

Social intelligence, human intelligence and niche construction

Kim Sterelny*

*Philosophy Program, Research School of the Social Sciences, Australian National University,
0200 Canberra, Australian Capital Territory, Australia and Philosophy Program,
Victoria University of Wellington, PO Box 600, Wellington, New Zealand*

This paper is about the evolution of hominin intelligence. I agree with defenders of the social intelligence hypothesis in thinking that externalist models of hominin intelligence are not plausible: such models cannot explain the unique cognition and cooperation explosion in our lineage, for changes in the external environment (e.g. increasing environmental unpredictability) affect many lineages. Both the social intelligence hypothesis and the social intelligence–ecological complexity hybrid I outline here are niche construction models. Hominin evolution is hominin response to selective environments that earlier hominins have made. In contrast to social intelligence models, I argue that hominins have both created and responded to a unique foraging mode; a mode that is both social in itself and which has further effects on hominin social environments. In contrast to some social intelligence models, on this view, hominin encounters with their ecological environments continue to have profound selective effects. However, though the ecological environment selects, it does not select on its own. Accidents and their consequences, differential success and failure, result from the combination of the ecological environment an agent faces and the social features that enhance some opportunities and suppress others and that exacerbate some dangers and lessen others. Individuals do not face the ecological filters on their environment alone, but with others, and with the technology, information and misinformation that their social world provides.

Keywords: evolution of cooperation; niche construction; social intelligence; division of labour; strong reciprocity

1. THE EXPLANATORY TARGET

Our australopithecine ancestors had approximately chimp-sized brains and a technological toolkit that was not much more complex than that of contemporary chimps. Nor is there reason to suppose that their social lives were more complex than those of surviving great apes. Over the next 4.5 Myr, a lot happened. The geographical and ecological range of these primates expanded greatly and diets changed. Hominins depended increasingly on meat and high-value plant foods, and processing food after its acquisition became increasingly important. In particular, cooking detoxified much plant food, reduced the physical stresses of chewing and released more nutrients (Wrangham *et al.* 1999; Wrangham 2001). Hominin technology increased greatly in complexity and variety. Hominin social life became obligatorily cooperative, as the acquisition of crucial resources came to depend on a division of labour. Beginning with *Homo ergaster*, expansion into new habitats began. As this expansion continued, it co-occurred with, and sometimes depended on, an expansion of expertise and cooperation. The deserts and tundras into which early sapiens and its immediate ancestors expanded were not otherwise survivable. Our ancestors of 4 Myr

ago lived in a world as they found it. We have transformed our physical, biological, social and informational environments. Humans of one generation bequeath an engineered world to the next generation, who often alter it further before transmitting it to their successors (Odling-Smee *et al.* 2003; Sterelny 2003). With these ecological, economic and cognitive changes, a transformation occurred in hominin morphology and life history. Humans are less sexual dimorphic than australopithecines, but we are larger, with relatively larger brains. Our cortical regions, especially, have expanded, despite the expense of these tissues and the life-history price they carry with them. We live longer and are dependent on adult provisioning longer. We have become a singleton. Through most of hominin evolution, there were a number of hominin species extant at any one time, but not now. There is certainly something to explain. All species are unique, but some, including ours, are more unique than others (for a recent overview of hominin evolution, see the five linked entries on hominid evolution in Pagel 2002).

The social intelligence hypothesis is one candidate explanation of this extraordinary transformation. This idea has been pressed into service to explain the distinctive features of primate, great ape and human intelligence; its service in this final role will be my concern. The social intelligence hypothesis dates to papers by Jolly & Humphrey (Jolly 1966; Humphrey 1976); it became central to theories of cognitive

*kim.sterelny@vuw.ac.nz

One contribution of 19 to a Discussion Meeting Issue 'Social intelligence: from brain to culture'.

evolution as a result of two very salient collections edited by Byrne & Whiten (Byrne & Whiten 1988; Whiten & Byrne 1997). The crucial idea is that the sophistication of primate (ape, human) intelligence is an adapted response to the complexity of the social environment in which primates (apes, humans) act. Different versions of the social intelligence hypothesis focus on different dimensions of this complexity. Robin Dunbar, for instance, emphasizes the pressure social stress management imposes on an animal's time budget as group size increases (Dunbar 1996, 2003). Humphrey's original paper emphasizes competitive manoeuvring: the anticipation and counter-anticipation of social chess as agents compete for scarce resources in generationally complex environments. Jolly's much earlier paper centres on socially mediated learning rather than Machiavellian manoeuvring.

The plausibility of these models of hominin evolution depends on two linked thoughts: on intuitions about the sheer complexity of human social worlds, and the idea that there is a feedback loop between human cultural and cognitive complexity that drives the elaboration of each. Human sociality is spectacularly elaborate, and of profound biological importance. Our social groups are characterized by extensive cooperation and division of labour, with different individuals specializing in different tasks. There is cooperation within the family: males invest in their (presumptive) children, and there is often extensive cooperation, resource sharing and division of labour between sexual partners. There is intergenerational cooperation, too, when adults provision children and when middle age women forgo reproduction to invest instead in their younger children and their grandchildren. These economic and sexual forms of human sociality are interwoven with our complex systems of communication and affiliation. We are ultrasocial.¹

There is much plausibility in the suggestion that human social worlds are extremely complex, and McShea has shown how to make this idea precise (McShea 1996; Anderson & Franks 2001; Anderson & McShea 2001; Anderson *et al.* 2001). In McShea's framework, we measure complexity in two dimensions. Social groups are hierarchically structured: individuals are embedded in families, extended families, sometimes in clans or villages as well as tribes and in tribal alliances. Hence, one dimension ('vertical complexity') measures the depth of the hierarchical organization an agent experiences. Another dimension 'horizontal complexity' measures size and differentiation at a level. As Dunbar has emphasized, numbers matter, in part because the number of relationships in a group grows much faster than group size itself (very much faster, if every member of a group interacts significantly with every other member). But differentiation matters too. The more the individual agents differ from one another, the more complex the agent's social world. These differences may be in expertise, economic role, physical capital, dispositions to cooperate or not and mate choice and life-history strategies. Vertical complexity measures structure between the level of individuals and that of the group as a whole. In a vertically simple environment, the social world consists of just individuals and the group as a whole. Add kin

groups, clans and totem groups, economic/ecological teams—for instance, the cooperative whale-hunting groups studied by Alvard (Alvard 2002; Alvard & Nolin 2002)—and the social environment becomes vertically complex. For an agent's prospects will depend in part on his interactions with these proto-institutions. Thus, the complexity of an agent's social environment depends both on its horizontal and vertical complexity.

Given this framework, it is evident that there has been a massive expansion of the social complexity of hominin life. It is one thing to construct a mental map of an australopithecine band of 20, or so, individuals, with fairly homogenous technical and foraging skills but with (say) differing sexual politics (keep an eye on that just-subadult male). It is another to do the same for 150 individuals with quite varied technical and foraging expertise, and divided into kin groups and totem alliances. Recent hominin social worlds are not just large great ape worlds. They are more vertically complex, and they are far more differentiated.

