The ‘problem of altruism’ has remained a thorn in the side of evolutionary biology since Darwin. In *On the origin of species* (1860), Darwin clearly recognized that the widespread existence of altruistic behavioural adaptations was a potential problem for his theory of natural selection. The general problem is that, if nature is ‘red in tooth and claw’ and natural selection produces adaptations by virtue of competitive elimination of the less fit, how could it produce the many examples of cooperation found in nature in which individuals sacrifice some degree of fitness for another? Since Darwin’s time, evolutionary biologists have tried to explain altruism within the natural selection framework. This has resulted in many different efforts to explain how altruism could be maintained under selection. These many theories all appear to successfully demonstrate ways that altruistic behaviours might be sustained against ‘invasion’ by non-altruistic alternatives. These are relevant to our approach, but only as *post hoc* adaptive consequences of the emergence of altruism. We will argue below that the standard natural selection approach does not do an adequate job of explaining the origins of such adaptations.

The selection framework itself is an incomplete explanation for the evolution of altruism because it necessarily avoids answering the question of how altruistic behaviours initially arise in a non-altruistic context, and instead explains how they might be stabilized or modified with respect to alternatives in a given environment. This is because natural selection theory is intrinsically agnostic to how a given trait initially arises. Nevertheless, this does not mean that the question of how modification of traits is generated is entirely irrelevant. This agnosticism can lead to the expectation that random mutation, recombination and genetic drift are sufficient mechanisms to explain the creativity that is evident in evolution. It has been easy to avoid addressing the question of the source of variant forms in contexts where a new adaptation can be traced to prior
trait states that could have been incrementally modified to reach the known end state. There are, however, adaptive transitions where certain directions of modification should have been blocked by countervailing factors, apparently requiring a discontinuous jump. In such cases, it is common for evolutionary theorists simply to imagine that the transition occurred due to a ‘hopeful monster’ mega-mutation or some other accidental radical reorganization of the genome. This can strain the dependency on accident as an explanation, especially as the adaptive complexity of the transition increases. This is most obviously problematic in the case of what Maynard Smith and Szathmáry (1995) have described as major transitions in evolution, such as the transition to multicellularity in plants, animals, and fungi (e.g. Buss 1987). In such transitions, there has been a shift from autonomy to codependence, with the result that a higher-order unit of evolution emerges, organized around a novel synergy of multiple lower-order units that previously would have been in competition. Both the combinatorial complexity of hitting upon a sufficient complementarity of interdependencies and the dangers due to loss of autonomy in the process pose a high barrier to achieving such a transition.

In general terms, the problem of explaining the origin of an altruistic adaptation is a paradigm case of such a major transition. First we will argue that a shift to codependence maintained by altruistic adaptations cannot be fully explained by natural selection alone. Natural selection acts as a limitation on variety, but does not account for the generation of the variant forms that are its substrates. Since the form of the relevant variation in the case of altruism involves potentially high costs, incremental transition is more problematic. Second, we will suggest instead that relaxation of selection may be an important factor due to the degradation of autonomy that can result, and because this creates conditions which both allows for and aids in the emergence of new potential interdependencies.

To exemplify the general mechanism involved we will examine two cases of reorganization effects due to relaxation of selection: an increase in the complexity and neural control of song in a domesticated bird and the evolution of dependency on dietary vitamin C in anthropoid primates and its consequences for other adaptations. Both examples demonstrate how relaxation of selection may lead to a degradation of autonomy, and how this may contribute to the emergence of functional codependence. Neither matches the problem of altruism exactly, but both are informative in different ways. Borrowing insights from these two examples, we extrapolate a novel approach to the origins of altruism.
OVERVIEW OF THE PROBLEM

Darwin himself recognized that examples of evolved altruism such as that of hive bees posed problems for his theory (1860). His solution was to suggest that a form of ‘community selection’ might occur when traits that undermine an individuals’ reproduction turn out to be adaptive in terms of the reproduction of a group, which is likely to contain family members of the altruistic individual. This explanation was developed by Petr Kropotkin who, based on his observations of wildlife communities in Siberia (1902), argued that limited resources would select for a tendency to cooperate rather than compete. Subsequent work drew further links between environmental structure and social behaviour; Wynne-Edwards (1962), for example, argued that if resources are clumped and can only be obtained or protected by multiple individuals working in concert, then selection pressures are likely to favour cooperative behaviours over selfish individual behaviours.

However, some difficulties with group selection approaches remained, notably the assumption that groups can be treated as a type of individual with respect to natural selection. Critics pointed out that in fact many groups tend to have rather fluid memberships (e.g. Williams 1966), and that group selection arguments lacked an explanation for how group benefits may arise.

The discovery of DNA and its integration with Darwinian theory allowed Hamilton (1964a, 1964b) to solve Darwin’s problem with eusocial insects by demonstrating that the close genetic relatedness of bees explained the altruism of sterile workers. Subsequent work attempted to generalize from kin altruism among genetically related individuals to a broader theory of evolved altruistic behaviour, showing that reliably reciprocated altruistic behaviours between unrelated individuals could also serve to maintain social cooperation (e.g. Trivers 1971). More recent developments generalized this work still further by considering direct reciprocity a special case of indirect reciprocity within a population of two (Nowak 2006), as aid given within groups is not necessarily limited to pairs of individuals engaging in repetitive or exclusive interactions.

