Experimental Studies of Modern	1
Human Social and Individual Learning	2
in an Archaeological Context: People	3
Behave Adaptively, But Within Limits	4

## Alex Mesoudi

## 5

#### Abstract

It has been proposed that one reason for the success of *Homo sapiens* is our advanced learn-7 ing abilities. Theoretical models suggest that complex cultural adaptations can arise from 8 an optimal mix of (1) individual learning that is of sufficient accuracy plus (2) social learn-9 ing that is of sufficiently high fidelity and is payoff-biased. Here I review the findings of a 10 series of experimental studies of human learning, designed to simulate the kind of technol-11 ogy-based tasks that our ancestors would have faced. Results of these studies support the 12 predictions of the models, and show that contemporary humans' learning strategies are 13 broadly adaptive. Performance typically improved through effective individual learning and 14 payoff-biased social learning. The latter crucially allowed participants to escape low-fitness 15 locally optimal artifact designs and jump to higher-fitness designs, assuming a realistic 16 multimodal adaptive landscape underlying artifact fitness. On the other hand, people also 17 exhibited predictable flaws in their learning, such as the copying of neutral traits exhibited 18 by successful models along with their functional traits (i.e., cultural hitchhiking), and an 19 unwillingness to share information with others under certain circumstances. 20

Keywords		
Cultural evolution	• Cumulative culture • Individual learning • Social learning	

#### 21 22

6

#### 23 8.1 Introduction

In a relatively brief period of evolutionary time, our species 24 has successfully colonised and inhabited virtually every ter-25 restrial environment on the planet, from the driest deserts to 26 frozen tundra, from high-altitude mountain ranges to remote 27 28 island chains, such that we now account for about eight times the biomass of all other wild terrestrial vertebrates combined 29 (Hill et al. 2009). Other hominin species such as the 30 31 Neanderthals have gone extinct, possibly due in part to the success of Homo sapiens, while our closest living relative 32

species, chimpanzees, are limited to a few small, scattered 33 populations across Africa. What accounts for the extraordinary evolutionary success of our species? 35

One possibility, proposed by the Replacement of 36 Neanderthals by Modern Humans (RNMH) Project (Akazawa 37 2012), is that anatomically modern Homo sapiens possessed 38 superior learning abilities compared to their fellow hominins 39 and other primates. This hypothesis has its roots in theoretical 40 modelling work in the field of cultural evolution going back 41 several decades, which has linked evolutionary rates of change 42 and phenotypic adaptation to learning strategies (Aoki et al. 43 2005, 2011; Boyd and Richerson 1985; Cavalli-Sforza and 44 Feldman 1981; Rogers 1988). A primary focus of these models 45 has been the interplay between individual (or asocial) learning, 46 in which novel solutions to problems are invented by a single 47 individual, and social learning (or cultural transmission), in 48 which solutions are copied from one or more other individuals 49 in the population. The latter can take on different modes, 50

A. Mesoudi (🖂)

Department of Anthropology and Centre for the Coevolution of Biology and Culture, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK e-mail: a.a.mesoudi@durham.ac.uk

A. Mesoudi

115

such as vertical transmission from one's biological parents (Cavalli-Sforza and Feldman 1981), conformist transmission of the most popular solution in one's group (Henrich and Boyd 1998), or payoff/prestige biased transmission in which the most successful/prestigious individual in one's group is preferentially copied (Boyd and Richerson 1985; Henrich and Gil-White 2001).

Although the results of these models are varied, a gen-58 eral finding seems to be that some mix of individual and 59 social learning is adaptive in fluctuating environments that 60 change too rapidly for innate, genetic responses to evolve, 61 yet not so rapid that previous generations' solutions to 62 63 problems are out-of-date (Aoki et al. 2005; Boyd and Richerson 1988). Moreover, if individual learning is suffi-64 ciently accurate, and social learning is of sufficiently high 65 66 fidelity and is payoff-biased such that adaptive solutions are preferentially copied, then this mix of social and indi-67 vidual learning can result in cumulative cultural evolution 68 69 (Aoki et al. 2012; Ehn and Laland 2012; Enquist et al. 2008; Mesoudi 2011b; Powell et al. 2009). Just as cumula-70 tive genetic evolution can result in complex genetic adapta-71 tions such as eyes or wings, cumulative cultural evolution 72 can similarly generate complex cultural adaptations that 73 most likely underlie our species' success, from bow-and-74 arrows, kayaks and celestial navigation to agriculture, air-75 planes and quantum physics (Richerson and Boyd 2005). 76

Did anatomically modern humans uniquely possess an 77 optimal mix of sufficiently accurate individual learning plus 78 sufficiently high fidelity, payoff-biased social learning? Was 79 one of these ingredients missing in other hominin, or other 80 primate, species? It is, of course, extremely difficult to infer 81 82 the learning abilities of extinct hominin species from the incomplete and often ambiguous artifactual record. We can, 83 however, test these predictions in contemporary humans. If 84 groups of people solve problems in the way predicted by the 85 aforementioned theoretical models, then we can be more 86 confident in the validity of those models, and more confident 87 in asserting that our species' learning capacities are evolu-88 tionarily adaptive. Just as importantly, if people do not 89 behave as predicted (e.g., if they eschew payoff-biased social 90 learning in favour of, say, conformist or random copying), 91 then this requires modification of the assumptions of the 92 93 models and/or modification of the original hypothesis that modern humans possess adaptive learning capacities. 94

With this aim in mind, in this paper I will review the 95 results of a series of experimental studies conducted by 96 myself and collaborators that have probed the learning abili-97 ties of contemporary humans when faced with a novel and 98 complex task-what we have dubbed the Virtual Arrowhead 99 Task-that is designed to resemble technology found in the 100 material record. Hopefully, the findings of these experiments 101 can inform both theoretical models of the evolution of human 102 learning capacities, and interpretation of the often ambiguous 103

archaeological record. This is not to say that experimental 104 simulations are a perfect tool: far from it. While they offer 105 many advantages, such as the ability to control extraneous 106 conditions, manipulate variables, replicate findings and gen-107 erate complete behavioural datasets, they are limited by their 108 lack of external validity, such as their short time spans, lower 109 incentives, restricted social interaction and the assumption 110 that the behaviour of contemporary humans can be extrapo-111 lated to that of past people. I therefore conclude with an 112 extended discussion of the limitations and real-life applica-113 tions of experimental methods in this context. 114

