.
- Braun, Anna, and Thomas Bugnyar. "Social Bonds and Rank Acquisition in Raven Nonbreeder Aggregations." *Animal behaviour*, 84. 6 2012: 1507-15.
- Braun, Anna, Thomas Walsdorff, Orlaith N Fraser, and Thomas Bugnyar. "Socialized Sub-Groups in a Temporary Stable Raven Flock?". *Journal of Ornithology*, 153. 1 2012: 97-104.

- Bugnyar, Thomas, and Bernd Heinrich. "Pilfering Ravens: *Corvus Corax* Adjust Their Behaviour to Social Context and Identity of Competitors." *Animal Cognition*, 9 2006: 369–76.
- Bugnyar, Thomas, Maartje Kijne, and Kurt Kotrschal. "Food Calling in Ravens: Are Yells Referential Signals?". *Animal Behaviour*, 61. 5 2001: 949-58.
- Crist, Eileen. *Images of Animals: Anthropomorphism and Animal Mind* (Philadelphia: Temple University Press, 1999).
- Dawkins, Richard. A Devil's Chaplain Selected Essays (New York: Houghton Mifflin Company, 2003).
- ---. *The Selfish Gene* (Oxford: Oxford University Press, 2006).
- de Waal, Frans B.M. "Putting the Altruism Back into Altruism: The Evolution of Empathy." *Annual Review of Psychology*, 59 2008: 279–300.
- Despret, Vinciane. "The Enigma of the Raven (Translated by Jeffrey Bussolini)." *Angelaki*, 20. 2 2015.
- Dugatkin, L.A. *Cooperation among Animals: An Evolutionary Perspective* (New York: Oxford University Press, 1997).
- Fedigan, Linda, and Laurence Fedigan. "Gender and the Study of Primates." In *Critical Reviews of Gender and Anthropology : Implications for Teaching and Research*, edited by Sandra Morgan. (Washington, D.C.: American Anthropological Association, 1989).
- Ghiselin, Michael T. *Economy of Nature and the Evolution of Sex* (University of California Press, 1974).
- Goodwin, Derek. Crows of the World, Vol. 2 (London: British Museum, 1986).
- Gordon, Deborah M. "What We Don't Know About the Evolution of Cooperation in Animals." In *Cooperation and Its Evolution*, edited by Kim Sterelny, Richard Joyce and Brett Calcott: MIT Press, 2013).
- Gould, S. J., and R. C. Lewontin. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society B*, 205 1979: 581-98.
- Hamilton, William D. "The Genetical Evolution of Social Behaviour, I and Ii." *Journal* of Theoretical Biology, 7. 1 1964: 17-52.
- Haraway, Donna. "Animal Sociology and a Natural Economy of the Body Politic, Part 1 : A Political Physiology of Dominance." In *Women, Gender and Scholarship*, edited by Elizabeth Abel and Emily Abel. (Chicago: Chicago University Press, 1983).
- – . Primate Visions: Gender, Race, and Nature in the World of Modern Science (New York & London: Routledge, 1989).
- Heinrich, Bernd. "Food Sharing in the Raven, *Corvus Corax.*" In *The Ecology of Social Behavior*, edited by C.N. Slobodchikoff. (San Diego, CA: Academic Press, 1988).
- ---. *Ravens in Winter* (New York: Summit Books, 1989).
- - -. "Winter Foraging at Carcasses by Three Sympatric Corvids, with Emphasis on Recruitment by the Raven, *Corvus Corax*." *Behavioral Ecology and Sociobiology*, 23 1988: 141-56.
- Heinrich, Bernd, and JM Marzluff. "Do Common Ravens Yell Because They Want to Attract Others?". *Behavioral Ecology and Sociobiology*, 28. 1 1991: 13-21.
- Heinrich, Bernd, and John Marzluff. "Why Ravens Share." *American Scientist*, 1995: 342-49.
- Hustak, Carla, and Natasha Myers. "Involutionary Momentum: Affective Ecologies and the Sciences of Plant/Insect Encounters." *differences*, 23. 3 2012: 74-118.

Keller, Evelyn Fox. "Competition: Current Usages." In *Keywords in Evolutionary Biology*, edited by Evelyn Fox Keller and Elisabeth A. Lloyd. (Cambridge, MA: Harvard University Press, 1992).

- – . "Feminism and Science." In *Women, Gender and Scholarship*, edited by
  Elizabeth Abel and Emily Abel. (Chicago: Chicago University Press, 1983).
- Lancaster, Jane. *Primate Behavior and the Emergence of Human Culture* (New York: Holt, Reinhart and Winston, 1975).
- Latour, Bruno. "A Well Articulated Primatology: Reflections of a Fellow Traveler." In *Primate Encounters: Models of Science, Gender and Society*, edited by S. Strum and L. Fedigan. (Chicago: University of Chicago Press, 2000).
- Lewontin, Richard C. "Adaptation." Scientific American, 1978: 212-31.