The second feature of the social intelligence hypothesis is its identification of a putative feedback loop: an increase in social intelligence selects for yet further increases by increasing the complexity of the social environment. This feedback loop depends on a fundamental problem in human society: that of enjoying the benefits of cooperation without being exploited by others. Cooperation can be very profitable, because a group acting jointly can generate a higher return than the sum of each of them acting individually. Brian Skyrms' *The Stag Hunt* is a game-theoretic exploration of such synergies. Two hunters acting together can capture a stag, whereas each hunting individually can take only a hare apiece. Cooperation is favoured because a stag is worth more than twice a hare (Skyrms 2003). Collective defence, likewise, will typically be far more effective than individual defence. So there is a potential benefit to cooperation, but only if the costs of defection can be contained. For cooperative actions are not free, and the benefits of cooperation often do not fully depend on every agent paying the full cooperation cost. Collective defence can still be successful even if one defender lurks in the rear. These circumstances generate a temptation to avoid the costs of cooperation while collecting the benefits. For cooperation to be stable, the costs of defection need to be contained. Machiavellian versions of the social intelligence hypothesis focus on the cognitive challenge of managing cooperation in an environment in which defection is a threat. The feedback loop between individual capacity and social complexity makes the social intelligence hypothesis a niche construction hypothesis: the evolution of hominin cognition depends on features of the environment that hominins have created themselves.

In such an environment, the socially adept agent must calculate and police reciprocal bargains, scrutinize signals for their honesty, decide on her own disclosure principles, negotiate alliances and calculate whether it is worth defecting herself. These challenges lead to a feedback loop between individual cognitive capacity and social complexity. A crucial element of this model is that an increase in individual cognitive sophistication generates further social complexity. That

link is well-motivated in Machiavellian versions of the social intelligence hypothesis. For increases in cognitive sophistication bring improved strategies of deception, counter-deception and cabal formation. This is the *Machiavellian loop* through which social chess generates social complexity. This mechanism was clearly identified by Humphrey, who wrote of the feedback loop as a ratchet, a 'self-winding watch to increase the general intellectual standing of the species' (Humphrey 1976, p. 311). For a recent version of this view, see Flinn *et al.* (2005). The link is less well motivated if social worlds are mostly cooperative. For in that case, the challenges of social life mostly consist of coordination problems, and increases in intelligence can make coordination easier. Signals become less ambiguous, plans more explicit and coordination can be organized by negotiating norms and customs. The social environment can thus become more informationally transparent, and selection for further intelligence would be self-limiting.

Contemporary social life can make the Machiavellian loop seem more central to human cognitive evolution than it really is. For the problems of deception and defection are far more serious in contemporary mass societies than in the social worlds in which the cooperative framework of human life evolved. Mass societies are anonymous. Many interactions are one-off, with strangers. Communication is often disembodied and decontextualized, via arms-length media. Perhaps, most important of all, agents are highly mobile, making a defect-shift strategy available. The attraction of that strategy has been boosted by the invention of money. Money may not be the root of all evil, but it facilitates the defect-shift strategy by making resources extremely portable, and by making immense gains from a single interaction possible. These are all novel facets of human worlds. We cannot project our institutional policing mechanisms back in time to explain the stability of hominin ultrasociality in the face of defection. But nor can we project the contemporary risk back in time as a threat to that sociality. Hominin ultrasociality was assembled in smaller and far from anonymous social worlds; and social worlds in which shifting between groups was not a routinely available, low-cost option.

Even on these more intimate scales, defection is a serious threat, and containing its costs takes cognitive investment. But I shall argue that the Machiavellian loop rests on a misconceived view of the evolution of cooperation in hominin life. Cooperation did not survive and expand in hominin worlds as a result of individuals vigilantly policing reciprocal exchanges of cooperative benefit. It did not evolve as a result of each individual efficiently scrutinizing their rate of return from cooperative exchanges in iterated prisoner's dilemmas, using the threat of withdrawing cooperation to keep others honest. Human cooperation has been seen too much through the lens of reciprocal altruism modelled as an iterated prisoner's dilemma. As with the social intelligence hypothesis, I shall suggest a model of human evolution in which niche construction plays a central role. In altering their social, biological and technological environment, we transformed the selective forces acting on our lineage. But I shall suggest that

crucial early forms of cooperation were hunting and defence coalitions. These do raise defection problems, and hence generate a commitment problem. An agent should join a defence coalition only if he is sure others will join too. But since the benefits of cooperation, if achieved, are delivered immediately and since participation in a cooperative alliance, when it happens, is typically unambiguous, the cognitive demands on partner choice and partner assessment are contained. Moreover, traditional forager societies have been organized (and probably adapted) in ways that minimize the cognitive price of policing while still reducing temptations to defect. There is public information about the agents in these worlds, and that makes the problem of partner choice more tractable. Norms regulate cooperation: they reduce the calculative load on honest cooperators, and make defection, when it occurs, unambiguous. They thus make these small-scale social worlds more informationally transparent. Human psychology has evolved in conformity to that social organization. Most humans are *default* rather than *calculating reciprocators*: they enter social relations with the intention of cooperating if they expect other agents to do the same (Fehr & Fischbacher 2003, 2004). The cognitive cost of policing is not trivial. But social worlds in which there are cheap heuristics for detecting likely defectors, and in which most agents are default cooperators and which are organized to reduce temptations to defect are not dominated by a deception/counter-deception arms race. Or so I argue in §2.

I shall argue, instead, that the cognitive expansion of the later hominin was driven by positive feedback loops between social and ecological competence. As a consequence, the distinction between social and foraging domains has been undermined. For the great apes and, I assume, early hominins, that distinction is valid: the cognitive demands ecology imposes on great ape intelligence can vary independently of the demands imposed by sociality. Indeed, the great apes vary very considerably in their social lives: gorillas live in extended family groups; orang-utans live fairly solitary lives (though probably they are more social than was once supposed); and the two chimp species live in complex fission–fusion social worlds. But Byrne has argued that they face a similar kind of ecological challenge: they all depend on defended or elusive resources. As a result, they are all skilled foragers. Gorillas and orang-utans, for example, harvest plant foods that defend themselves with spines, thorns or stings. Eating them safely takes skill and dexterity: anyone who doubts this can try their hand at preparing stinging-nettle salad. In particular, Byrne argues that processing highly defended plant foods requires the mastery of an appropriate behavioural programme incorporating precision handling with bimanual role differentiation, a regular, sequential and arguably hierarchically organized task structure (Byrne 1997, 2003, 2004). In short, the great apes have expertise, and they have expertise as a result of ecological selection. Though social and ecological innovative capacities tend to covary with one another (Reader & Laland 2002), social and technological competence are more decoupled among the great apes than in our lineage.

We cannot draw this distinction for the later hominins, for they have evolved into cooperative technological foragers, and the social and ecological domains have fused. Our distinctive intelligence is not due to the complexities of our social lives, though those lives are complex. Nor is it due to the fact that our lifeways have long depended on information and technology-intensive resource harvesting. It is due to the fact that our working lives have become our social lives. Cooperative social environments can evolve if agents can solve two problems: those of the generation and distribution of benefit. To generate benefit, agents need to solve coordination and differentiation problems. For cooperation to be stable, the profit of cooperation has to be distributed in ways that maintain incentives to cooperate. In the evolution of cooperation literature, there has been an inordinate focus on the distribution of benefit. I shall argue, in §3, that the generation of cooperative benefit drove hominin cognitive evolution.