#### 8.2 The Virtual Arrowhead Task

The Virtual Arrowhead Task was originally designed by 116 myself and archaeologist Michael O'Brien to capture the 117 key aspects of North American projectile points (Mesoudi 118 and O'Brien 2008a, b), although we have since used it to 119 explore the learning of complex technology in general 120 (Atkisson et al. 2012; Mesoudi 2008, 2011a). One limitation 121 of many of the theoretical models of cultural evolution dis-122 cussed above, as well as some experimental tests of such 123 models (e.g., McElreath et al. 2005), is that the 'task' or 124 'problem' that must be solved is unrealistically simple: 125 often it is assumed that individuals can exhibit just one of 126 two possible discrete traits, with one of those traits giving a 127 higher payoff than the other trait as specified by the state of 128 the environment. Even the simplest of human technology, 129 however, comprises multiple component traits, some of 130 which might be continuous (e.g., the length or width of a 131 handaxe: Lycett and von Cramon-Taubadel 2008), others 132 discrete but with more than two states (e.g., arc-shaped vs. 133 curved vs. triangular base shapes of projectile points: 134 O'Brien et al. 2001); some might be functional (e.g., the 135 thickness or length of arrowheads: Cheshier and Kelly 2006) 136 and some might be functionless (e.g., decorative patterns on 137 canoes: Rogers and Ehrlich 2008). The overall 'cultural fit-138 ness' of an artifact will be a combination of these compo-139 nent trait values, each of which interacts with one another, 140 as well as with the skill of the manufacturer/user, and sto-141 chastic factors such as weather conditions. 142

We therefore sought to design a task that was simultane-143 ously complex enough to give us insights about how people 144 solve real-life technology-based problems, and simple enough 145 to be able to inform the theoretical models described above 146 and yield tractable findings. In our task (see Mesoudi and 147 O'Brien 2008a for a full description), participants in small 148 groups of 5-6 each design an arrowhead via a computer pro-149 gram (Fig. 8.1). This virtual arrowhead is composed of three 150 continuous traits (Height, Width and Thickness), which can 151 each take any value from 1-100 arbitrary units, and two dis-152 crete traits (Shape and Colour), which can each take one of 153

8 Experimental Studies of Modern Human Social and Individual Learning...



**Fig. 8.1** A screenshot of the Virtual Arrowhead Task. Participants can choose to directly change the traits in the box at the *top* (individual learning) or copy the design of another participant in the

box on the *left* (social learning). Feedback is given in calories depending on how close the design is to one or more hidden optimal designs

four categorical values. Over a series of trials (or 'hunts'),
participants can improve their arrowhead by either individual
trial-and-error learning, by directly altering the values of one
or more of the traits, or social learning, by copying the design
of another group member. The form of this social learning
(e.g., payoff bias, conformity) can be manipulated.

On each hunt the participant tests their arrowhead in a 160 virtual hunting environment, receiving a score in calories out 161 of 1,000. The closer their design is to one or more hidden 162 optimal designs pre-specified by us using fitness functions, 163 the higher the score ('fitness' is used here to refer to cultural 164 fitness of an artifact, which may, or may not, correspond to 165 the biological fitness of the individual using that artifact). 166 167 The overall fitness of the arrowhead is given by the sum of the separate fitness functions for the constituent traits 168 (Fig. 8.2). The discrete trait Shape has a step fitness function, 169 with the four shapes randomly assigned either 100 %, 90 %, 170 66 % or 33 % of the maximum possible fitness from that 171 trait. Colour is neutral and does not contribute to fitness in 172 any way. The continuous traits (Height, Width and Thickness) 173 each have bimodal fitness functions. For each, one randomly 174 chosen value gives 100 % of the fitness contribution (the 175 global optimum), and another random value gives 66 % of 176 that maximum (the local optimum). 177

When added together, these bimodal functions generate a 178 multimodal adaptive landscape (Wright 1932), where each 179 coordinate represents a different arrowhead design and the 180 height of the landscape represents the fitness of that design. 181 With three bimodal traits there are  $2^3 = 8$  peaks in our adap-182 tive landscape, with each peak varying in its maximum pay-183 off. For example, an arrowhead with Height, Width and 184 Thickness all at their globally optimal values gives the full 185 1,000 calories; an arrowhead with Height and Width at their 186 global optima and Thickness at its local optimum gives a 187 slightly lower maximum payoff; an arrowhead with Height, 188 Width and Thickness all at their local optima gives the lowest 189 maximum payoff. Given that most real-life problems can 190 typically be solved in multiple ways, with some solutions 191 better than others, this is likely to be representative of real-192 life technological fitness (Boyd and Richerson 1992). Note, 193 however, that participants were told nothing about these fit-194 ness functions (just as, presumably, real-life hunter-gathers 195 have no a priori knowledge of the effectiveness of most of 196 the technology they use). Finally, there is always a small ran-197 dom error in the score, simulating stochastic conditions such 198 as weather or prey availability. 199

After each hunt, participants are informed of their score 200 out of 1,000 calories. Participants go through three seasons 201





**Fig. 8.2** Fitness functions for the constituent traits. The overall fitness of an arrowhead was given by the sum of these fitness functions. The continuous traits (Height, Width and Thickness) had bimodal

of hunting, with each season comprising 30 hunts. Optimal 202 values change between seasons, but not during seasons, and 203 participants are informed about both of these facts. During 204 205 each season the participant can see their cumulative score (the sum of the scores on every hunt up to that point), and in 206 group conditions their relative rank compared to other group 207 members' cumulative scores. Motivational reward has varied 208 across the studies described below: in some studies partici-209 pants were rewarded monetarily based on their absolute 210 score, in others based on their relative rank, and in others no 211 monetary reward is given at all (interestingly, no obvious dif-212 ferences have been observed across these different motiva-213 tional regimes). 214