Such indirect reciprocity may also include more complex forms of interaction; language, for example, allows gossip and the exchange of information about cooperators and cheaters alike, so that individuals are able to weigh the likely costs of giving against even indirect benefits. In this scenario, natural selection should favour cooperation (as groups of
cooperators do better than their cheating counterparts) as well as better forms of communication, as offsetting the costs of group living.

However, language and communication more generally must themselves be the result of a complicated evolutionary history; thus indirect reciprocity approaches require that a whole slew of elements come together to form both a cohesive system of behavioural predispositions for maintaining group cohesion and expelling cheaters, some of which (such as language) are symbolic processes probably restricted to human cooperative groups.

Indirect reciprocity also generally assumes that interactions among group members are relatively equiprobable. However, this is generally not the case in actual biological systems as inter-individual distance is usually quite variable and non-symmetric, and more recently network reciprocity theory has used graph theory to take into account the statistical nature of interactions limited by spatial constraints (Nowak 2006). In this approach, each individual communicates/interacts with a limited number of other members of the population who may be either cooperators or defectors (cheaters). It is assumed that when members gain direct knowledge of a cheater they will attempt to shift their interactions to a different neighbour. As neighbouring cooperators discover one another in this manner they begin to share information amongst themselves, i.e. in a local sub-network within the group that will have a better overall fitness than the sub-networks of cheaters.

In recent decades such approaches have been complemented by work investigating the issue from a standard economic perspective which attempts to explain how cooperators can maintain their populations against cheaters. Organisms do better as cheaters only if they subsequently avoid associating with the organism they cheated: if information on cheaters’ reputations is available, cheaters are forced into drifting. Cooperators, however, repeat cooperative interactions with other cooperators and thereby eventually benefit from the occasional costs of being cheated, thus maintaining their populations through group selection.

This perspective has been used in several different game theory approaches pre-dating many network reciprocity approaches, including the ‘Prisoner’s Dilemma’ and ‘Stag Hunt’ type games which alter the relative costs and benefits of cooperating or defecting (cheating). Research on which algorithms of play did best at the Prisoner’s Dilemma (PD) game (Axelrod 1984) established several stable solutions: briefly, groups of cooperators can maintain group cohesion and keep out cheaters if they maintain a strategy of cooperating until the other player cheated, as well
as occasionally cooperating even when the strategy dictated cheating. In this way, mistakes that throw the interaction into a series of cheating interactions can be corrected.

Therefore, work on problem of altruism has suggested several mechanisms through which cooperation, when it occurs, can be maintained in a variety of populations of cooperators and defectors. More recent co-evolutionary approaches have also investigated aspects of altruism that are transmitted socially, or that involve niche construction effects influencing subsequent generations. These co-evolutionary approaches differ primarily in their addition of non-genetic components that are transmitted independent of an organism’s biological lineage and which may even affect an organism’s genetic reproduction. We will return to these human-specific variants on the altruism problem below, but first we consider some special circumstances that aid the evolution of pro-social behaviour in animals.

Social spiders offer an interesting case in which cooperation can emerge due to advantages of maintaining proximity. Sociality has arisen in several different groups of spiders, and researchers have been concerned with why this might be the case. Generally all populations of animals must balance the dual constraints of population density and its link to the distribution and accessibility of environmental resources. Thus spiders working together can capture larger prey than solitary individuals (Nentwig 1985), but how spiders become habituated to social living so that they can take advantage of this synergistic benefit provides additional insight into conditions favoring the evolution of altruism. The Allee effect, named for Warder Clyde Allee (1951), examines conditions under which population density and the resulting proximity of individuals can have a positive correlation with survival and reproduction of that population. Living in groups can be advantageous under certain conditions, and if there are collective effects through which cooperating individuals can gain access to special resources, then generally the larger your numbers the better off you are. But there are usually costs to group membership as well, due to the need to share resources. Allee was primarily concerned with group effects such as predatory protection and group hunting, but the theory also suggests that if a group is brought together there could be multiple ways in which maintaining the group could be reinforced. For instance, if group size is correlated with better survival, then selection for sex ratios would heavily bias the production of females so that the optimal population size can be reached at a faster rate than a population without this bias.
A recent study (Bilde et al. 2007) shows that in one social spider group, Stegodyphus dumicola, reduced female body size and corresponding smaller clutch sizes would seem to be a cost to group living. However, overall lifetime reproductive success in these same individuals increases with colony size due to the greater percentage of offspring that survive the juvenile to adult transition and persist to form the basis of the next generation. Other examples from social spiders show some of the integrated functions that can occur with prolonged group living. Matriphagy (eating the mother) occurs at the end of each season so that the offspring from the previous year now have a source of food upon which to begin the new season of colony development. In addition, there appears to be shared care for offspring. Presumably, non-cooperative behaviours that benefit individuals at the expense of other members of the group do not arise because the benefit of cooperative behaviour always outweighs any benefits that would arise due to defection. Thus social spiders demonstrate that cooperative group living can provide many benefits accruing from population density effects, such as collective resource acquisition and reproductive support, and that these benefits can be a source of selective advantages which will also select against non-cooperative and defecting behaviours.

