

This work originally appeared in:

Dennett, Daniel C. "Tarbutniks Rule: Review of Animal Traditions: Behavioural Inheritance in Evolution, by Eytan Avital and Eva Jablonka." *Journal of Evolutionary Biology* 15, no. 2 (March 2002): 332-34.

This is Daniel C. Dennett's final draft before publication. It has been modified to reflect the pagination of the published version of the work.

## Tarbutniks Rule

A review by Daniel C. Dennett

Animal Traditions: Behavioural Inheritance in Evolution,  
By Eytan Avital and Eva Jablonka. Cambridge University  
Press, 2000. £50.00/US\$80.00. ISBN 0 521 66273 7.

For thousands of years, we have been captivated by the cleverness of animals, the elegant *ways* in which birds of different species build their nests, the circumspection and efficiency with which predators stalk their chosen prey. The genius of 'instinct' comes in abundant variety, and breeds true. 'It must be in the genes' - that's what we tend to conclude. But when we do, we may be jumping to conclusions, because there are other possibilities: the clever behaviour we observe *could* be the do-it-yourself invention or discovery of the individual behaviour or it *could* be a clever trick copied from an elder member of its species, most likely one of its parents. The book provides a wealth of examples drawn from studies of literally hundreds of species (almost all mammals and birds); and it addresses the theoretical problems posed for evolutionary theory by cultural transmission and its interaction with genetic transmission. But also, by the very strenuousness of its efforts to overcome the prejudice against its main thesis, it inadvertently throws a spotlight on the way received opinion in science can close investigators' minds. Some sidelong enquiries convinced me that the mindset they seek to overturn is actually quite common. So this is an important book, potentially a major investigation-shaper in the years to come, for in addition to the widespread work they discuss, they point to a much larger array of still-to-be-done studies, eminently possible, that have never been done simply because nobody thought to do them.

The first task of the authors is to establish the theoretical possibilities of cultural transmission, which they do with a delightful thought experiment about an imaginary species of small mammals, *tarbutniks* (from the Hebrew word *tarbut*, meaning *culture*). These are declared by fiat to be all clones of each other, with zero genetic diversity and hence zero genetic evolution by natural selection. The population comes to be divided, as populations so often do, and in one group a pioneer digs a hole in the ground (it might just be an accident, or the result of a 'bad' habit of this individual) and this novel act happens to inspire some of the onlooking conspecifics to

do likewise. Why? Just because the tarbutniks are postulated to have a genetically maintained penchant for imitation, unlike a less fortunate strain of tarbutniks that were restricted to individual, risky, trial-and-error learning, and became extinct. Because it happens that hole-digging is beneficial in their local environment (it provides some protection, or gives access to a good underground food source), those who dig holes do better than those who do not. The habit spreads, *but not genetically*: the young pick it up by 'social learning' from their parents, or others in their community. Hole-digging leads to tunnel-digging that leads to giving birth in the underground tunnels, and in due course this lineage of tarbutniks have all adopted behaviours and a diet of the sort observed in moles. The other population takes up berry-picking, living in the protection of the underbrush, and its diet and habits are likewise moulded by natural selection of behavioural tradition, not genes. One group has a problem with the acidity of its diet, corrected by eating a bit of dirt, a trick pioneered by one and copied by others, which then opens up other food sources heretofore toxic, and so on. Eventually they have become as different as two closely related but distinct species can be - all without any genetic change at all. The authors want us to notice that there is a broad-band informational pathway that runs roughly parallel to the genetic pathway that can transmit adaptations just as well as - sometimes better than - genes can.

The next task is to demonstrate that the contributions of transmitted tradition or culture to animal behavioural design are in fact substantial. Here the authors provide more informed speculations than conclusive demonstrations, but in addition to the wealth of circumstantial evidence they cite, they do point to key studies that point the way to confirmation. The way to test their claims is to interrupt one transmission channel or another and see what gets through. Cross fostering is the most obvious manipulation: to see if young exhibit the behaviours of their foster parents instead of their 'biological' parents. (Notice how strong the association has become between genes and biology - as if there were nothing in biology except genes!) The authors report the results of cross fostering studies already undertaken, as well as studies that block the paths of social learning in one way or another, and the results they cite certainly support their contention, but there is much more to be done.

Before researchers can be enlisted to embark on these long-term investigations, they have to be persuaded that they are likely to hit paydirt. That is where the thought experiments and speculative scenarios come in. Time and again, the authors offer a persuasive redescription of the setting of some well-studied behaviour - food preferences, predation techniques, nest-building, danger-avoidance, mating tactics - and consider what could be the case about how it is installed in each generation. Along the way, *they* consider and disarm a host of objections, and present reasons for thinking that evolution ought to

avail itself of cultural transmission whenever possible. In the first place, such social learning is clearly safer - less risky - than individual trial 'nd error by novices, surely a large benefit that would be recognized by natural selection. Moreover, the cultural transmission of newly discovered Good Tricks (*my* term, not theirs) is orders of magnitude swifter than the incorporation into the genome of whatever it takes to specify the Good Trick genetically. Cultural transmission works as an enhancement of pure trial and error: when an old trick outlives its usefulness because of a change in environment, the lineage does not have to wait for many generations for the right new combinations or mutations to come along. The individual animals can revert to trial and error immediately, and as soon as one explorer finds a new trick in the right direction, others can copy it and abandon their riskier explorations. Of course they may also be led down the path to destruction by copying an innovation that is only apparently an improvement; social learning has its own risks.