This task is intended to capture the key aspects of most 215 216 complex technology, including that used by both modern humans and Neanderthals around the time of their coexis-217 tence: a technology composed of multiple constituent traits 218 (some continuous and some discrete, some functional and 219 some neutral), that is cognitively opaque (there is no obvi-220 ous, intuitive relation between an artifact and its effective-221 ness: Gergely and Csibra 2006) and which has multiple 222 locally optimal alternative designs (i.e., a multimodal adap-223 tive landscape). In a series of studies we have explored how 224 contemporary humans engage with this task, with the fol-225 lowing key findings. 226

functions, generating a multimodal adaptive landscape. A fifth trait, Colour, was neutral and did not affect arrowhead fitness. From Mesoudi and O'Brien (2008a)

## 8.3 Key Findings 227

### 8.3.1 People Are Effective Individual 228 Learners, But Can Get Stuck on Local 229 Optima 230

While much theoretical modelling work has looked at a 231 diverse range of social learning strategies (Laland 2004), 232 individual learning is often under-theorised in models, where 233 it is often assumed that individuals come up with the correct 234 solution to a problem with some fixed probability. We were 235 interested in opening this 'black box' and exploring the strategies that people use when engaging in individual learning. 237

When playing alone, participants on average show effective 238 individual learning. Figure 8.3 shows that mean score increases 239 over successive hunts, plateauing to a level significantly higher 240 than that of the starting (random) design. Analyses of these 241 data revealed that participants appear to engage in a simple but 242 effective reinforcement learning, or 'win-stay-lose-shift', strat-243 egy (Mesoudi and O'Brien 2008a, b): pick a trait at random 244 (e.g., Width), modify the trait (e.g., increase Width), if the 245 payoff increases then keep modifying the trait in that way 246 (e.g., increase Width further); if the payoff decreases then do 247 the opposite (e.g., decrease Width). This is repeated until the 248

Author's Proof

8 Experimental Studies of Modern Human Social and Individual Learning...



**Fig. 8.3** The mean score of a sample of individual learners (N=27) showing a gradual increase and plateauing over successive hunts (*black line with squares*), along with the simulated performance of the reinforcement learning strategy with d=1 and c=5 (*red line with triangles*)

payoff no longer changes, at which point the whole process
is repeated for the next trait. In terms of the multimodal
adaptive landscape, this simple hill-climbing algorithm
results in the participant converging on the nearest peak in
the landscape.

Formally, we can define two parameters in this strategy: 254 d, which we defined as the number of traits that a participant 255 changed on a single hunt (0 < d < 5), and c, the amount by 256 257 which a continuous trait is modified during one hunt  $(0 \le c \le 99)$ . If more than one continuous trait was changed in 258 a hunt then c represents the mean of these traits, and we 259 focus on the continuous traits because these are responsible 260 for most of the improvement and variation in payoffs. 261 Empirically, our participants typically had a d of 1 262 (mean = 1.43, median = 1, mode = 1) and a c of 5 (mean = 9.50, mean = 9.50)263 median=5, mode=5), meaning that on each hunt they 264 changed one trait by 5 units. To test our hypothesised indi-265 vidual learning strategy, an agent-based model was con-266 structed that followed the rules specified above with d=1267 268 and c=5 (Mesoudi and O'Brien 2008b). As shown in Fig. 8.3, the simulated values match well with the actual data 269 from participants, reaching virtually identical end points and 270 showing a similar gradual increase then plateau. 271

Interestingly, the participants do best relative to the simulation during early hunts (see hunts 4, 5 and 6 in Fig. 8.3). Further analyses showed that this is because c was not, in fact, constant across all hunts, as suggested by the slightly higher mean of 9.50. During earlier hunts, when participants generally had low scores, they responded by increasing c, i.e., making larger modifications to their arrowheads.

Consequently, score was negatively and significantly corre-279 lated with c ( $r_s = -0.368$ , p<0.01). In a multimodal adaptive 280 landscape this is an adaptive individual learning strategy: if 281 your score is low, you are most likely to be in a low-fitness 282 valley, and large modifications may well transport you to a 283 higher-fitness part of the landscape. If your score is high, 284 then modifications should be small, otherwise you may move 285 off your peak and into a valley. 286

Note also from Fig. 8.3 that the maximum mean score at 287 hunt 30 of around 750-800 calories, which appears to have 288 levelled off at a kind of equilibrium, falls quite short of the 289 maximum possible 1,000 calories. This, again, is because of 290 the multimodal adaptive landscape. The individual learning 291 strategy followed by our participants, and simulated in the 292 model, leads participants uphill from a random starting point 293 to the top of the nearest peak. This might be the globally 294 optimal peak, but equally might be one of the seven other 295 locally optimal but globally suboptimal peaks. So even 296 though participants saw that their score was less than the 297 maximum of 1,000, the majority chose to stick with their 298 pretty-good-but-not-perfect design, what Simon (1956) 299 called 'satisficing'. This represents a disadvantage of pure 300 individual learning in a multimodal adaptive landscape: 301 independent individual learners can get stuck on locally opti-302 mal, but globally suboptimal peaks. 303

Note also that this individual learning strategy was 304 employed for a range of randomly generated optimal arrowhead designs, with these random optima changing between 306 seasons and across studies. Participants did not exhibit any intuitive notion of what an effective arrowhead design looked 308 Fig. 8.4 The mean score of individual learners (*black line with squares*) compared to payoff-biased social learners (*blue line with circles*). The latter could copy one another only during the last five hunts, during which their score significantly increased relative to the individual learners, who could not copy on any hunt



like, or if they did, it was (1) different for each participant 309 given that they each started at different points in the land-310 scape (see Mesoudi and O'Brien 2008b), and (2) quickly 311 overridden when the a priori intuitively good arrowhead 312 design was found to perform poorly in the experiment. In 313 this case, then, general-purpose learning rules override any 314 pre-existing intuitive content biases or cultural attractors 315 (Sperber 1996) regarding projectile point characteristics (at 316 least in our non-expert participants; we explicitly excluded 317 archaeology students and amateur replica-arrowhead-makers 318 from the studies to avoid too specialised knowledge). 319

# 8.3.2 People Use Payoff-Biased Social Learning to Jump to Higher-Fitness Designs

We can now ask how social learning, and in particular payoff-323 biased social learning, changes participants' performance on 324 the task. Payoff-biased social learning was implemented by 325 allowing participants to view the arrowhead design of another 326 member of their group, given information about those group 327 328 members' cumulative scores up to that point. When this is allowed, either after a long period of individual learning 329 (Mesoudi and O'Brien 2008a) or concurrently with individual 330 learning (Mesoudi 2008), participants readily engage in pay-331 off-biased social learning, copying the design of the most suc-332 333 cessful person in their group rather than copying a random group member or continuing with individual learning. The 334 result of payoff-biased social learning is a significant jump in 335 the mean score relative to individual learners (Fig. 8.4). 336