2. A MACHIAVELLIAN LOOP?

The evolution of cooperation has typically been explained as a form of reciprocal altruism and modelled in the framework of an iterated prisoner's dilemma. This framework makes Machiavellian versions of the social intelligence hypothesis plausible: cooperation seems both valuable and risky. In the right circumstances, cooperation can be very rewarding, and an agent who missed out on these rewards would be in real trouble, for example in many forager environments, hunting failures are frequent,² and cooperating hunters can insure one another against these failures. It makes sense for an agent who catches a pig to share, if he can be confident that his favour will be returned. For a pig is a large food package, but one that (in traditional societies) cannot be stored. The marginal value to the hunter of his remaining pig parts will decline as he and his family eat generously; so the last half of the pig will be much more valuable to those still hungry than to the successful hunter. In an environment in which one's own success is unpredictable, and not synchronized with the success of others, and in which one is likely to have a long history of interaction, cooperative food sharing is highly beneficial. So if families interact with one another regularly and if they are able to monitor one another's continued cooperation, the threat of withdrawing cooperation is likely to be important enough to make defection irrational.

On this model, cooperation is sustained (and occasionally fails) by the calculation of self-interest in a community of self-interested maximizers. Mutual scrutiny and the shadow of the future keep us honest. But we are always under selection to evade the scrutiny of others, thus gaining the rewards of cooperation without paying its full cost. Even more, we are under selection to ensure that others do not evade our scrutiny. And effective scrutiny is cognitively demanding (Stevens & Hauser 2004). Reciprocation obviously relies on identifying agents and representing their past actions, and these demands on memory become significant in multi-player interactions. Moreover, the cooperating agent needs to be able to judge his own

investment and an expected return on it from his partner. This task of assessing return on investment is made more difficult by the need to discount future benefits. The cooperating agent needs to be able to represent the temporal gap between investment and payback, and to apply an appropriate discount rate.

If this is the right model of cooperation and its evolution, it would be true that the increasing complexity of human social worlds, and the increasing cognitive complexity of other agents, would ramp up the cognitive costs of cooperation. But in the past few years, an alternative to this calculative model of human cooperation has been developed. This model consists of three elements: (i) humans are (mostly) *strong reciprocators*: they enter social situations disposed to cooperate if they expect others to cooperate in return, without this disposition being dependent on their expectation that cooperation is economically optimizing for them. Humans are typically default rather than calculative cooperators. Moreover, they respond to defection with punishment, not just withdrawal (Fehr *et al.* 2002; Fehr & Fischbacher 2003). (ii) Humans live in 'symbolically marked' groups: groups which have common and distinctive customs, norms and values. This population structure makes cooperation more stable by making defecting more expensive. Shifting between symbolically marked groups is often impossible and is never routine. Some symbolically marked groups are now large enough for agents to try a defect-shift strategy within such a group, but this is a recent phenomenon. (iii) Norms help solve coordination problems: it is easier to anticipate what others will do and what they expect of you. But they also help solve problems that arise through the distribution of benefit, for cooperation is often channelled through norms and customs. Norm-regulated cooperation, and especially of norm-regulated distribution of benefit, reduces the calculative burden of strong reciprocation. In regulated interaction, no one has to try to calculate the fair return of cooperative investment in a joint product, taking into account temporal discounts, differential contributions to success and the like. Even in a community of honest cooperators, a fair negotiation of every joint product would be difficult, time consuming and conflict generating. Norms disambiguate a social environment: in norm-governed interactions, what is expected of an agent is public knowledge. This helps a strong reciprocator: he or she knows what to do and what expectations he or she should have of others. And it makes defection more obvious. Someone who fails to conform to a norm is defecting: the violation of expectations cannot be explained as an honest difference in view as to the fair contribution to or from a joint effort. Norms make the social environment more transparent.

Thus, Bowles, Gintis, Fehr and their collaborators have argued that *strong reciprocation* is the distinctive form of human cooperation. In strategic interactions, strong reciprocators cooperate if they expect other agents to cooperate too, even though they could gain by defecting. Their cooperation is not conditional on the expectation that their cooperation has the highest economic reward of their available options. Strong reciprocators enter a social situation disposed to begin by cooperating; they respond to cooperation by further,

perhaps even enhanced, cooperation. They also punish failures to cooperate. They respond to defection not only by not cooperating in return, but also by punishment, even when punishment comes at a price and with no expectation of future benefit (Bowles & Gintis 2001; Fehr *et al.* 2002; Bowles & Gintis 2003, 2004; Fehr & Fischbacher 2003).

Experimental economists have revealed this behavioural syndrome by studying interactions in strategic games, where the experimental subjects had real gains and losses to make. It is striking that in these interactions, humans do not act like calculating cooperators: they do not cooperate if and only if they expect it to pay (for an overview, see Bowles & Gintis 2003), for example in a 'public goods game', N players simultaneously decide their contribution to a joint pool from an endowment. That joint pool grows (modelling the synergy of cooperation) and is then divided into N equal shares. Each agent keeps their non-donated contribution plus an equal share of the joint product. A calculating reciprocator would contribute nothing. A typical player contributes 50% of their stake in a one-shot game. But if the game is iterated, the donation declines to nothing over time. For the typical response is not universal, some defect. So agents reciprocate expected cooperation and only expected cooperation. The situation changes if communication and especially punishment are added to the game. In this form of the game, at the end of a round, agents can invest in punishment that reduces the take of defectors. If punishment is effective and not too expensive, agents punish, even when they will not interact with the punished player again, and that increases and stabilizes cooperation. Very strikingly, if subjects are allowed to choose between participating in a public goods game with punishment and one without (after experience), they almost all end up choosing a punishment game and cooperating maximally. When agents choose a game which allows punishment of defection, they contribute more of their stake to the common pool. They take the choice to enter such a regime to be an honest signal of willingness to contribute and to punish, and hence they ramp up their own contributions (Fehr & Rockenbach 2004).

This pattern is not an artefact of this particular game. Ultimatum and dictator games show a similar picture of our strategic dispositions. In the ultimatum game, player A proposes a division of a fixed resource to B, who can accept the proposal or decline it. If B declines the offer, both get nothing. If the interaction is one-off and anonymous, if both A and B were calculating cooperators, A would offer B the minimum possible fraction of the resource and B would accept the offer. In fact, most offers are between 0.3 and 0.5; about 50% of offers under 0.25 are rejected. A's knowledge that unfair offers are likely to be rejected constrains his strategy, but that is not the whole story (there is extensive cross-cultural research on this game; see Henrich *et al.* 2004). The dictator game is like the ultimatum game except B has no power to veto the decision. Even here, A typically offers B something. There is a lot of variation, but the average offer is about 0.25 of the stake. In the third-party punishment game, A and B play a dictator game. C observes and can

punish A, at some cost, if she so chooses. Again, if everyone were calculating cooperators, A would give B nothing, and C would never punish A. In fact, the less A gives B, the more the C punishes A. Agents respond to perceived unfairness by punishing it, so long as it is effective and not too expensive (Fehr & Fischbacher 2004). There is good reason to believe that human agents are typically strong reciprocators.

Strong reciprocation, Bowles, Gintis and Fehr all argue, itself depends on prosocial emotion. Agents are disposed to cooperate with other cooperators through some combination of affiliative and empathetic emotions. We cooperate because we know that we can identify with our partners in cooperation. And we cooperate through a sense of fairness and justice. Prosocial emotions induce an agent to act prosocially and to motivate punishment when others fail to act prosocially. They induce some mix of guilt/regret and shame when the agent himself/herself fails to act prosocially. The victim of defection might punish through anger and resentment. But third-party punishment must be based on judgement of unfairness, and motivated by anger (and even disgust) at violations of norms of unfairness.