If this is all so obviously adaptive, why have investigators been so prejudiced against it as a major possibility? There are many reasons. As 'culture' is commonly taken to be one of the prime idiosyncrasies distinguishing *Homo sapiens* from all other species, anything that smacks of the exploitation of culture by non-human species promises to blur a boundary many want to keep as hard-edged as possible. Then there is the ever-present fear of lapsing into 'Lamarckian' heresy. But the main source of covert resistance comes from the genocentric assumptions that have apparently swept to fixation in the minds of many biologists.

A mistaken ground for suspicion of the idea of transmission of behavioural tradition is the hunch that since there is no proprietary code (like A, C, G, T) in which such information is couched, transmission cannot be sufficiently high-fidelity to count as replication.

Codes do indeed make a big difference. We human beings have symbolic codes - natural languages composed of finite vocabularies of words anchored to norms of both production and meaning - and this gives our practice of cultural transmission a hugely different profile of competence compared with other species. 'Since animals cannot represent information symbolically, .... the focus must be the social and ecological conditions that lead to the manifestation and re-generation of essentially similar patterns of behaviour' (p. 95). Or, to turn the point around, symbolic representations (of behaviours and other topics) have built-in self-stabilizing features (the norms) that can permit them to survive drastic changes in supporting ecological conditions essentially intact, something quite impossible in the animal world.

The comparison with human cultural transmission presents a delicate problem for the authors. Choosing their battles carefully, they go somewhat overboard in distancing themselves from the controversial topic of *memes*, which arouses blind animosity in so many

(Dawkins). What they are mainly concerned to argue is that transmitted tradition is another path to genetic fitness of behaving organisms - it is information that creates adaptations in the extended phenotype. They are not concerned with the fitness as replicators of such designed behaviours themselves. One cannot blame them for wanting to secure a little good will *by* hastening to endorse some of the standard (but inconclusive) objections to memes, but in fact their own account is consistent with the more careful formulations about memes, and they make many of the favourite points of memeticists in their own terms. They point to the possibility of the spread of traits with no fitness advantage (pp. 131-136), and stress (as Dawkins did) the fact that transmission is via copying the phenotype. They point to the ease of remembering as a factor in transmission of a trick that may move it away from what otherwise would be the 'engineering' optimum (p. 135). But right here they might benefit from the memeticists' perspective, for it is easier to see that memorability is itself just as much a question of 'engineering' if one is thinking of the fitness of the remembered items themselves, instead of their possible contribution to the fitness of their hosts. And *by* concentrating on vertical transmission of culture (from parent to offspring), they ignore the predictable prospect of virulent, parasitic habits being more readily spread obliquely, an insight that beckons once one adopts the meme's-eye point of view. (See also the review *by* Matteo Mameli of this book in *Biology and Philosophy* 16(5),2001.)

Occasionally, the authors overstate their best case. For instance, wishing to provide a striking alternative to the received wisdom about parent-offspring conflict in, e.g. tits (p. 173) they ask 'who really controls the allocation of resources in the tit family?' and go on to argue that there is an alternative story to the story of genetic conflict that can be told, in which the parents are teaching their offspring, not being blackmailed *by* them. There may well be something to their perspective on this, but the question they do not address is this: is there also an argument *against* the existence of genetic conflict? If we already have reason to believe that there should be genetic conflict, their alternative might be a useful supplement, but not an alternative. They say 'Translating agonistic behaviour among family members into evolutionary conflict may mislead us' (p. 182). This is true. The question is: does it mislead us in fact? They say that the conflict theory's assumptions 'are not substantiated *by* any data' (p. 185)-

because their alternative fits the data equally well - but then they are equally in no position to assert, as they do. 'Looked at in this way, the squabbles between parents and young are not an outcome of evolutionary conflict, but are inevitable results of the learning process and the somewhat painful transition to the youngsters' independence' (p. 184). The bland truth may turn out to combine both ideas, with the genetic conflict harnessed into an opponent process system of teacher and learner.

Some of the most exciting suggestions appear in their discussion of the Baldwin effect, or Waddington's genetic assimilation, and the possibilities of a sort of teamwork between cultural and genetic transmission in the design of elaborate adaptations.

One final comment was inspired by the authors' occasional lapses of overselling. A brute fact about evolution that is *rhetorically inconvenient*, when confronting skeptics, is that it is ... shy about displaying its powers. It works when it works, but usually it does not. Every time a parent gives birth to offspring, this is potentially the initiation of a speciation event, but it almost never is. Similarly, every time a habit is picked up by one animal from another, a potential cultural tradition is 'born, but it almost never is. Only slightly less rare, presumably, are ephemeral group habits, commonalities in behaviour that spread through a neighbourhood or population, but that are too minor and evanescent to count as traditions, passing fancies that do not even rise to the status of fads. One should not be put off by this; it would be theoretically tidy to be able to say that whenever such and such happens, a tradition results. But it is a fool's errand to try to prescribe the sufficient conditions for such momentous innovations. The likeliest candidates almost never pan out, in fact. But sometimes they do. When it happens, it happens. Tradition-creation in evolution, like speciation, can be both an all but invisibly rare event and a highly significant force in the design processes that create the cleverness we observe.<sup>1</sup>

Daniel C. Dennett  
Centre for Cognitive Studies  
Tufts University  
Medford, MA 02155, USA

<sup>1</sup>I am indebted to Matteo Mameli for discussions of this book and an earlier draft of this review.