Payoff-biased social learning is adaptive here because itallows participants to abandon their locally optimal designs

and jump, almost instantaneously, to the globally optimal 339 peak, or at least the highest peak found by anyone in the 340 group. Payoff-biased social learning has this effect almost by 341 definition, because participants who have found higher peaks 342 will have higher scores, and they are preferentially copied. 343 To confirm that the multimodal shape of the adaptive land-344 scape was responsible for the advantage of social learning, it 345 was shown that (1) there were significantly more participants 346 with designs at or near a locally optimal peak immediately 347 before social learning is allowed than after, and conversely, 348 significantly more participants at globally optimal peaks 349 after social learning than before (Mesoudi and O'Brien 350 2008a), and (2) when the adaptive landscape was made uni-351 modal (by removing the local optima from the fitness func-352 tions for Height, Width and Thickness shown in Fig. 8.2, to 353 create a single globally optimal design/peak), the advantage 354 of social learning disappeared, and individual learners 355 achieved mean scores identical to multimodal social learners 356 (Mesoudi 2008). 357

Moreover, just as a participant's individual learning 358 strategy changed in response to the participant's score, so 359 too did their social learning. The lower a participants' 360 score, the more use they made of social information 361 (Mesoudi 2008). This was indicated by a significant and 362 negative correlation (r = -0.29, p < 0.001) between partici-363 pants' scores and a measure of social influence, defined as 364 the amount by which a participant changed their existing 365 arrowhead to make it more similar to the arrowhead of the 366 participant who they had chosen to view. 367

This performance-dependent payoff-biased social learning, or "copy-successful-individuals-when-behaviour-isunproductive" (Laland 2004), is again adaptive. Boyd and Richerson (1995) showed that this flexible and selective 371

8 Experimental Studies of Modern Human Social and Individual Learning...

learning strategy of engaging in social learning only when 372 individual learning is particularly costly or difficult is one 373 way of solving 'Rogers' paradox' (Rogers 1988). Rogers 374 375 suggested that social learners can be seen as 'information scroungers' free-riding on the costly efforts of individual 376 learners (or 'information producers'), with a net result that a 377 mixed population of social and individual learners will never 378 have a higher mean fitness than a population solely com-379 prised of individual learners. Boyd and Richerson (1995) 380 showed that making learners selective, engaging in social 381 learning only when individual learning is costly or difficult, 382 removes this problem, allowing social learning to evolve and 383 mean fitness to increase. That our participants behave in this 384 way, only engaging in social learning when their scores are 385 low (which we can infer is because they are finding individ-386 387 ual learning difficult), is encouraging. It is also encouraging that other studies using different tasks have found similar 388 effects, such as Morgan et al.'s (2012) finding that the lower 389 a participant's confidence in their performance, the more 390 they rely on social learning. 391

## 8.3.3 Payoff-Biased Social Learning Is Preferred to Other Forms of Social Learning

The Virtual Arrowhead studies discussed so far compared 395 individual learning with payoff-biased social learning, with 396 alternative social learning strategies difficult or impractical 397 for participants to use. In a recent study (Mesoudi 2011a), 398 participants were given the option to engage in three addi-399 400 tional strategies: random copying (copying the arrowhead of a randomly-chosen fellow group member), conformity 401 (in which continuous traits were divided into 10-unit inter-402 vals, i.e., 1-10, 11-20, 21-30..., and the conforming par-403 ticipant is assigned the mid-value of the most popular 404 interval in their group) and averaging (in which participants 405 were assigned the arithmetic mean of everyone in the 406 groups' values for each trait, similar to Boyd and 407 Richerson's (1985) blending inheritance), along with pay-408 off bias (copying the arrowhead of the highest-scoring 409 group member) and individual learning (directly changing 410 411 the traits with no social influence) as before.

Payoff-biased social learning was the clear favourite com-412 pared to the other social learning strategies. Across all hunts 413 played by all participants, 78 % involved individual learning, 414 19 % payoff-biased social learning, and only around 1 % 415 each of conformity, random copying and averaging (Mesoudi 416 2011a). Again, this choice of social learning strategy is adap-417 tive in the multimodal adaptive landscape implemented here. 418 As shown using agent-based models simulating each of these 419 strategies (Mesoudi and O'Brien 2008b), only payoff-biased 420 social learning outperforms individual learning, due to the 421

aforementioned reason that individual learners stuck on 422 locally optimal peaks can jump to higher-fitness peaks found 423 by more successful group members. Random copying also 424 allows participants to jump peaks, but to a random, not nec-425 essarily high, peak. Conformity allows participants to jump 426 to the most popular peak, but again there is no reason that 427 this most-popular peak is the highest (unless payoff-bias has 428 already acted). Averaging is particularly bad, as the mean 429 trait value of several peaks is likely to be mid-way between 430 all of them, i.e., in a valley. 431

## 8.3.4 Payoff Biased Social Learning Leads 432 to "Cultural Hitchhiking" 433

In Sects. 3.2 and 3.3 we saw how payoff-biased social learn-434 ing is adaptive, allowing participants to jump to high-fitness 435 peaks in the multimodal adaptive landscape. Yet this social 436 learning strategy also comes with disadvantages. As noted 437 above, the Colour trait was neutral and had no effect on the 438 score shown to participants. Despite this, Colour was copied 439 by our participants just as faithfully as the other functional 440 traits during payoff-biased social learning (Mesoudi and 441 O'Brien 2008a). 442

This was measured by calculating pair-wise inter-trait 443 correlations across all participants in a group, i.e., the corre-444 lation between all participants' Height and Width, the corre-445 lation between all participants' Height and Thickness, and so 446 on. Following periods of individual learning, these inter-trait 447 correlations were found to be quite low, around r=0.1-0.3. 448 This is to be expected, as different individual learners would 449 diverge to different peaks in the adaptive landscape, thus 450 reducing between-participant similarity. Once payoff-biased 451 social learning was permitted, however, the inter-trait corre-452 lations increased significantly to around r=0.3-0.9. This is 453 because all participants in the group copied the single most-454 successful group member (apart from that most-successful 455 participant him or herself, of course, who could not copy 456 themselves), thus all participants ended up with extremely 457 similar arrowheads. Colour showed the same pattern of inter-458 trait correlations as the other traits, indicating that Colour 459 was copied along with the other functional traits in a com-460 plete package. 461