Human ultrasociality depends on the fact that most humans are default cooperators, but not only on that: cooperation is supported by demographic structure. Throughout most of the species lifespan, humans have lived in relatively small, 'symbolically marked' populations. The signature of modern human ecology—extensive, regionally varied toolkits, the capacity to invade most habitats and spread geographically, a broad foraging niche—emerged in rough synchrony with archaeological signs of symbolic group marking, i.e. of groups identifying themselves and being identified by others by their distinctive norms and customs. An archaeological signature of ideology is inevitably much more ambiguous than that of ecology, but there is such a signature. Camp sites begin to show the use of ochre. We find stylistic variation in, and decoration of, tools. Totem-like objects appear in the record. The dead are buried, sometimes with grave goods. Later, there is clear evidence of cave paintings and the like. Collectively, this foraging and ideational complex is known as behavioural modernity, and it seems to have emerged gradually and roughly synchronically (though there is considerable debate about the extent to which it is a true linked package; Henshilwood & Marean 2003) in Africa between 200 000 and 50 000 years BP (McBrearty & Brooks 2000; Foley & Lahr 2003; Henshilwood & Marean 2003).

Norms often directly support prosocial action (Fehr & Fischbacher 2004). Human motivational mechanisms do not seem to have kept pace with our increased lifespan and capacities to plan. Even by our own lights, we too readily trade future harms against current pleasure. Norms incentivate our own preference functions: violating a norm against (say) drunkenly groping your superior's partner will have immediate and hence motivationally salient costs, not just distant disutility. But norms can also stabilize behaviour by making the informational environment of strong reciprocation transparent. Norms make explicit the requirements of reciprocity. In doing so, norms reduce the cost of

calculation among strong reciprocators, and by making the expectations of others unambiguous and explicit, they make failures to cooperate both salient and negatively marked.³ So norms can support adaptive action by cognitively limited agents (Boyd & Richerson 2001). Alvard's portrait of the Lamalera is a lovely example of norm-regulated division which solves coordination and division problems of this kind. When a whale is caught, it is divided into shares (anatomical parts) which then go to particular stakeholders, for example whole shares go to the crew, and there are further norms about how the crew's share is divided among harpooner, his assistant, the helmsman, the bailers and the rest of the crew. Likewise, craftsmen also receive shares as of right: these go to the smith, the sailmaker, the carpenter and the boat manger, in addition to any entitlement they may have qua crewmember (Alvard & Nolin 2002). Having norms of division of this kind is not unusual, for example in group hunts by Efe Pygmies, shares depend on specific roles in the hunt: the hunter who shoots the first arrow gets about 35% of the prey, the hunter who shoots second about 10% and the owner of the dog gets 20% (Gurven 2004, p. 557). Importantly, these divisions of the hunt often involve rewards to invisible members: to the Lamalera craftsmen and to those Ache who cut trails, carry game and provision the hunting party rather than foraging directly (Gurven 2004, p. 558).

Moreover norms, together with customs and other forms of social life that are distinctive of particular groups can play an indirect role in stabilizing cooperation. For the result of symbolic marking in a human population is divided into groups which tend to be internally homogenous while varying one from another. Furthermore, movement between such groups is restricted. These are conditions which make cultural group selection effective, and cultural group selection, presumably, will favour groups which police norms promoting effective coordination and cooperation (Sober & Wilson 1998; Boehm 1999). Moreover, individual level selection in favour of defecting from norms of cooperation will be weak. There will be no selection in favour of disobeying norms like those which regulate the division of a jointly caught whale. For violating these norms would incur punishment. If there is a temptation to defect, it will be defecting from paying the costs of punishing norm violation. But for those, the costs of punishment are likely to be low; perhaps very low. In a world that is already cooperative, some punishments cost little while effectively penalizing their target. Withdrawing social esteem and prestige are cheap punishments that impose a serious cost. Moreover, most of the population are strong reciprocators, so the cost of punishment is shared. Finally, punishment is rarely necessary because the threat of it is effective (Boyd & Richerson 1992). The individual cost of cooperation may well be very low; group selection in favour of cooperation will not be counted by strong individual selection in favour of defection. Thus, this demographic structure—populations divided into smallish groups, each group with a distinctive set of norms and customs—favours the evolutionary stability of cooperation.

Both iterated prisoner's dilemma and strong reciprocity models of cooperation share a common core:

their paradigm of cooperation is the sequential exchange of favours over time. I share some of my pig with you today; in two weeks I receive a chunk of armadillo from you. An alternative paradigm for the evolution of cooperation is collective action (Alvard & Nolin 2002). Agents generate a joint benefit acting together in hunting large game, in the coordinated harvesting of large amounts of small game, in collective defence and, perhaps, in coalitional enforcement of egalitarian social orders against would-be alpha males. Hunting coalitions, collective defence and (perhaps) enforcement coalitions are plausible early forms of hominin cooperation. These are examples of mutualistic interaction. And they sidestep the cognitive costs of policing reciprocity. If joint action is successful, the profit is shared jointly and simultaneously (and shared automatically, in the case of successful collective defence). Dividing the spoils after a successful buffalo hunt is not difficult. It is not delayed in time. The buffalo can be dismembered on the spot in circumstances in which each is monitored by all.

These are not pure coordination games in the sense of Schelling's *The Strategy of Conflict*; there is a temptation to cheat. The cooperation problem with a buffalo hunt is to manage coordination and wholehearted participation in the hunt itself. As with reciprocity over time, there is a defection threat to joint action, for it is very important to avoid the sucker's pay-off. You do not want to be the only agent standing your ground against the charging buffalo or the attacking predator. Frank (1988) has written impressively on the role of the emotions in solving the class of coordination problems; in signalling trust and trustworthiness. These emotions and their signals are difficult to fake, especially between agents who have interacted regularly (Frank 1988). Moreover, some emotional signalling problems are ancient and predate the establishment of highly cooperative social worlds, for example establishing that threats are credible. This helps make collective action a plausible model for an early form of cooperation. One set of prosocial emotions that are not typically discussed in the evolution of cooperation literature, but which are important in this context, are those manifest in contemporary team sports. We find successful joint action intrinsically rewarding: perhaps especially when it is a high-energy, high-stress, high-arousal activity. Such collective activities both depend on and fuel affiliative bonds between the players; the more dangerous the activity, the more intense this affiliation cycle. Virtually, every memoir of infantry service centres on this affiliation circle and the role it plays in motivating action in combat (e.g. Graves 1929; Sassoon 1930; Fraser 2001).