McIntosh, Robert. "Competition: Historical Perspectives." In *Keywords in Evolutionary Biology*, edited by Evelyn Fox Keller and Elisabeth A. Lloyd. (Cambridge, MA: Harvard University Press, 1992).

- Mesterton-Gibbons, Michael, and Lee Alan Dugatkin. "On the Evolution of Delayed Recruitment to Food Bonanzas." *Behavioral Ecology*, 10. 4 1999: 377-90.
- Noble, Denis. "Neo-Darwinism, the Modern Synthesis and Selfish Genes: Are They of Use in Physiology?". *Journal of Physiology*, 589. 5 2011: 1007–15.
- Oyama, Susan. Evolution's Eye: A Systems View of the Biology-Culture Divide (Durham & London: Duke University Press, 2000).
- Plumwood, Val. *Environmental Culture: The Ecological Crisis of Reason* (London & New York: Routledge, 2002).

---. *Feminism and the Mastery of Nature* (London & New York: Routledge, 1993). Ratcliffe, Derek. *The Raven* (A&C Black, 2010).

- Roughgarden, Joan. *The Genial Gene* (Berkeley and L.A.: University of California Press, 2009).
- Rowell, Thelma E. "The Concept of Social Dominance." *Behavioral biology*, 11. 2 1974: 131-54.

Sachs, Joel L, Ulrich G Mueller, Thomas P Wilcox, and James J Bull. "The Evolution of Cooperation." *The Quarterly Review of Biology*, 79. 2 2004: 135-60.

Seed, Amanda M, Nicola S Clayton, and Nathan J Emery. "Cooperative Problem Solving in Rooks (Corvus Frugilegus)." *Proceedings of the Royal Society B: Biological Sciences*, 275. 1641 2008: 1421-29.

Shiebinger, L. *Has Feminism Changed Science?* (Cambridge, Mass: Harvard University Press, 1999).

Sober, Elliott. "The Abcs of Altruism." In *Altruism and Altruistic Love: Science, Philosophy, and Religion in Dialogue,* edited by Stephen G Post, Lynn G Underwood, Jeffrey P Schloss and William B Hurlbut: Oxford University Press, 2002).

Stengers, Isabelle. *Power and Invention: Situating Science* (Mineapolis: University of Minnesota Press, 1997).

Szipl, G, and T Bugnyar. "Craving Ravens: Individual 'Haa'call Rates at Feeding Sites as Cues to Personality and Levels of Fission-Fusion Dynamics?". Animal Behavior and Cognition, 1. 3 2014: 265-80.

- Szipl, Georgine, Markus Boeckle, Claudia AF Wascher, Michela Spreafico, and Thomas Bugnyar. "With Whom to Dine? Ravens' Responses to Food-Associated Calls Depend on Individual Characteristics of the Caller." Animal Behaviour, 99 2015: 33-42.
- Trivers, Robert L. "The Evolution of Reciprocal Altruism." *Quarterly review of biology*, 1971: 35-57.
- Zahavi, A., and A. Zahavi. *The Handicap Principle: A Missing Piece of Darwin's Puzzle* (Oxford: Oxford University Press, 1997).

#### Endnotes

<sup>5</sup> Ghiselin, Economy of Nature and the Evolution of Sex, 247.

<sup>6</sup> Lewontin, 'Adaptation'; Gould and Lewontin, 'The Spandrels of San Marco and the Panglossian Paradigm.'

<sup>7</sup> Gordon 'What We Don't Know,' 195.

<sup>8</sup> Sachs et al., 'The Evolution of Cooperation.'; Axelrod and Hamilton, 'The Evolution of Cooperation.'

9 Sober, 'The ABCs of Altruism.'

<sup>10</sup> It is debatable to what extent we can meaningfully think about a (singular) bottom line here. See Gordon, 'What We Don't Know.'; Oyama, *Evolution's Eye*, 208-10..

<sup>11</sup> Baglione et al., 'Does Year-Round Territoriality.'; Goodwin, Crows of the World.

<sup>12</sup> Seed, Clayton, and Emery, 'Cooperative Problem Solving in Rooks.'