This is an example of a neutral trait hitchhiking on func-462 tional traits, and represents the downside of payoff-biased 463 social learning: while copying a successful individual will on 464 average lead to the acquisition of adaptive behaviour, occa-465 sional neutral or even maladaptive traits might also be cop-466 ied. This hitchhiking was explored formally by Boyd and 467 Richerson (1985) as 'indirect' bias, which encompasses 468 payoff-biased social learning, in which successful people are 469 preferentially copied, and prestige bias, in which people with 470 high social status are preferentially copied (which may, or 471

A more recent study illustrates further the power of pres-479 tige bias. Henrich and Gil-White (2001) suggested that peo-480 ple often identify from whom to copy based on quite minimal 481 and subtle cues of prestige, such as looking times. Highly 482 prestigious individuals should be looked at more by others 483 than less prestigious individuals because they are good 484 sources of information, and so looking times might consti-485 tute a cheap and quick cue regarding who to copy. Atkisson 486 487 et al. (2012) tested this prediction in the Virtual Arrowhead Task, presenting participants with objective success informa-488 tion-the scores of other group members-as before, but 489 also fictional looking time information concerning how long 490 each group member had chosen to view every other group 491 members' arrowheads. Even though the looking times were 492 fictional and therefore useless, this marker of prestige was 493 used at least as much as the objective success information 494 when participants were choosing from whom to copy. So 495 again, while this prestige-biased social learning may be 496 broadly adaptive, it can easily misfire. 497

Further studies might look more systematically at the 498 conditions under which we would expect neutral or maladap-499 tive to hitchhike via generally prestigious models. We might 500 predict hitchhiking to be particularly prevalent when it is dif-501 ficult to directly assess the efficacy of different traits. In the 502 503 arrowhead task, the constant random error in feedback likely obscured the fact that Colour had no systematic effect on 504 payoffs; future studies might vary the size of this feedback 505 error to determine whether hitchhiking disappears below 506 some error threshold. Whether maladaptive traits hitchhike, 507 meanwhile, is likely dependent on their cost relative to the 508 fitness benefits of the adaptive traits exhibited by prestigious 509 demonstrators. One might predict that highly maladaptive 510 traits would not spread beyond an initial accidental copying 511 event after which their negative effects are detected (although 512 cases such as kuru [Durham 1991] or celebrity-driven copy-513 514 cat suicides [Mesoudi 2009] might suggest otherwise).

## 5158.3.5Informational Access Costs Block Social516Learning

517 In the Virtual Arrowhead experiments discussed so far, par-518 ticipants could freely view other participants' arrowhead 519 designs. This is unlikely to hold true for all real-life situa-520 tions, however. Henrich and Gil-White (2001) suggested that 521 even though many hunter-gatherer societies are relatively

egalitarian, highly skilled individuals will often receive 522 material benefits (e.g., food) or non-material benefits (e.g., 523 status) from letting others watch them engage in their skilled 524 activity. Stout (2002) found that knowledge of stone tool 525 production in adze makers of Indonesian Irian Java was care-526 fully protected through the use of highly selective appren-527 ticeships. Similarly, in industrialised societies, it is 528 commonplace for highly skilled or knowledgeable people, 529 from car mechanics to lawyers, to set prices for access to 530 their skills or knowledge. Moreover, the level of skill and 531 knowledge often covaries with their price: more knowledge-532 able lawyers set higher fees than less knowledgeable law-533 yers, for example. These prices can be seen as 'informational 534 access costs', which potential social learners must pay in 535 order to access social information. 536

In one study, I therefore added informational access 537 costs to the Virtual Arrowhead Task (Mesoudi 2008). Each 538 participant could set their own access cost, in terms of calo-539 ries, that other group members had to pay in order to view 540 their arrowhead design. These costs were added and sub-541 tracted to the participants' actual cumulative scores. For 542 example, if Participant 1 set an access cost of 450 calories 543 and Participant 2 chose to copy Participant 1, then 450 cal-544 ories would be deducted from the cumulative score of 545 Participant 2 and 450 calories would be added to the cumu-546 lative score of Participant 1. 547

As expected, participants with higher scores set higher 548 informational access costs than participants with lower 549 scores. Participants were clearly aware, then, that their fellow 550 participants will engage in payoff-biased social learning and 551 preferentially copy the highest-scoring participant, such that 552 their information would be in the highest demand and there-553 fore be most valuable. But unexpectedly, rather than seeking 554 to profit from the access costs of potential copiers, the high-555 est-scoring participants in the group typically set excessively 556 high access costs (mean = 2,500 calories, although ranging up 557 to 23,000 calories) which no other group member was willing 558 to pay. Consequently, the frequency of social learning 559 dropped, and the frequency of payoff-biased social learning 560 dropped to almost zero. At the group level, the overall increase 561 in mean score illustrated in Fig. 8.4 disappeared, and groups 562 of social learners with informational access costs performed 563 no better than groups of individual learners. 564

In a sense, this use of informational access costs to block 565 social learning is a product of the competitive nature of the 566 task as it was set up in that study. Participants were informed 567 not only of their absolute score but also their relative rank in 568 their group (although participants in this particular study 569 were unpaid, they seemed to be motivated primarily by rank 570 rather than absolute performance). It was therefore in the 571 interest of high-scoring participants to maintain their advan-572 tage by protecting their high quality information. If the 573 incentives were to be changed such that participants are only 574

8 Experimental Studies of Modern Human Social and Individual Learning...

shown or rewarded for their absolute performance and not 575 provided with information about relative performance, then 576 access costs might be lower and copying more frequent 577 (although there would still be no positive incentive to sharing 578 one's information, just no negative consequence). 579 Alternatively, if groups rather than individuals are rewarded 580 for their overall relative group score, then we might expect 581 more information sharing to occur between group members 582 (but not with members of other groups, if permitted). Adding 583 environmental change might also encourage information 584 sharing even in the most individually competitive situation, 585 as participants might seek to profit from their high-quality 586 information before it becomes out-of-date. 587

Nevertheless, this study is valuable in demonstrating that people (at least Western people) are not indiscriminately egalitarian with their information. Indeed, the apprenticeships observed by Stout (2002), as well as other institutions such as guilds, might be seen as following the same principles, with high-quality skills and knowledge protected from outsiders.