If this is an important model of early hominin cooperation, two implications follow. First, vertical complexity is a key aspect of social complexity. Teams—coordinated work groups, often with specialist roles—generate important benefits, which flow preferentially to members of the team. Gurven and his colleagues note that in near-contemporary forager societies, the first division of spoils from big game hunting typically goes to members of the hunting partnership, though there may be a secondary flow

from those hunters to others. Teams and their formation are important. In turn, this implies that partner choice models rather than partner control models are crucial in explaining the initial growth of cooperation in hominin life. Iterated prisoners dilemma models and their relatives are *partner control* models of cooperation. Agents improve their net benefit from cooperation by inducing favourable changes in partner behaviour; conditional willingness to cooperate and/or punishing defection induces partner cooperation. But as Ronald Noë has pointed out, these models are not biologically plausible: in real biological interactions, agents do not act simultaneously, each in ignorance of the other's act. So Noë argues that it is important to develop accounts of cooperation structured around *partner choice* models (Noë 2006). Forming hunting teams and enforcement coalitions is a partner choice problem, not a partner control problem. This changes our model of the cognitive demands of cooperation. The task becomes that of identifying the honest cooperators in your social world—if there are any to choose—and pursuing your joint endeavours with them, rather than monitoring reciprocation and its failure. If such partners can be identified and recruited, the intractable tasks of micro-managing and micro-accounting interactions disappear. In intimate social worlds in which there is mutual knowledge of the behavioural and emotional profiles of others, partner assessment is not cognitively intractable.

3. THE GENERATION AND DISTRIBUTION OF BENEFIT

The evolutionary biology of the evolution of cooperation has generated a massive literature on the distribution of benefit. But there is much less on the generation of benefit for an exception, see Alvard & Nolin (2002); for the importance to evolutionary theory of this neglect, see Calcott (2006). Yet, this too can require major cognitive investment. Synergies of cooperation sometimes depend just on joint action: a pack of African wild dogs hunting together can kill a wildebeest without role specialization by swamping that animal's defence. Very often though, the generation of benefit involves both specialization and coordination. Anderson & Franks (2001) review teamwork—collective activity with role differentiation—in animal social life; hominins have gone a long way down this road. Behaviourally modern human foraging depends on coordination and specialization. In turn, coordination, specialization, technology and the skills to use it require an investment in cognitive resources. Teams must act in unison, in coordinated fashion, often while being aware of, and adjusting to, the acts of others. Collective action itself can be cognitively challenging. Moreover, human foraging is technologically enhanced, for example Inuit foraging would simply be impossible without kayaks and umiaks, harpoons, sewn clothing and footwear, and sleds. Technological dependence adds invisible partners to the hunt: those that provide the technology and informational tools without which the hunt would be impossible. Behaviourally modern foragers need a major investment to assemble the skill base on which

coordinated technologically enhanced action rests. Boyd, Richerson and their students have made this point strikingly and in detail (though for some of the problems we face in testing such evolutionary models of cooperation, see Rosenberg & Linquist 2005). They show that traditional societies depend on the skills, technologies and information that have been accumulated over many generations and which are transmitted, as critical cognitive capital, to the next generation (Henrich & McElreath 2003; Richerson & Boyd 2005). As this culturally transmitted skill base becomes more important, selection for the capacity to acquire and transmit such information intensifies; humans alter our environment in ways that transform the selective forces acting on us.

This investment in cooperative technological foraging collapses the distinction between social and ecological expertise, and generates feedback loops selecting for the further development of expertise. For coordinated foraging, and especially coordinated hunting, requires a fusion of social and ecological skills. The regular exploitation of large game like Cape Buffalo is often taken to be one signature of the appearance of behaviourally modern humans, for such large and potentially dangerous animals can be harvested only with appropriate ecological information, technology and coordinated action. Hunting requires foraging expertise: hunters need to be aware of the animal, its capacities, and its likely responses to threat. They need a precise understanding of their technology, its limits and their power to use it. But joint hunting is also an intensely social activity: hunters must have mutual knowledge of one another. Each hunter must know what others are doing and are likely to do; they must understand both their intentions and their capacities. Moreover, each must be aware of what others expect of him. Effective safe action depends on the smooth integration of social and ecological expertise (Laland & Hoppitt 2003). Plants, shellfish, animals down burrows and under rocks do not impose such heavy demands on fast-response decision making, though while trees do not fight back or run away, they can fall on you. But even harvesting these resources requires communication, planning and coordination. For one synergistic benefit of cooperation is *efficient search*. A group will forage more effectively, if they divide both targets and territory and if foragers ensure that every likely spot is searched, but that the same spot is not picked over twice. The social skills of communication and negotiation need to be allied with knowledge of natural history and local geography. The sexual division of labour typical in foraging societies is adaptive for this reason. Each gender specializes in the role for which it has a comparative advantage, though it is not clear whether traditional foraging societies routinely benefit in other ways as well from these search synergies. For foraging for plants and small items of animal food tends to be more individualistic, both in the search itself and in sharing the product (Boehm 1999).

A similar fusion is evident in the acquisition of foraging skills. Traditional lifeways depend on the accurate intergenerational transfer of foraging expertise: of information about the local geography, with its

resources and dangers; natural history information; and information about the technology needed to acquire and process the resources on which those lifeways depend. Human minds and social worlds are adapted to enhance the reliability of inter-generational information transfer (e.g. Tomasello 1999a,b; Alvard 2003). Imitation, language and theory of mind all play key roles in this intergenerational transfer of information. Language, for example has many utilities, but learning and teaching is surely one. It is a crucial medium for pure cultural learning: in conversation, information is pumped from one mind to another. But much human learning is hybrid learning. The trial-and-error learning of the one generation is structured by its parental generation, making exploration safer and more productive. Apprentice craftsmen, hunters, foragers get advice and instruction as they practice. Moreover, they often get this advice and instruction from the most expert members of the previous generation (though they often have to pay a price in deference and respect to these experts (Henrich & Gil-White 2001)). Many traditional societies are organized so that information flows collectively from one generation to the next; many members of the upstream generation contribute to the cognitive capital of each member of the downstream generation. Language plays an important role in structuring and supporting exploration learning. It is well suited to encoding forager expertise, incorporating rich natural history and technical vocabularies (as ethnobiologists have shown; Atran 1990; Berlin 1992). It enables agents to describe environmental features qualitatively, quantitatively and probabilistically. Moreover, language allows the parental generation to substitute social signals for those from the world itself. As warnings ('no, that one is poisonous') substitute for error, the cost of exploration falls (Castro & Toro 2004; Castro *et al.* 2004).

Imitation, likewise, plays its most central role in hybrid learning. In contrast to young apes, human children are early and incorrigible imitators (Tomasello 1999a,b). Even so, few life skills are learned by imitation alone. Rather, adult demonstration is combined with practice, trial-and-error exploration and instruction in skill acquisition. Language and imitation show that human minds are extensively adapted for cultural learning. But they also show that the tools for cultural learning are not used just for learning *about* culture. Our adaptations for cultural learning allow us to use others' mind as sources of information about the non-human world. The same is true of human theory of mind capacities. Machiavellian versions of the social intelligence hypothesis emphasize the role of mind-reading in social chess; mind-reading allows one agent to anticipate what others are likely to do and say. But it also allows one agent to use another as a source of information about the world, and it adds to the efficiency of other adaptations for cultural learning. For a theory of mind makes teaching more efficient (Brockway 2003). Teaching is more effective if a teacher recognizes a student's existing capacities and understands what they find easy and what they find difficult, and when they are highly motivated and when they are beginning to lose motivation. But the effective

transfer of craft and natural history skills is also promoted by a reflective understanding of the task domain itself. It is hard to pass on a skill that has become obligatorily automatized. To effectively teach a behavioural programme, that programme needs to be articulated. A performance needs to be slowed down; crucial subroutines need to be exaggerated or repeated; the programme as a whole needs to be decomposed into elements which can be taught and practiced independently, and hence demonstrated and described independently. Being able to disarticulate a skill is not an automatic consequence of having it. An effective teacher of a skill has to understand his or her own skill. Perhaps this reflective understanding is not an introspective theory of mind, but it is some form of cognitive self-awareness. It is also important that a student understands the teacher's demonstrations as demonstrations: she understands that a particular element of a skill is slowed down and exaggerated, and why, and also understands the crucial element of the total behavioural suite to which she should attend. Critical cognitive tools of human culture exist (I hypothesize) owing to selection for their use in the acquisition and deployment of ecological skills. In the lives of ancient humans, selection pressures generated by ecological complexity do not act independently of those derived from social complexity.⁴