<sup>13</sup> For instance, the term 'harem' usually refers to a group composed of one male mating with several females. This semantic choice implies a particular scenario: that of a dominant male exercising control over his females. However, who says that the male chooses the females? That he appropriates them, that he takes possession of them? Nothing does; it is only the term 'harem' that encourages this meaning. Another way of describing this type of organization has been proposed, however, notably by some feminist researchers working in the framework of the Darwinian theory of sexual selection. See Lancaster, *Primate Behavior*, 34.. <sup>14</sup> One of us, VD, has already written about these ravens and Heinrich's work with them. The other of us, TvD, started work on this chapter without having read that paper – which has only recently been translated into English. Both being captivated by the same ravens, we continued this conversation together and this chapter is the result. See Despret, 'The Enigma of the Raven.'

<sup>15</sup> Latour, 'A Well Articulated Primatology.'

<sup>16</sup> Zahavi and Zahavi, *The Handicap Principle*.

<sup>17</sup> Thelma Rowell, Interview in the document base 'Non sheepish Sheep', Vinciane Despret and Didier Demorcy, document made for the exhibition 'Making Things Public,' 2003. <sup>18</sup> Hamilton, 'The Genetical Evolution of Social Behaviour.'

<sup>19</sup> Ackerman, *Chance in the House of Fate*, 141.. This statement is a good example of a general tendency in many evolutionary discourses that is discussed in more detail below. Haldane's overly rational, overly quantified, claim, bleeds over into a motivational space. While insisting that behaviour is the result of evolutionary forces (ultimate causes) and cannot be equated with conscious motives (proximate causes), framing like this – 'I would lay down my life...' – ends up presenting the motivational drives of individuals as mere copies of evolutionary forces: as if cooperative actors were some kind of rational economic agents 'really' just taking care of their genetic patrimony.

<sup>20</sup> Sachs et al., 'The Evolution of Cooperation,' 137.

<sup>21</sup> Trivers, 'The Evolution of Reciprocal Altruism.'; Axelrod and Hamilton, 'The Evolution of Cooperation.'

<sup>22</sup> Sachs et al., 'The Evolution of Cooperation.'

<sup>23</sup> As is discussed further below, this understanding has been challenged in recent work by Thomas Bugnyar and colleagues.

<sup>24</sup> Heinrich, 'Food Sharing in the Raven,' 294.

<sup>25</sup> Ibid.. But see the discussion of the work of Thomas Bugnyar below for an alternative account of group formation amongst this species in Austria. It remains an open question as to whether Common Raven food sharing in New England is at all similar to that practiced in the Austrian Alps. The question needs to be asked, but we certainly can't assume commonality of behaviour on the basis of species.

<sup>26</sup> de Waal, 'Putting the Altruism Back into Altruism,' 280.

<sup>27</sup> Keller, 'Competition,' 69.

<sup>28</sup> Plumwood, Feminism and the Mastery of Nature, 143.

<sup>&</sup>lt;sup>1</sup> Heinrich, 'Food Sharing in the Raven,' 290.

<sup>&</sup>lt;sup>2</sup> Heinrich, *Ravens in Winter*, 12.

<sup>&</sup>lt;sup>3</sup> Ibid., 11.

<sup>&</sup>lt;sup>4</sup> Ibid., 12.

<sup>29</sup> Plumwood, Environmental Culture, 34.

<sup>31</sup> See also McIntosh, 'Competition.'.

34 Roughgarden, The Genial Gene, 12; Noble, 'Neo-Darwinism.'

<sup>35</sup> Roughgarden, *The Genial Gene*.

<sup>36</sup> Ibid., 12.. We have omitted some of the more 'gene centric' phrasing in this quote from Roughgarden which, in our opinion, overemphasises the significance of genetic inheritance in these processes. This change has not altered the relevant aspects of this quote for the purposes of the current discussion. In addition, we remain uncertain about this characterisation which seems to imply a hard – even if complex – distinction between cooperation and competition (as is discussed in more detail below).

<sup>37</sup> Dugatkin, Cooperation Among Animals.

<sup>38</sup> Heinrich, 'Food Sharing in the Raven,' 306.

<sup>39</sup> Mesterton-Gibbons and Dugatkin, 'On the Evolution of Delayed Recruitment.'

<sup>40</sup> Heinrich and Marzluff, 'Why Ravens Share.'

<sup>41</sup> Heinrich, 'Winter Foraging.'; 'Food Sharing in the Raven.'; *Ravens in Winter*; Heinrich and Marzluff, 'Do Common Ravens Yell.'; Heinrich and Marzluff, 'Why Ravens Share.'

<sup>42</sup> Heinrich and Marzluff, 'Why Ravens Share,' 342.

<sup>43</sup> Heinrich and Marzluff, 'Do Common Ravens Yell.'