## 595 8.4 Limitations and Applications

There are, of course, many limitations of laboratory experi-596 ments. Generally, experiments lack 'external validity', the 597 degree to which the experimental situation resembles the 598 real-life situation of interest. This is true of all experiments, 599 but particularly so when seeking to simulate past techno-600 logical change in traditional societies, as we are here. The 601 computer-based task described above is obviously a highly 602 603 abstracted and simplified version of real-life artifact design practiced by past hunter-gatherers. The task lacks any kind 604 of motor activity and physical object affordances. The 605 incentive (a few pounds or dollars) is very different to the 606 incentive to feed oneself and one's family. The partici-607 pants-typically Western college students-are different in 608 many ways to the long-dead hunter-gatherers responsible 609 for manufacturing artifacts found in the archaeological 610 record. The time-frame is very different: an hour or so in the 611 experiment versus years or decades acquiring the skills 612 needed to manufacture complex artifacts such as arrow-613 614 heads or handaxes. So too is the social structure: a closed and small group of unrelated strangers in the experiments 615 versus a much larger kin-based society with overlapping 616 generations, migration from other groups, and so on. 617

All of these limitations should be recognised. Yet experiments make up for their obvious lack of external validity by having high 'internal validity', the degree to which they afford experimental control (Mesoudi 2007). In experiments we can isolate and manipulate specific variables in order to test their causal effect; we can randomly assign participants into different conditions in order to test hypotheses; we can re-run situations in multiple groups to determine whether 625 observed effects are robust or historically contingent; and we 626 can obtain complete and unbiased data regarding our partici-627 pants' behaviour. None of these are possible with historical 628 or ethnographic methods for both practical and ethical rea-629 sons. Archaeologists cannot 're-run' history or manipulate 630 key variables to see how history would have changed in 631 response to that variable, and seldom have uninterrupted or 632 unbiased historical data sets. Ethnographers cannot ran-633 domly assign contemporary hunter-gatherers into different 634 control and experimental societies to see how a key variable 635 affects behaviour. Essentially, historical and observational 636 methods are limited in being correlational, whereas experi-637 ments can test causal hypotheses. 638

Experiments can therefore be seen as a useful bridge 639 between theoretical models and historical/ethnographic 640 methods. The key point is that these methods should be used 641 in combination. Theoretical models and experiments that are 642 not informed by real-life historical and observational data 643 will simply reflect the uninformed and probably incorrect 644 intuitions of the modeller/experimenter. Conversely, histori-645 cal and observational data alone cannot be used to test causal 646 hypotheses due to their non-interventionist and correlational 647 nature. 648

This interplay is hopefully illustrated in our previous 649 application of the Virtual Arrowhead Task to a specific 650 archaeological case study. Bettinger and Eerkens (1999) 651 documented how projectile points from the Great Basin 652 region of the south-western United States from around 300-653 600 AD exhibited systematic differences between two sites. 654 In one site, in central Nevada, the inter-trait correlations 655 were very high, indicative of a small number of uniform 656 types. In eastern California, in contrast, inter-trait correla-657 tions were significantly lower, such that there were no sys-658 tematic links between the dimensions of different arrowheads. 659 Having ruled out any differences in prey or material type 660 between the two sites, Bettinger and Eerkens (1999) sug-661 gested that the difference lay in learning strategies: prehis-662 toric Nevada featured strong payoff- or prestige-biased social 663 learning, such that hunters copied a small number of designs 664 exhibited by a few high-status individuals, whereas prehis-665 toric California featured much more individual learning, 666 which increased variation as different hunters experimented 667 in different ways. 668

As noted above, our experimental simulation supported 669 this hypothesised scenario (Mesoudi and O'Brien 2008a): 670 when our participants were allowed to engage in payoff-671 biased social learning then inter-trait correlations increased 672 (like in Nevada), and when our participants had to rely on 673 individual learning then inter-trait correlations were low 674 (like in California). This supports Bettinger and Eerkens 675 (1999) hypothesis, and shows that it is consistent with actual 676 human behaviour. 677

Yet we also showed that this hypothesis only works under 678 certain assumptions that were not specified by Bettinger and 679 Eerkens (1999). For example, the hypothesis only works 680 681 under the assumption of a multimodal adaptive landscape. If there is a single optimal point design, then individual learn-682 ers will converge on this design, and inter-trait correlations 683 will remain high. Indeed, independent work testing the func-684 tional characteristics of projectile points suggests that mul-685 tiple locally optimal designs are a reasonable assumption. 686 Cheshier and Kelly (2006) found that long, thin points were 687 easier to aim and hit prey with but less likely to result in a kill 688 due to the small wounds they create, whereas thick, wide 689 points were harder to fire but more likely to result in a kill 690 because they created a larger wound. Here we have at least 691 two optima: one maximising firing power, the other maxi-692 693 mising the likelihood of a kill.

Moreover, our experimental programme suggests possi-694 ble reasons why prehistoric Nevada might have featured 695 696 more social learning than prehistoric California. Perhaps individual learning was more costly in Nevada due to its 697 harsher environment making social learning more adaptive, 698 or perhaps informational access costs were higher in 699 California therefore blocking social learning. These hypoth-700 eses, suggested by our experiments, can hopefully guide fur-701 ther archaeological research. In sum, the interplay of 702 theoretical models, archaeological data and lab experiments 703 provides a richer understanding of the past than any one of 704 these methods alone. 705

### 706 8.5 Conclusions

The aim of this series of studies (Atkisson et al. 2012; 707 Mesoudi 2008, 2011a; Mesoudi and O'Brien 2008a, b) was 708 to test the predictions of theoretical models concerning the 709 adaptiveness of contemporary humans' learning strategies, 710 using a complex task designed to be representative of real-711 life human technology. Participants in small groups designed 712 virtual arrowheads via individual and social learning, while 713 we manipulated key variables such as the form of the under-714 lying fitness functions, the possible social learning strategies 715 permitted, the cost of individual learning, and whether social 716 717 information was free or costly to access.