Turning our attention to the role of social transmission on the evolution of altruism, there have been a number of approaches that demonstrate how processes of social transmission can augment the stabilization of altruistic behaviours in social groups. Many have been motivated by the evolutionary analogy drawn between genes and social traits, such as the concept of memes introduced by Richard Dawkins (1976). Despite criticisms with respect to how to categorize memes and whether or not discrete units of socially transmitted information are obtainable or transmissible, there are aspects of these general principles that are relevant to our discussion. With respect to evolution, an advantage of social transmission, and particularly cultural evolution (memetic or otherwise), is that it can occur at rates that are orders of magnitude faster than biological evolution due to its de-coupled relationship from genetic material that has to be passed from parents to offspring. Social transmission is also not limited to related individuals, but can travel across individuals. Co-evolutionary theories share this blending of behaviour and biological evolution, and work to understand their relationships to one another.

One example of an account of the evolution of altruism that depends on social transmission effects is Lehmann’s (2007) notion of trans-generational altruism. Lehmann argues that by assuming that the altruism is
occurring among contemporaries we tend to ignore the role of behaviours that provide altruistic benefits (as well as potential costs) across generations. This is particularly relevant with respect to niche construction effects (e.g. Laland et al. 1996, 2000) where an environmental modification may persist across generations. In the extreme case of humans, extensive man-made modifications of both local living environments and global socio-economic context of social life over the past century have radically altered the conditions affecting social behaviours of future generations in both beneficial and deleterious ways. But even in more typical cases, such as nests that are maintained across generations, trans-generational altruism and selfish behaviours are possible. Consider the example of matriphagy (discussed above), in which mothers die to leave a carcass for their offspring to eat. Thus, not only can an altruistic benefit be paid forward to future generations, but selfish behaviours such as resource depletion can also have cross-generational effects. These considerations greatly enlarge the scope of the evolutionary problem of determining what constitutes an evolutionary stable altruistic strategy.

Heylighen (1992) argues that theories restricted to biological evolution are incapable of explaining true unselfish altruism, and that only memetic or dual inheritance approaches can achieve this result. Although we will not pursue this hypothesis below, the role of biologically uncoupled cultural processes is not incompatible with the approach we will pursue. An evolutionary mechanism that can achieve some degree of altruistic behaviour even at the cost of individual or kin selection advantage would provide a foundation for the evolution of socially transmitted biologically disadvantageous altruistic behaviours.

CODEPENDENCY

These co-evolutionary and niche construction considerations demonstrate that the problem of the evolution of altruism is far more general than merely sacrificial and helpful interactions between pairs of interacting organisms. Formulated more abstractly, they demonstrate that the underlying issue is whether higher-order synergistic interdependencies with distributed advantages can emerge and be maintained in the face of costs imposed by breakdowns in this synergy, either because of a failure to maintain an equal distribution of costs and benefits or because of invasion by non-cooperative elements. Framing the problem in these more general terms, however, highlights the fact that this is not merely an issue
concerning animal social behaviour, but also a more general problem concerning the evolution of synergistic codependency relationships in biology at all levels.

Of course, explaining the maintenance of such synergies and the emergence of novel synergies are distinct evolutionary problems. Identifying the classes of stable interactive strategies that maintain such higher-order synergistic social organizations does not necessarily provide insight into how they could form in the first place. Nevertheless, perhaps exploring cases in which higher synergistic relationships have emerged in physiological systems can shed light on how analogous relationships can emerge socially.

Below we describe two examples in which synergistic physiological interactions have emerged from previously non-interacting components. Although physiological mechanisms are not in reproductive competition with each other as social interactions are, one similarity between social and physiological cooperation is that in both circumstances synergistic interactions emerge from statistically unlikely combinatorial relationships before any functional advantage is exhibited. The relevance of these cases to our present problem is that functions depending on the interaction of distributed components require those components to co-occur reliably. Therefore, irrespective of whether the problem is the prevention of a synergistic combination of phenotypes from becoming dissociated, or the defence of codependent individuals in a social group from defectors, the combinatorial interdependency itself must come under selection. For this to happen, the synergistic interaction must emerge and persist in a sufficiently robust manner.