44 Heinrich, 'Food Sharing in the Raven.'

<sup>45</sup> See, for example, Braun and Bugnyar, 'Social Bonds and Rank Acquisition.'; Braun et al., 'Socialized Sub-Groups.'; Bugnyar, Kijne, and Kotrschal, 'Food Calling in Ravens.'; Szipl et al., 'With Whom to Dine?'; Szipl and Bugnyar, 'Craving Ravens.'. This work challenges the foundation of Heinrich's solution to this puzzle, discussed further below.

<sup>46</sup> Barlow and Rowell, 'The Contribution of Game Theory.'

<sup>47</sup> Nor can this be taken up as straight forward comparison in which the question is 'do they benefit more from sharing than not sharing?' This question assumes that both options are open to them, it ignores all of the other social, environmental, etc, constraints that play a role in the emergence of the behaviour. This is a general problem with this scholarship on cooperation.

<sup>48</sup> Szipl et al., 'With Whom to Dine?'

<sup>49</sup> Ratcliffe, *The Raven*, 104.

<sup>50</sup> Szipl et al., 'With Whom to Dine?'

<sup>51</sup> Heinrich and Marzluff, 'Why Ravens Share.'

<sup>52</sup> Ibid., 349.

<sup>53</sup> Heinrich, Ravens in Winter; Heinrich and Marzluff, 'Why Ravens Share.'

54 Heinrich, 'Food Sharing in the Raven.'

<sup>55</sup> Ibid., 302-3.

<sup>56</sup> In part this approach is also a product of the practicalities of doing science: it is much harder to isolate and test if multiple causes are part of the explanation. In this context, good explanations require purified causes. There is a related pattern at work in the desire to understand altruism and selfishness themselves in black and white terms: from this perspective both are easier to give an account of, to predict and measure. When both parties benefit in complex mutualisms, when both parties' interests must be weighed and balanced, there are now two (sets of) reasons. Two reasons is too many.

<sup>57</sup> In corvid worlds it is remarkable how much public relations work is grounded in efforts to cultivate human respect and care on the basis that these birds are intellectually and emotionally complex creatures.

<sup>58</sup> Keller, 'Competition,' 71.

<sup>59</sup> Questioning the centrality of competition in this way also draws our attention to the assumed priority of 'individualism' in our accounts, the two having tended to go hand in hand ibid.. It is, therefore, no surprise that underlying a great deal of work on the evolution of cooperation is an assumption that 'life in common' is fragile and fleeting; that it readily breaks down and disintegrates without constant maintenance. Unfortunately, we do not have

<sup>&</sup>lt;sup>30</sup> Keller, 'Competition,' 68-73.

<sup>&</sup>lt;sup>32</sup> Keller, 'Competition.'

<sup>&</sup>lt;sup>33</sup> Ibid., 72.

the space here to offer a detailed analysis of the problematic nature of assumed individualism in evolutionary theory.

<sup>60</sup> Crist, Images of Animals, 139.

<sup>61</sup> de Waal, 'Putting the Altruism Back,' 281.

<sup>62</sup> Ibid., 282.. As de Waal notes here, there are many forms of empathy; not all of them involve clear motivational states or intentions to help others.

<sup>63</sup> Dawkins, *The Selfish Gene*, 2.

<sup>64</sup> Dawkins, A Devil's Chaplain, 9.

<sup>65</sup> See, for example, Fedigan and Fedigan, 'Gender and the Study of Primates.'; Keller, 'Feminism and Science.'; Haraway, 'Animal Sociology.'; Haraway, *Primate Visions*; Shiebinger, *Has Feminism Changed Science*?.

<sup>66</sup> Keller, 'Competition,' 69.

<sup>67</sup> Crist, Images of Animals, 141-2.

68 Ibid., 142.

<sup>69</sup> Heinrich and Marzluff, 'Why Ravens Share,' 342.

<sup>70</sup> Ibid., 349.

<sup>71</sup> Heinrich and Marzluff, 'Do Common Ravens Yell.'

<sup>72</sup> Ibid., 13.

<sup>73</sup> Some of these findings – which it should be noted were generated within the confines of an aviary with all of the associated social consequences (see Rowell, 'The Concept of Social Dominance.') – differ from those of Bugnyar and colleagues who, for example, found that subordinates did most of the calling amongst free living ravens in Austria. See Szipl et al., 'With Whom to Dine?'.

<sup>74</sup> Stengers, Power and Invention.

75 Rowell, 'The Concept of Social Dominance.'

<sup>76</sup> Bradshaw and White, 'Rapid Development of Cleaning Behaviour.'

77 Hustak and Myers, 'Involutionary Momentum.'