This fusion of the social and the ecological has an important informational effect. The more coordinated action becomes part of the life of a group, the more agents know about each other. Joint foraging generates social information as a side effect. When individuals are engaged in a collective activity, they broadcast information about their personality, emotional states, skills and capacities, and reliability as an informant. The longer the association, the more often it is repeated, the greater the variety of circumstances in which joint activity is pursued, the more agents advertise themselves. Time-pressured, stressful or dangerous activities are especially revealing (for in those circumstances, inhibition is less effective). Agents disclose their personalities, because information leaks through cues rather than signals; through actions whose primary purpose is ecological rather than communicative. Agents reveal their patience or its absence, their temperament in a crisis and their capacity to function when wet, tired and hungry. Interactions with an unforgiving and indifferent world are natural signs of the psychological dispositions of an agent. Extended joint activity gives every agent extensive exposure to a large repertoire of such natural signs. A workplace—and a Pleistocene foraging band was a workplace—is simultaneously a social and an ecological domain. Team formation leads to better team formation: good partners are able to recognize one another increasingly well over time. As collective foraging is established, it will become increasingly difficult to seem like a good partner without being a good partner. If, therefore, it is important to be chosen, selection will favour the psychology of strong reciprocation.

Section 2 developed a sceptical view of the Machiavellian positive feedback loop, of the idea that cognitive sophistication breeds social complexity which breeds further cognitive sophistication, as managing

reciprocal cooperation becomes ever more necessary and ever more demanding, as hominin social worlds become ever more complex. However, hominin cognitive complexity does depend on feedback loops, and that social complexity is part of that loop. However, the loop involves ecological as well as social complexity. It is the combination of the increasing information requirements of hominin resource extraction and the increasing social complexity of hominin worlds that drives the evolution of late hominin intelligence. One positive feedback loop is between ecological innovation, social complexity and cultural transmission. One major shift among the hominin is a change in the pattern and the magnitude of cultural learning. Among most animals, social learning typically takes place between members of the same generation, the information that flows has a short shelf-life, and it flows as a side effect of agents' ordinary ecological lives. Among the later hominin, there is extensive inter-generational flow of information with a long shelf-life (Reader & Laland 2002; Laland & Hoppitt 2003). This rich form of cultural transmission, characteristic of behaviourally modern humans, depends on the extension of human childhood, the invention of adolescence and the concomitant extension of human lifespans. Those changes in human life history, in turn, depend on ecological innovation. Cross-generational information flow both depends on and helps sustain the cross-generational flow of physical resources. The extension of human lifespan and the investment in a long childhood depended on controlling extrinsic causes of mortality: reducing threats of death through predation or accident and reducing the risk of starvation when ill, injured or unlucky (Hill & Kaplan 1999). For these human life-history patterns depend on within-family and between-generation resource transfers, on the fact that adults (and especially adult males) generate far more resources than they consume themselves. For human populations to be viable, the adults of generation $N+1$ must survive long enough to pump resources to generation $N+2$ equivalent to those they received from generation N . So, human life-history characteristics coevolve with technological competence and cultural learning. The technological and informational bases of cooperative technological foraging typically require deep educations. Foragers do not peak in their resource acquisition powers until they are about 30; they do not begin to produce more than they consume until about 18. The resource debt that individuals acquire as children and adolescents is not paid off until around 50. Extensive, apprentice-style cultural transmission supports the development of technological foraging skills that generate very rich returns; the life history that makes such cultural transmission possible is paid for by those same skills (Robson & Kaplan 2003; Kaplan *et al.* 2005).

In addition to this feedback relationship between human life-history patterns, cultural transmission of information and information-intensive foraging, there is also a feedback loop between innovation and group structure, especially group size. Technology and foraging competence impact on group size. Group size, in turn, impacts on vertical complexity and the division of labour. Many adaptations are zero-sum:

they change the distribution of traits within a population without affecting the size of that population at equilibrium. A mutation that makes an individual resistant to malaria can spread through a group exposed to that disease without changing population size at all. The adaptations that made technological cooperative foraging possible were not zero-sum adaptations. When technology and cooperation are combined, their profit drives population growth. Cooperative technological foraging gives a group access to resources that were previously unavailable, and allows more efficient harvesting of previous targets. The same adaptive complex gives better protection against predators. As a consequence, groups in which this complex establishes are less tied to specific habitats, for example good anti-predator defences might mean that grasslands—areas without natural refuges—can be exploited, and lesser predators can be driven from their kills (for the importance in hominin evolution of this habitat, see Potts 1996). The resource envelope increases; predation causes less mortality: the population expands. This population growth allows specialization. A band of 20 or so probably cannot afford a knapping specialist or a specialist fire-maker. The specialist will not have enough customers to support his/her skill; a band of twice that size may well do so (Ofek 2001). Size improves access to the enormous benefits of the division of cognitive labour. Moreover, larger groups maintain their cognitive resources more reliably. It is much safer to have a few old heads that know where water is to be found in dry times than have that knowledge restricted to one, vulnerable, old head (Henrich 2004). Much more speculatively, an expanding energy budget fuelled by the marriage of technology and cooperation might explain how hominin afforded their expensive brains (Aiello & Wheeler 1995).

As group size increases, the selective environment favours a further expansion of cognitive resources. Expansion can never be unchecked. At some stage, population expansion will put pressure on the existing resource base. For there is likely to be a population overshoot rather than a new equilibrium: the invention of a new technology (say, a first fish trap) is likely to lead to resources being harvested faster than the rate at which they are replenished. That pressure will select for a more intense exploitation of currently used resources. It also selects for adding resources: for geographical and/or ecological expansion. As resources are added, and exploited intensely, further specialization becomes economically viable. If wildfowl are eaten only occasionally as lucky windfalls, it will not pay to develop the specialist skills and tools needed to take them most efficiently. If they are regularly exploited, these special skills and technologies pay their way. Finally, expansion must eventually lead to more frequent and/or more intense intergroup conflict. Thus, geographical expansion, increasing resource breadth and more severe intergroup conflict all select for social or technological improvements in foraging and defence. Both the growth phase triggered by innovation and the constraint phase that follows it select for further innovation. Selection need not be efficacious: appropriate variations may not appear.

Stasis and extinction are both possible. But if appropriate innovations are found and established, the cycle will iterate. Technological innovation will tend to cause populations to expand in numbers and area. Such expansion, in turn, tends to select for further innovation.