This poses what we will call the ‘Secretariat problem’ (named for a horse that was a spectacular Triple Crown winner a few generations back). Though bred from the same stock as many of the horses he competed against, Secretariat seemed to run effortlessly away from the competition. The traits brought together in his breeding had produced an unprecedented synergy, resulting in just the right balance of strength, body proportions, metabolism and coordination to be an ideal racehorse—every breeder’s dream. But breeding Secretariat would not produce an offspring with this same synergy of traits, because sexual reproduction reshuffles the combination and passes on only 50 per cent of the relevant genes to be mixed with those from a mate in his progeny. So, whether in groups or in individuals, the emergence and evolution of high-level synergistic functions depends on the possibility not merely of ‘discovering’ a reciprocal complementarity among traits, but having this
condition occur with sufficient reliability for selection to emerge with respect to it.

Thus, while we do not dispute the importance of natural selection for the stabilization of the synergistic interdependency of cooperatively acting individuals in a group, we will argue that such interdependencies must arise and be regularly present before natural selection can begin to shape and stabilize their supportive conditions. We hypothesize that—counterintuitively—this requires a relaxation of selection. Below we will show how relaxing selection pressures, as demonstrated in the ‘evolution’ of socially acquired song in a domesticated finch and in the evolution of dietary vitamin C dependency in primates, can lead to the emergence of complex functional interdependencies that may become subject to stabilization and further shaping by natural selection. In these cases relaxation of selection produces degradation of the autonomy of some function which leads spontaneously to dependency on a more distributed realization of that function—a kind of addiction—and out of this a complex and codependent function can arise. Invoking a similar mechanism of relaxed selection, self-organization of current behaviours, and a reintroduction of natural selection, we will suggest a possible mechanism for the generation of altruistic-like behaviours.

**COMPLEXIFICATION OF BIRD-SONG**

Recent work examining the neuroanatomy of song-learning in birds has shown some unexpected effects that we believe exemplify the results of relaxed selection (Deacon 2009). Kazuo Okanoya (2004) has studied the singing behaviour of the Bengalese Finch, which has been domesticated for 250 years in Japan. Breeders have kept documents of their breeding process, so we know that this bird was not domesticated for its song but was bred for traits such as coloration and ability to breed in captivity. Okanoya has also studied the finch’s wild cousin, the White-backed Munia. One of the major differences between the two species is that the White-backed Munia has a very stereotypic song, which means that song structure is very predictable in that song element A is always followed by song element B. In other words, the transition probability between song elements is nearly 1.0 (completely predictable). The Bengalese finch has a song that is more complex than its wild cousin in three ways. First, the transition probability between song elements has equalized, which means that the predictability of the next song element in a singing bout has
decreased significantly, resulting in considerable variability. Second, the song of a Bengalese finch is strongly influenced by songs sung by other Bengalese finches during its development, whereas White-backed Munia songs are produced irrespective of social influence. Third, Okanoya found that the number of forebrain structures and the complexity of the neural connections involved in song production in the Bengalese finch is greater than the relatively simple motor output found in the White-backed Munia. The White-backed Munia has essentially one forebrain nucleus (the nucleus RA), providing the motor output controlling song production. The Bengalese finch, by contrast, depends on several different forebrain nuclei in addition to RA for the acquisition and control of song.

It has generally been assumed that bird song complexity, like other display behaviours, increases as a function of the importance and intensity of sexual selection in a species. Likewise, it is believed that complex functional organization of a physiological function—such as a complex, context-sensitive, coordinated behaviour and its neurological substrates—can only result from intense selection favouring this capacity. But in the case of Bengalese finch domestication, there appears to have been neither artificial nor sexual selection on singing behaviour, nor selection favouring complex reorganization of this brain function. This poses a conundrum for more traditional neo-Darwinian accounts: how might the Bengalese finch's abilities have arisen so rapidly (250 years is a mere blink in evolutionary time) without intense and specific artificial or natural selection favouring these consequences? We suggest that the breeding process shielded singing behaviour from the effects of selection that were present in the wild (a ‘masking’ of selection), causing its highly constrained structure and motor control to degrade by a process of genetic drift (Deacon 2009). This degradation is what we believe to be responsible for allowing song complexity to increase, song structure to become dependent on experience, and brain control of song to become more distributed.

Much of the background research on the song development and its neural control was pioneered by Fernando Nottebohm and colleagues (Nottebohm 1970, 1980, 1996). He found that if birds with stereotyped songs were deafened at hatching so that they could not hear either their own singing or the singing of their conspecifics, they would still sing a crude version of their species' subsong at puberty. The notes were distorted and in some cases only vaguely resembled the appropriate note, but there was still some resemblance to the species-typical song. Thus these birds have an internal bias to sing particular notes in particular
sequences. The motor template of their song is highly constrained and is under strong stabilizing selection that requires little outside influence to maintain, though being able to hear oneself sing does matter. This is supported by comparison of deafened birds’ singing to that of normal birds raised in isolation. While isolated birds could not hear other birds, they could hear themselves sing and as a result they produced notes and song sequences that were much more like those of normal, socialized birds, demonstrating that the innate song template is effectively distributed to both auditory and motor systems. In species that depend more on social learning for normal song development, still other forebrain nuclei are critical. These include brain structures contributing pre-motor and striatal-like motor learning functions (including most critically, the nuclei designated HVC, iMAN and Area X). While these structures play a small or non-existent role in species with stereotyped song, they increase in importance in species engaging in complex song learning and song production. So although all these brain structures and their interconnection exist in both social learners and stereotypic singers, they only seem to play a significant role in song behaviour in the species that acquire a normal song by listening to other singers. In these latter species, often there are also differences in these brain structures and their connections that appear to be correlated with selection augmenting their functioning.