Our findings demonstrated that people approached this 718 task in a broadly adaptive manner. They used a simple but 719 effective reinforcement-based individual learning strategy 720 that improved their payoff by leading them to a locally-721 optimal arrowhead design. They engaged in payoff-biased 722 social learning in preference to alternative and less effective 723 social learning strategies such as conformity, random copy-724 ing and averaging, with this payoff-biased social learning 725 uniquely allowing participants to jump from low-fitness 726 locally optimal designs to high-fitness globally optimal 727

designs that had been found by more successful group 728 members. At a larger scale, payoff-biased social learning is 729 especially likely to lead to cumulative cultural evolution 730 (Aoki et al. 2012; Enquist et al. 2008; Mesoudi 2011b; 731 Powell et al. 2009) by selectively preserving and building on 732 effective cultural traits. It is therefore encouraging that our 733 participants readily and preferentially engaged in this par-734 ticular social learning strategy. 735

Moreover, both individual and social learning flexibly 736 responded to the participants' performance in real-time. 737 When participants were performing poorly, they made larger 738 changes to their arrowhead when learning individually, and 739 they were more likely to engage in payoff-biased social 740 learning. This latter 'selective learning'-copying others 741 only when individual learning is costly or difficult-has 742 been shown to be adaptive relative to a mix of pure individ-743 ual learners and pure social learners, allowing our partici-744 pants to avoid the detrimental effect of information 745 scrounging (Boyd and Richerson 1995). 746

Yet there were also flaws in our participants' learning strat-747 egies. Payoff-biased social learning was indiscriminate such 748 that participants readily copied functionless traits from suc-749 cessful individuals alongside their functional traits. Indirect 750 cues to prestige, such as looking times, were used as guides to 751 who to copy as much as objective measures of success, even 752 when it was inappropriate to do so, which may exacerbate the 753 spread of neutral or even maladaptive traits. Finally, when par-754 ticipants were allowed to set access costs that others had to pay 755 in order to see their arrowhead, they used these to block all 756 social learning. At a population level, this may be detrimental 757 to the overall preservation and accumulation of knowledge, 758 and highlights how the cooperative motivation to share infor-759 mation on the part of the demonstrator is just as important as 760 the social learners' choice of who to copy. 761

A comparison of contemporary humans' learning abilities 762 with those of prehistoric hominins (either anatomically mod-763 ern humans or Neanderthals) is beyond the scope of this 764 paper, and will be left to those expert in interpreting the 765 archaeological record. It is instructive, however, to compare 766 the results of these studies with similar learning studies of 767 chimpanzees. Some studies suggest that, in contrast to our 768 human participants, chimpanzees are less likely to switch to 769 superior solutions to tasks. Marshall-Pescini and Whiten 770 (2008), for example, found that chimpanzees will readily 771 copy and use a quite-good method for extracting honey from 772 a puzzle box (sticking a wand into the box and licking honey 773 off the end) but, when shown an even better method (using 774 the wand to open the top of the box to expose all of the 775 honey), fail to switch to this superior solution (see also 776 Hrubesch et al. 2009). This stands in contrast to our partici-777 pants, who readily abandoned their own arrowheads and 778 switched to superior designs. This lack of payoff-biased 779 social learning in chimps might explain why their cultural 780

8 Experimental Studies of Modern Human Social and Individual Learn

traditions remain non-cumulative (Tennie et al. 2009), if they 781 fail to selectively copy and switch to superior traits. 782

On the other hand, more recent studies suggest that chim-783 784 panzees will switch to superior methods if they are dissatisfied with their current payoff (Dean et al. 2012; Yamamoto et al. 785 2013), suggesting that they do exhibit some form of payoff-786 biased social learning. Dean et al. (2012) attributed a lack of 787 cumulative culture in chimpanzees instead to a lack of teach-788 ing, imitation and/or prosociality. The latter finding in particu-789 lar might be of particular importance. Chimpanzees have been 790 shown to be inordinately self-interested, failing to share food 791 with others even when there is no cost to sharing (Jensen et al. 792 793 2007; Silk et al. 2005). As we showed in our studies using informational access costs, a lack of cooperation can severely 794 block social learning. Human cumulative culture may there-795 796 fore be intimately tied to our cooperative motivations (Dean et al. 2012; Hill et al. 2009; Mesoudi and Jensen 2012). 797

Assuming that chimpanzees are closer behaviourally to the 798 common ancestor of chimpanzees and humans that lived 799 around 6 million years ago (which is, admittedly, a contestable 800 assumption), we can speculate that somewhere in the hominin 801 lineage the capacities for high fidelity and flexible payoff-802 biased social learning, tied to cooperative motivations to allow 803 individuals to copy one other, evolved and facilitated the emer-804 gence of cumulative cultural adaptations. As illustrated in 805 Sect. 4, it is possible to detect the signatures of different learn-806 ing strategies in the archaeological record, as we did in the 807 Great Basin by inferring payoff-biased social learning from 808 high inter-trait correlations and individual learning from low 809 inter-trait correlations. Perhaps the same might be possible 810 with earlier material culture to determine, say, whether 811 Neanderthals exhibited payoff-biased social learning. The 812 appearance of culturally hitchhiking neutral or maladaptive 813 traits might also serve as an indication of payoff-biased social 814 learning. In sum, hopefully the further interplay of lab experi-815 ments and theoretical models, along with comparative studies 816 of non-human primates and the archaeological study of pre-817 historic hominin material culture, will lead us to a better 818

understanding of our species' success story. 819

#### References 820

- 821 Akazawa T (ed) (2012) Replacement of Neanderthals by modern 822 humans (RNMH) project series, vol 1. RNMH Project Group, Kochi University of Technology, Tokyo 823
- Aoki K, Wakano JY, Feldman MW (2005) The emergence of social 824 825 learning in a temporally changing environment: a theoretical model. Curr Anthropol 46:334-340 826
- Aoki K, Lehmann L, Feldman MW (2011) Rates of cultural change and 827 828 patterns of cultural accumulation in stochastic models of social 829 transmission. Theor Popul Biol 79:192-202
- 830 Aoki K, Wakano JY, Lehmann L (2012) Evolutionarily stable learning 831 schedules and cumulative culture in discrete generation models. 832
- Theor Popul Biol 81:300-309