4. CONCLUSION

Richard Potts has argued that hominin evolution is a response to an increasingly challenging because increasingly variable physical and biological environment (Potts 1996). This might be the correct view of early hominin evolution, but there is a rough consensus that later hominin evolution is not explained in an externalist, adaptationist mode, as a lineage's adaptive response to an externally caused change in the environment. Both the social intelligence hypothesis and the social intelligence–ecological complexity hybrid I have proposed are niche construction models. Hominin evolution is hominin response to selective environments that earlier hominin have made. In contrast to social intelligence models, I have argued that hominins have both created and responded to a unique foraging mode, a mode that is both social in itself and which has further effects on hominin social environments. In contrast to the social intelligence model recently defended by Flinn *et al.* (2005), on this view, hominin encounters with their ecological environment continue to have profound selective effects. Flinn and his allies doubt this: they argue that the ecological dominance of humans results in humanity being 'its own principal hostile force of nature' (Flinn *et al.* 2005, p. 14). Selection on humans is the result of action by other humans. This is a mistake. For one thing, the fossil record of Neanderthals suggests that even technological and cooperative hunting is physically stressful and accident prone (Klein 1999, pp. 474–475). Even though Neanderthal rates of trauma reflect the extremely hostile nature of their environment, foraging is not safe. It results in significant mortality and morbidity. But even if that were not true, differential success (of both individuals and groups) in interaction with the non-human environment has selective consequences. However, though the ecological environment selects, it does not select on its own. Accidents and their consequences, differential success and failure, result from the combination of the ecological environment an agent faces and the social features that enhance some opportunities and suppress others; that exacerbate some dangers and lessen others.⁵ Individuals did not face the ecological filters on their environment alone, but with others, and with the technology, information and misinformation that their social world provides. Ecological and social complexity became fused, as the ecological problem of extracting resources as individuals from a world we did not make became the economic problem of extracting resources collectively from and in a human world.

Thanks to Nick Shea, Kevin Laland and audiences at Victoria University of Wellington, the Royal Society Discussion Meeting and the ANU for feedback on earlier versions of this paper.

ENDNOTES

¹Indeed, Foster & Ratnieks (2005) have suggested (perhaps not wholly seriously) that humans are a second eusocial mammal.

²Kaplan *et al.* (2005) note that Ache hunters return empty-handed 40% of the time; Hazda, hunters of large game, return with meat on only 3% of their hunting days.

³In discussing, the Ache and reporting on the !Kung, Kaplan, Gurven and their colleagues note that reservation life, based on cultivation, made the issue of sharing and cooperation among the Ache much more fraught. Even in a culture with strong traditions of sharing and reciprocity, it is hard to hammer out a consensus conception of what counts as being fair, what counts as being cooperative, but not a sucker (Kaplan *et al.* 2005, Part III).

⁴It is important here to recall that the social intelligence hypothesis is a view of the selective environment of hominin evolution, not cognitive architecture. In particular, the social intelligence hypothesis does not share the controversial assumptions of the 'massive modularity hypothesis'. According to this hypothesis, the distinctive features of human intelligence depend on an ensemble of special purpose cognitive subsystems rather than enhanced domain general learning and problem solving capacities (Barkow *et al.* 1992; Pinker 1997; Sperber & Hirschfeld *in press*). One view of this cognitive architecture, we have a 'mind-reading' module: an innately based specialist subsystem that enables us to anticipate the actions of others by representing their cognitive and affective states. These nativist theories of cognitive architecture are committed to the idea that the informational bases of adaptive action in a particular domain are stable over evolutionary time. Neither social intelligence hypothesis nor this idea about the ecological–social feedback loop has any such commitment. We may well have enhanced general purpose problem solving capacities as a result of selection favouring enhanced capacity to solve the problems posed by our social environments.

⁵Social facts, for example, profoundly affect the pathogens to which a population is exposed (Ewald 1994).

REFERENCES

- Aiello, L. C. & Wheeler, P. 1995 The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221. (doi:10.1086/204350)
- Alvard, M. 2002 Carcass ownership and meat distribution by big-game cooperative hunters. *Soc. Dimensions Econ. Process* **21**, 99–131.
- Alvard, M. 2003 The adaptive nature of culture. *Evol. Anthropol.* **12**, 136–149. (doi:10.1002/evan.10109)
- Alvard, M. & Nolin, D. 2002 Rousseau's whale hunt? Coordination among big game hunters. *Curr. Anthropol.* **43**, 533–559. (doi:10.1086/341653)
- Anderson, C. & Franks, N. 2001 Teams in animal societies. *Behav. Ecol.* **12**, 534–540. (doi:10.1093/beheco/12.5.534)
- Anderson, C. & McShea, D. W. 2001 Individual versus social complexity with particular reference to ant colonies. *Biol. Rev.* **76**, 211–237. (doi:10.1017/S1464793101005656)
- Anderson, C., Franks, N. R. & McShea, D. W. 2001 The complexity and hierarchical structure of tasks in insect societies. *Anim. Behav.* **62**, 643–651. (doi:10.1006/anbe.2001.1795)
- Atran, S. 1990 *Cognitive foundations of natural history*. Cambridge, UK: Cambridge University Press.
- Barkow, J. H., Cosmides, L. & Tooby, J. 1992 *The adapted mind: evolutionary psychology and the generation of culture*. Oxford, UK: Oxford University Press.
- Berlin, B. 1992 *Ethnobiological classification: principles of categorization of plants and animals in traditional societies*. Princeton, NJ: Princeton University Press.
- Boehm, C. 1999 *Hierarchy in the forest*. Cambridge, MA: Harvard University Press.
- Bowles, S. & Gintis, H. 2001 *Prosocial emotions*. Working paper. Santa Fe, NM: Santa Fe Institute.