How could relaxation of selection, at the hands of breeders interested in feather coloration, have produced effects analogous to those undergone by complex song-learning birds? We are not suggesting that new brain structures emerge, that these many nuclei become augmented in their functionality, or that a series of new neural connections is made in this process. We merely argue that the existing structures and their direct and indirect inputs to the nucleus RA can begin to have an increased influence on this song output nucleus as its specificity of function degrades.

We suggest that this change in brain function is a result of a shift from a template-based song that is highly constrained to mechanisms intrinsic to the nucleus RA to a learned song with many more inputs affecting the nucleus RA. Learning is a distributed function that requires strong links across sensory and motor modalities and their memories. For this reason, learning cannot reside in a single nucleus. We suggest that relaxation can occur in multiple ways, one of which is through domestication as in the Bengalese finch example. Due to the effects of long-term breeding that masked the selection pressures typical of life in the wild, the song template of the Bengalese finch was no longer under strong stabilizing selec-
tion. In the wild, we would expect that aspects such as predation and sexual selection play a role in stabilizing the song template, and the relative autonomy of nucleus RA control of song. With breeding comes a relaxation of those constraints so that selection no longer plays a role in maintaining tight constraints on the functional autonomy of the nucleus RA. As the integrity of the RA-based template degrades due to the effects of drift, the inputs to RA from other structures change their effective weighting and can begin to exert influence on the song template. With weakened intrinsic constraints on song structure, various extrinsic influences, both from other brain functions and from indirect environmental influences, can begin to influence song. Thus both the flexibility and the conditionality of song structure with respect to other factors can begin to emerge.

Since these other systems are themselves serving complex functions that have evolved for various other reasons, these influences are not merely random but carry with them some trace of these functional consequences. As a result, novel coupling between singing and other functions becomes more likely. Therefore, despite emerging irrespective of selection on any synergistic function, synergistic interactions may be more likely to result than by chance alone. The tendency for epigenetic processes to compensate for changes in organization due to damage or mutation altering typical anatomical features may also play a role in ensuring that the resulting neural outcome is functionally well integrated.

The point of this example is to show how relaxation of selection pressures can allow for the generation of variation through drift that can lead to self-organizing effects with organized functional consequences, even though functional correspondence of these changes with the environment is not shaped by selection (for more details see Deacon 2009).

**LOSS OF ENDOGENOUS VITAMIN C PRODUCTION**

Another way that this relaxation effect can occur in the wild is through a functional duplication. As an exemplar of this, we turn to something relevant to us—our addiction to fruit. Among mammals, anthropoid apes are some of the few that lack the ability to endogenously produce ascorbic acid or vitamin C (Chatterjee 1973). To better understand this, researchers in Japan examined the gene for the final catalyst in the production of ascorbic acid, called L-gulano-lactone oxidase (GULO), in rats (Nishikimi et al. 1994). They used this gene sequence as a probe to
search for a homologous GULO gene in humans, and demonstrated its existence, albeit in a greatly degraded form. In humans, this once-functioning gene has accumulated many loss-of-function mutations such as the deletion of coding segments (exons) and the insertion of ‘stop’ codons, making it a pseudogene.

This poses an interesting problem. How can the degeneration of a gene with a necessary functional product, gain a foothold within a lineage? Selection on the essential ascorbic acid in the body is maintained, so how can mutations that occur which render the GULO homologue useless not only occur, but spread throughout the lineage?

In part, the answer lies in the evolutionary timing of this genetic degeneration. We know from phylogenetic research that the GULO mutations date back to approximately 35 million years ago. A series of other primate morphological changes began to take place at roughly the same time, such as the development of colour-vision and changes in tooth structure to better handle frugivory. We suggest that if primates, 35 million years ago, are able to eat foods rich in vitamin C regularly, then genetic mutations that result in loss-of-function of their GULO catalyst will not affect their survival and reproduction. In other words, the change to frugivory does not begin as a functional adaptation because fruit is not necessary to the diet, although it may be a plentiful resource. In this sense, the early stage of fruit-eating can be considered facultative. However, as frugivory becomes habitual and is maintained over evolutionary time, it will mask selection that would otherwise maintain the genetic mechanisms necessary for endogenous production of ascorbic acid. This will allow the GULO gene to accumulate loss-of-function mutations, and consequently the lineage will become forced into maintaining frugivory in compensation. Currently, primates obtain vitamin C from dietary sources such as fresh fruits and vegetables. Transport and storage of foodstuffs are not significant factors when vitamin C is endogenously produced, as it is available at steady levels. If, however, it must be obtained purely from dietary sources, then the lack of storage means that the external sources of vitamin C must be relatively constant throughout the year. Given the importance of vitamin C, we can be fairly certain that there has been continuous selection on its antioxidant function. Therefore, when the gene for GULO became a pseudogene in the anthropoid primate lineage, primates became forced to maintain a frugivorous diet because of the negative reproductive consequences for those that do not maintain healthy levels of ascorbic acid.

In this example, something that was entirely endogenous to the organ-
ism has become fully 'off-loaded' onto the environment. An animal must either produce vitamin C endogenously, or acquire it extrinsically. Unlike bird song, vitamin C foragers are entirely dependent on acquiring vitamin C from their environment. In this sense there is a dependency roughly analogous to an addiction. It is an addiction in that it is reached while under constant selection. Unlike the relaxation of selection on Bengalese finch song, the function of ascorbic acid is not made irrelevant by its availability in fruit. There is merely a redundant way that this function can be fulfilled, one endogenous and one extrinsic. This redundancy could be the source of relaxation of selection on either source, but one—endogenous synthesis—is more susceptible than the other as mutations to the primate GULO gene do not negatively affect health and reproduction if the function can be met by eating enough fruit to maintain appropriate ascorbic acid levels in the body. Therefore it is not relaxation of selection on ascorbic acid function, but on the maintenance of constraints on endogenous ascorbic acid production that is occurring. Furthermore, whereas, periodic irregularities of frugivorous foraging behaviours can be easily redeveloped, functional degradation of the GULO genetic sequence can only be recovered with a very low probability inverse sequence of point mutation changes.

Unlike the complexification of song structure and control in the Bengalese finch, which was a spontaneous side-effect of degradation, the persistence of function in the case of the degradation of vitamin C synthesis creates a context for unmasking selection on other functions. Because extrinsic vitamin C is not as reliable as endogenously produced vitamin C, breakdown of endogenous synthesis and dependence on a dietary source can be a source of reintroduced selection affecting any adaptations that help to maintain this extrinsic source. These probably include the evolution of three-colour vision, changes in tooth structure, digestive adaptations, metabolic changes and probably many other primate-specific adaptations, all of which would have increased the reliability of access to and utilization of dietary vitamin C (Deacon 2009). Thus evolutionary addiction to extrinsic vitamin C probably unmasked selection on a variety of phenotypes not previously under selection for anything to do with this function, but which have subsequently come to function as an integrated suite.

The phenomenon of relaxation of selection is relevant to the evolution of altruism because it provides an evolutionary mechanism whereby codependent relationships can develop and become integrated. Below we argue that reciprocally altruistic behaviours can also be understood as a
form of codependence, and that the logic of relaxation of selection, degeneration and addiction, and re-distribution of selection can be applied to the problem of altruism in a way that complements earlier theories.

**IMPLICATIONS FOR ALTRUISM**

Taking the relationship between relaxed selection, reorganization and natural selection into account, let us reconsider the problem of explaining the evolution of altruism and its co-evolution with cheating behaviours. Earlier studies assuming the ubiquity of natural selection have demonstrated a number of ways that altruism can be maintained across generations despite being faced with cheating strategies. Presumably these various strategies evolved to overcome the challenge of cheating and so would have evolved as a consequence of a prior rise in altruistic behaviours and the presence of cheaters. The question that is not well addressed by these theories is how altruistic and pro-social behaviour can arise and become widespread in a population prior to the evolution of mechanisms to defend against non-cooperative and cheating behaviours.

What evolutionary mechanism can lead progressively from a non-cooperative state to cooperation before there are mechanisms for its maintenance via selection? Unless we invoke the unprecedented and sudden population-wide appearance of cooperation, we are forced to show how every incremental move towards increasing levels of cooperation within a population is more effective than prior non-cooperative behaviours. This raises a particularly difficult problem, because the shift from autonomy to codependence is at every stage susceptible to invasion by non-cooperators, and at any one moment the two strategies are mutually exclusive.

We argue that there is another way of dealing with the problem of competition, by removing the source of the competition. This is because cheating and various forms of cheating defence have evolutionary consequences only if they provide reproductive advantage over not doing so. When selection is removed, so are the adaptive values previously placed on these behaviours, and cheating, hoarding, competing over resources etc. lack differential reproductive consequences. Selection gives value to phenotypes by determining their fitted-ness with the world. Relaxing selection decreases the constraints on what counts as fitted-ness.

Although there are probably multiple ways that relaxation of selection
can lead to the diminution of non-cooperative behaviours we will explore only two: a change in environment that masks selection on certain competitive traits and the appearance of a redundant substitute for a competitive adaptation.