- Bowles, S. & Gintis, H. 2003 Origins of human cooperation. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 429–443. Cambridge, MA: MIT Press.
- Bowles, S. & Gintis, H. 2004 *The evolutionary basis of collective action. Santa Fe working papers*, pp. 1–20. Santa Fe, NM: Santa Fe Institute.
- Boyd, R. & Richerson, P. 1992 Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13**, 171–195.
- Boyd, R. & Richerson, P. 2001 Norms and bounded rationality. In *Bounded rationality: the adaptive toolbox* (eds G. Gigerenzer & R. Selten), pp. 281–296. Cambridge, MA: MIT Press.
- Brockway, R. 2003 Evolving to be mentalists: the ‘mind-reading mums’ hypothesis. In *From mating to mentality: evaluating evolutionary psychology* (eds J. Fitness & K. Sterelny), pp. 95–124. Hove, UK: Psychology Press.
- Byrne, R. W. 1997 The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In *Machiavellian intelligence II: extensions and evaluations* (eds R. Byrne & A. Whiten), pp. 289–311. Cambridge, UK: Cambridge University Press.
- Byrne, R. 2003 Imitation as behaviour parsing. *Phil. Trans. R. Soc. B* **358**, 529–536. (doi:10.1098/rstb.2002.1219)
- Byrne, R. 2004 The manual skills and cognition that lie behind hominid tool use. In *Evolutionary origins of great ape intelligence* (eds A. Russon & D. R. Begun), pp. 31–44. Cambridge, UK: Cambridge University Press.
- Byrne, R. & Whiten, A. 1988 *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford, UK: Oxford University Press.
- Calcott, B. 2006 Transitions in biological complexity. Ph.D. Thesis. Canberra: Australian National University.
- Castro, L. & Toro, M. 2004 The evolution of culture: from primate social learning to human culture. *Proc. Natl Acad. Sci. USA* **101**, 10 235–10 240. (doi:10.1073/pnas.0400156101)
- Castro, L., Medina, A. & Toro, M. 2004 Hominid cultural transmission and the evolution of language. *Biol. Philos.* **19**, 721–737. (doi:10.1007/s10539-005-5567-7)
- Dunbar, R. 1996 *Grooming, gossip and the evolution of language*. London, UK: Faber and Faber.
- Dunbar, R. 2003 The social brain: mind, language and society in evolutionary perspective. *Annu. Rev. Anthropol.* **32**, 163–181. (doi:10.1146/annurev.anthro.32.061002.093158)
- Ewald, P. W. 1994 *Evolution of infectious disease*. Oxford, UK: Oxford University Press.
- Fehr, E. & Fischbacher, U. 2003 The nature of human altruism. *Nature* **425**, 785–791. (doi:10.1038/nature02043)
- Fehr, E. & Fischbacher, U. 2004 Social norms and human cooperation. *Trends Cogn. Sci.* **8**, 185–189. (doi:10.1016/j.tics.2004.02.007)
- Fehr, E. & Rockenbach, B. 2004 Human altruism: economic, neural and evolutionary perspectives. *Curr. Opin. Neurobiol.* **14**, 784–790. (doi:10.1016/j.conb.2004.10.007)
- Fehr, E., Fischbacher, U. & Gächter, S. 2002 Strong reciprocity, human cooperation and the enforcement of social norms. *Hum. Nat.* **13**, 1–25.
- Flinn, M., Geary, D. C. & Ward, C. V. 2005 Ecological dominance, social competition, and coevolutionary arms races: why humans evolved extraordinary intelligence. *Evol. Hum. Behav.* **26**, 10–46. (doi:10.1016/j.evolhumbehav.2004.08.005)
- Foley, R. & Lahr, M. M. 2003 On stony ground: lithic technology, human evolution and the emergence of culture. *Evol. Anthropol.* **12**, 109–122. (doi:10.1002/evan.10108)
- Foster, K. & Ratnieks, F. 2005 A new eusocial vertebrate? *Trends Ecol. Evol.* **20**, 363–364. (doi:10.1016/j.tree.2005.05.005)
- Frank, R. 1988 *Passion within reason: the strategic role of the emotions*. New York, NY: WW Norton.
- Fraser, G. M. 2001 *Quartered safe out here: a recollection of the war in Burma*. London, UK: Akadine Press.
- Graves, R. 1929 *Goodbye to all that*. London, UK: Jonathan Cape.
- Gurven, M. 2004 To give and to give not: the behavioral ecology of human food transfers. *Behav. Brain Sci.* **27**, 543–583.
- Henrich, J. 2004 Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *Am. Antiq.* **69**, 197–221.
- Henrich, J. & Gil-White, F. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)
- Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123–135. (doi:10.1002/evan.10110)
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E. & Gintis, H. 2004 *Foundations of human sociality*. Oxford, UK: Oxford University Press.
- Henshilwood, C. & Marean, C. 2003 The origin of modern behavior. *Curr. Anthropol.* **44**, 627–651. (doi:10.1086/377665)
- Hill, K. & Kaplan, H. 1999 Life history traits in humans: theory and empirical studies. *Annu. Rev. Anthropol.* **28**, 397–430. (doi:10.1146/annurev.anthro.28.1.397)
- Humphrey, N. 1976 The social function of intellect. In *Growing points in ethology* (eds P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge, UK: Cambridge University Press.
- Jolly, A. 1966 Lemur social behaviour and primate intelligence. *Science* **153**, 501–506. (doi:10.1126/science.153.3735.501)
- Kaplan, H., Gurven, M., Hill, K. & Hurtado, A. M. 2005 The natural history of human food sharing and co-operation: a review and a new multi-individual approach to the negotiation of norms. In *Strong reciprocity: modeling the roots of cooperative exchange. The moral sentiments and material interests: the foundations of cooperation in economic life* (eds S. Bowles, R. Boyd, E. Fehr & H. Gintis). Cambridge, MA: MIT Press.
- Klein, R. G. 1999 *The human career: human biological and cultural origins*. Chicago, IL: University of Chicago Press.
- Laland, K. & Hoppitt, W. 2003 Do animals have culture? *Evol. Anthropol.* **12**, 150–159. (doi:10.1002/evan.10111)
- McBrearty, S. & Brooks, A. 2000 The revolution that wasn’t: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563. (doi:10.1006/jhev.2000.0435)
- McShea, D. W. 1996 Metazoan complexity and evolution: is there a trend? *Evolution* **50**, 477–492. (doi:10.2307/2410824)
- Noë, R. 2006 Cooperation experiments: coordination through communication versus acting apart together. *Anim. Behav.* **71**, 1–18. (doi:10.1016/j.anbehav.2005.03.037)
- Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. 2003 *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.
- Ofek, H. 2001 *Second nature: economic origins of human evolution*. Cambridge, UK: Cambridge University Press.
- Pagel, M. (ed.) 2002 *Encyclopedia of evolution*. Oxford, UK: Oxford University Press.
- Pinker, S. 1997 *How the mind works*. New York, NY: W. W. Norton.
- Potts, R. 1996 *Humanity’s descent: the consequences of ecological instability*. New York, NY: Avon.
- Reader, S. & Laland, K. 2002 Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441. (doi:10.1073/pnas.062041299)

- Richerson, P. J. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- Robson, A. & Kaplan, H. 2003 The evolution of human life expectancy and intelligence in hunter-gatherer economies. *Am. Econ. Rev.* **93**, 150–169. (doi:10.1257/000282803321455205)
- Rosenberg, A. & Linquist, S. 2005 On the original contract: evolutionary game theory and human evolution. *Anal. Kritik* **27**, 136–157.
- Sassoon, S. 1930 *Memoirs of an infantry officer*. London, UK: Faber and Faber.
- Skyrms, B. 2003 *The stag hunt and the evolution of social structure*. Cambridge, UK: Cambridge University Press.
- Sober, E. & Wilson, D. S. 1998 *Unto others: the evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.
- Sperber, D. & Hirschfeld, L. In press. Culture and modularity. In *The innate mind: culture and cognition* (eds T. Simpson, P. Carruthers & S. Stich). Oxford, UK: Oxford University Press.
- Sterelny, K. 2003 *Thought in a hostile world*. New York, NY: Blackwell.
- Stevens, J. & Hauser, M. 2004 Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* **8**, 60–65. (doi:10.1016/j.tics.2003.12.003)
- Tomasello, M. 1999a *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. 1999b The human adaptation for culture. *Annu. Rev. Anthropol.* **28**, 509–529. (doi:10.1146/annurev.anthro.28.1.509)
- Whiten, A. & Byrne, R. W. (eds) 1997 *Machiavellian intelligence II: extensions and evaluations*. Cambridge, UK: Cambridge University Press.
- Wrangham, R. W. 2001 Out of the Pan, into the fire: how our ancestors' evolution depended on what they ate. In *Tree of life* (ed. F. B. M. de Waal), pp. 121–143. Cambridge, MA: Harvard University Press.
- Wrangham, R. W., Holland Jones, J., Laden, G., Pilbeam, D. & Conklin-Brittain, N. L. 1999 The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.* **40**, 567–594. (doi:10.1086/300083)