Consider a situation where individuals must compete over resources because they are insufficient to sustain the entire population. If there is a change in the environment such that food becomes over-abundant, there will be relaxation of selection on competition over food. In this case, individuals who remain competitive over food do not gain with respect to reproduction and health over those who are non-competitive. The result of prolonged reduction in the stabilizing selection that previously maintained genetic predispositions to engage in food competition will be degradation and drift of those traits and their genetic supports. Thus, over time, relaxation of this selection pressure would cause the behaviour patterns of individuals to tend towards less and less competition with respect to food. Resource-defence behaviours such as hoarding, territory defence, aggressive displacement of competitors and so forth, would no longer confer any reproductive advantage. Although relaxation of selection only has an indirect effect on the possibility of the emergence of cooperative behaviours, by removing the advantages of maintaining competitive behaviours it significantly increases the likelihood of cooperation emerging and spreading in a population. Furthermore, relaxation of selection on resource competition could potentially also be an indirect source of selection against competitive adaptations if these diverted time and energy from other reproductively important tasks and exposed the actor to possible damage.

Though degradation and drift are probably more likely than specific selection against competitive adaptations under these conditions, neither mechanism explains how new pro-social behavioural tendencies might be predisposed to emerge: they merely relax selection against them. Is there reason to expect more than just a permissive effect? In the examples of finch song and vitamin C adaptations discussed above, we observed that synergistic interactions were actually facilitated. Is something analogous possible in the case of social behaviour?

In the example of prolonged relaxation of food competition, competitive predispositions and related adaptations will devolve to a degraded state, while the variety of non-competitive behaviours would proliferate in the population. We can imagine that this would also include various degrees of egalitarian behaviours related to food, such as food sharing among both kin and non-kin and tolerance of multiple individuals feed-
ing side by side without threat. Even if none of these behaviours makes any reproductive difference, the generation of ‘new’ behavioural variants can in effect ‘explore’ potential functional possibilities that could not be sampled previously. For example, adaptive options that were previously blocked or limited by the need to compete may now become subject to selection. There might be advantages for individuals who want to be near others for predator defence or temperature maintenance, for example. Such advantages would have been unrealizable in a context of intense competition over resources, but masking selection on this one feature will tend to unmask an array of selective differences in the population that were effectively ‘below the radar’ as long as competition was important. In other words, if new domains of selective advantages are unmasked by the removal of this competing selection pressure, then variations in social predispositions within the population that tended to be suppressed in the context of competition can now provide a source of variation upon which novel forms of fitted-ness can emerge. Moreover, since many of these variants will share in common features that were to some degree or other incompatible with competitive strategies, they will also be more likely to share non-competitive attributes in common and in this way be more likely to interrelate synergistically with one another (much as in the cases of finch brain structure interactions and vitamin-C-acquiring adaptations). So we need not merely assume that groups simply happen to be cooperative and then ask how they could maintain this state against cheaters: we can now begin to explore ways in which cooperation can incrementally emerge.

Here we have only described one context in which relaxation of selection might lead to the emergence of cooperative behaviours. There may be many others: for example, situations where social living is enforced for other reasons, such as when rookery sites are limited, food sources clumped, temperature must be maintained or predators defended against, and probably many more. However, the relaxation effect is only part of the story because selection probably never remains entirely relaxed. The degradation of competitive behaviours is only one consequence of relaxation of selection: group living may mask many other adaptations for living non-socially. So the availability of close group members can result in the degradation of the capacity to live autonomously. Analogous to the evolution of vitamin C dependency, merely the presence of multiple individuals acting as a buffer against environmental challenges such as predation can lead to degradation and an addiction to group living. Such an addiction will specifically favour adaptations for maintaining social cohe-
sion, even if there is some reproductive cost. This can further lead to selection for behavioural adaptations to minimize or police against potential sources of group disruption.

As discussed above, there are many reasons why individuals might be brought into close proximity with one another. Moreover, changes that result in the clumping of individuals into groups that persist over many generations may relax selection on the maintenance of those adaptations critical to solitary life. One factor that is often significantly affected is the probability of being preyed upon. Where individuals tend to be near one another, a likely common side-effect is a change in strategies of predator defence. If a predator normally targets lone, isolated individuals, there will be intense selection favouring the abilities to detect, escape from and ward off the predator, resulting in individual defences against predation that can be quite well developed. For example, vigilant monitoring of the surroundings is strongly selected for, because if an animal notices the predator before it is too close it may have a better chance at escape or defence.

In highly social conditions, where individuals are constantly and reliably near one another, a predator attack has an intrinsic ambiguity and uncertainty as to the intended target. In clustered groups, when an individual animal detects a predator it cannot necessarily determine whether it is the target, and so must react to diminish the chance of being the target and of being caught. Means of doing so are likely to be quite different in a social context than when solitary. For example, solitary animals cannot rely on the possibility of others being targeted, their monitoring of the surroundings or on the startle reactions of others to serve as an alert, nor on the additive effects of many individuals’ defensive behaviours. But if circumstances consistently cluster individuals together, the possibility of other individuals producing responses that are redundant to those an isolated individual would produce can lessen the selection pressure to maintain these more self-reliant predator defences.

For example, actively monitoring the surroundings for predators might be well developed in a population of independently foraging diurnal animals because those that spot predators from afar are likely to reproduce more reliably than those that do not. But in social contexts, where the target of predation is ambiguous and unclear to the prey animal, individual monitoring of the surroundings will be less critical. Many eyes periodically looking up from foraging etc. to scan the surroundings will diminish the amount of time any one individual needs to be doing so and yet increase the potential of early predator detection. In addition, the
The startle response and escape tendencies of other group members can be relied on when a predator is detected, and these can evolve to become surrogates for one's own constant attention to the possibility of predation. In addition, there are many more potential targets and potential defenders in a social group. We see this in examples of eagles attacking small monkeys that are feeding in trees and herd animals feeding in large numbers on the savanna. Increased prey densities will reduce the probability that any particular individual will be caught in a given attack. Higher densities allow individuals with more socially dependent predator detection or evasion abilities to enjoy both a greater degree of freedom from predation and some lessening of the costs which defensive adaptations would otherwise impose (in terms of time and energy diverted from other needs).

As we saw in previous examples, even partial masking of selection can cause degradation of phenotypes so long as the masking is relatively stable and reliable over a significant number of generations. In this sense, the side-effects of population density are similar to the effects of ubiquitous dietary vitamin C, in that partial protection from predation supplied extrinsically is analogous to an essential nutrient being available extrinsically. As masked selection for vitamin C led to degradation of intrinsic production capabilities, so masked selection on specific predation defences could lead to degradation of those most effectively masked by social conditions. Finally, degradation of the autonomous function in both cases can lead to increased dependency on the extrinsic support and an unmasking of other traits that play some role in maintenance of this offloaded function.

Consider the situation that would exist subsequent to the evolutionary degradation of autonomous predator defence capabilities as a result of long-term evolution of social foraging. Individuals with a slight reduction in the tendency to constantly monitor the presence of predators or with slightly degraded ability to physically ward off a predator, will be at a decided disadvantage if separated from the social group. This will make it extremely costly for individuals to forage outside a social group, and thus will create a context that makes group break-up a decided danger. In other words, the degradation of non-social protections can lead to a corresponding increase in need to stabilize those social contexts, and thus to selection favouring any behavioural variations that tend to minimize this possibility.

This suggests only one way in which a transition from solitary foraging to social living can lead to addiction to social living. As a result, there will be a shift from selection on individuals’ predator defence behaviours
to behaviours that take advantage of social redundancy and that at the same time will lead to selection on any features that contribute to group maintenance. These may include both affiliative and social monitoring behaviours such as those that have been identified in other analyses (discussed above), e.g. reciprocity, cheater defence, etc. But since the masking effect of groups affects both the development of cooperative behaviours and the degeneration of non-cooperative behaviours, it can also lead to conditions that favour other non-cooperative behaviours (e.g. cheating), which must be defended against. For this reason, it is not surprising to find both a social hierarchy and social cooperation side by side in nature. The competition found in social hierarchies can be seen as both remnant of earlier autonomous competitive behaviours (which never fully degraded and are now limited by the necessity of group living) and an evolutionary consequence of cooperation. The various forms of ‘cheating’ that evolve after group-living addiction will only confer selective advantage once codependent interactions amongst group members have been established. Thus the importance of degeneration of strong autonomy is that it can lead to addiction to social living, and this can contribute to the evolution of both anti-social and pro-social behaviours.

CONCLUSIONS

In this chapter, we have argued for the existence of a previously under-appreciated factor in the evolution of pro-social behaviours: the degradation of functional autonomy due to relaxed selection conferred by group living. This is not proposed as a mechanism in competition with other accounts of the evolutionary stabilization of altruistic adaptations, but as a mechanism that can explain how such stable cooperative adaptations might have arisen from previously non-cooperative conditions. This approach was suggested by the analogy between social cooperation and other intra-organismic synergistic functions. The demonstration that conditions of reduced selection resulting from redundancy effects can eventually lead to a redistribution of function and an increase of codependent relationships in physiological evolution is here generalized and extrapolated to apply to certain group living contexts. In other words, we argue for a parallel logic behind the evolution of synergistic interdependencies in both organismic and social domains.

What is unusual about this hypothetical mechanism is that it is not strictly Darwinian, but instead depends on the reduction of selection...
pressures in some domain and an ensuing degradation of function. Basically, it is an argument for the emergence of pro-social adaptations in defence of social dependency, and it explains the emergence of social dependency as a consequence of the degradation of functional autonomy. This particular account of a mechanism that can lead to the emergence of codependency from a condition of autonomy does not exclude other possible mechanisms, including the serendipitous emergence of conditions where group effort (such as in the social spiders discussed above) can provide advantage over individual effort. However, we would predict that the transition into such relationships will be more likely under conditions of relaxed selection; e.g. non-zero sum contexts. In this respect, this hypothesis is consistent with earlier theories, but additionally contributes a source of selection pressures favouring the evolution of group-maintaining adaptations via a kind of addiction to group living.

Based on these considerations, we predict more generally that higher-order units of evolutionary adaptation arise only after there has been a loss of functional or individual autonomy and consequent selection to maintain the stability of codependent synergies. This should be as true for intra-organismic synergies as inter-organismic synergies, and should even apply to the emergence of cultural adaptations supporting social cohesion which have arisen via social evolution.

References