ing	
Atkisson C. Mesoudi A. O'Brien MJ (2012) Adult learners in a novel	83
environment use prestige-biased social learning. Evol Psychol 10:519-537	83 83
Bentley RA, Hahn MW, Shennan SJ (2004) Random drift and culture	83
change. Proc R Soc B 2/1:1443–1450 Rettinger RI – Ferkens I (1999) Point typologies, cultural transmission	83
and the spread of bow-and-arrow technology in the prehistoric	83
Great Basin. Am Antiq 64:231–242	84
Boyd R, Richerson PJ (1985) Culture and the evolutionary process.	84
University of Chicago Press, Chicago	84
Boyd R, Richerson PJ (1988) An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall T, Galef BG	84 84
(eds) Social learning. Erlbaum, Hillsdale, pp 29–48 Boyd B. Bisharson BI (1002) How misroavolutionary processes give	84
rise to history. In: Nitecki M. Nitecki DV (eds) History and evolu-	04 84
tion. State University of New York Press, Albany, pp 178–209	84
Boyd R, Richerson PJ (1995) Why does culture increase human adapt-	84
ability? Ethol Sociobiol 16:125-143	85
Cavalli-Sforza LL, Feldman MW (1981) Cultural transmission and	85
Cheshier I Kelly RL (2006) Projectile point shape and durability: the	85
effect of thickness: length. Am Antig 71:353–363	85
Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN (2012)	85
Identification of the social and cognitive processes underlying	85
human cumulative culture. Science 335:1114–1118	85
Dunnell RC (19/8) Style and function: a fundamental dichotomy. Am	85
Anuq 55:505–519 Durham WH (1991) Coevolution: genes, culture, and human diversity	85
Stanford University Press, Stanford	86
Ehn M, Laland KN (2012) Adaptive strategies for cumulative cultural	86
learning. J Theor Biol 301:103–111	86
Enquist M, Ghirlanda S, Jarrick A, Wachtmeister CA (2008) Why does	86
human culture increase exponentially? Theor Popul Biol 74:46–55	86
nedagogy in the transmission of cultural knowledge. In: Enfield NI	86
Levenson SC (eds) Roots of human sociality: culture, cognition, and	86
human interaction. Berg, Oxford	86
Henrich J, Boyd R (1998) The evolution of conformist transmission and the	87
emergence of between-group differences. Evol Hum Behav 19:215–241	87
Henrich J, Gil-White FJ (2001) The evolution of prestige. Evol Hum Babay 22:165–106	87
Hill K Barton M Hurtado AM (2009) The emergence of human	87
uniqueness. Evol Anthropol 18:187–200	87
Hrubesch C, Preuschoft S, van Schaik C (2009) Skill mastery inhibits	87
adoption of observed alternative solutions among chimpanzees (Pan	87
troglodytes). Anim Cogn 12:209–216	87
mizers in an ultimatum game. Science 318:107–100	87
Laland KN (2004) Social learning strategies Learn Behav 32.4–14	00 88
Lycett SJ, von Cramon-Taubadel N (2008) Acheulean variability and	88
hominin dispersals: a model-bound approach. J Archaeol Sci	88
35:553–562	88
Marshall-Pescini S, Whiten A (2008) Chimpanzees (Pan troglodytes)	88
and the question of cumulative culture: an experimental approach.	88
McElreath R. Lubell M. Richerson PL Waring TM. Baum W. Edsten E.	00 88
Efferson C, Paciotti B (2005) Applying evolutionary models to the	88
laboratory study of social learning. Evol Hum Behav 26:483-508	89
Mesoudi A (2007) Using the methods of social psychology to study	89
cultural evolution. J Soc Evol Cult Psychol 1:35–58	89
Mesoudi A (2008) An experimental simulation of the 'copy-successful-	89
nonviouals cultural learning strategy: Adaptive landscapes, producer-scroupger dynamics and informational access costs Evol	89
Free serveringer a frankres and informational access costs. Ever	

Hum Behav 29:350-363 896 Mesoudi A (2009) The cultural dynamics of copycat suicide. PLoS One 897 4:e7252 898

- Mesoudi A (2011a) An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. Evol Hum Behav 32:334–342
  Mesoudi A (2011b) Variable cultural acquisition costs constrain cumu-
- Mesoudi A (2011b) Variable cultural acquisition costs constrain cumu lative cultural evolution. PLoS One 6:e18239
- Mesoudi A, Jensen K (2012) Culture and the evolution of human sociality. In:
   Vonk J, Shackelford T (eds) The oxford handbook of comparative evolutionary psychology. Oxford University Press, Oxford, pp 419–433
- Mesoudi A, O'Brien MJ (2008a) The cultural transmission of Great
   Basin projectile point technology I: an experimental simulation. Am
   Antiq 73:3–28
- Mesoudi A, O'Brien MJ (2008b) The cultural transmission of Great
   Basin projectile point technology II: an agent-based computer simulation. Am Antiq 73:627–644
- Morgan TJH, Rendell LE, Ehn M, Hoppitt W, Laland KN (2012) The evolutionary basis of human social learning. Proc R Soc B 279:653–662
- Neiman FD (1995) Stylistic variation in evolutionary perspective inferences from decorative diversity and interassemblage distance
   in Illinois woodland ceramic assemblages. Am Antiq 60:7–36
- O'Brien MJ, Darwent J, Lyman RL (2001) Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the southeastern United States. J Archaeol Sci 28:1115–1136
- Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demogra phy and the appearance of modern human behavior. Science
   324:1298–1301

ncorrected

- Richerson PJ, Boyd R (2005) Not by genes alone. University of Chicago 924 Press, Chicago 925
- Rogers AR (1988) Does biology constrain culture? Am Anthropol 926 90:819–831 927
- Rogers DS, Ehrlich PR (2008) Natural selection and cultural rates of 928 change. Proc Natl Acad Sci U S A 105:3416 929
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS,
  Lambeth SP, Mascaro J, Schapiro SJ (2005) Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437:1357–1359
  933
- Simon HA (1956) Rational choice and the structure of the environment. 934 Psychol Rev 63:129–138 935
- Sperber D (1996) Explaining culture: a naturalistic approach. Oxford 936 University Press, Oxford 937
- Stout D (2002) Skill and cognition in stone tool production. Curr 938 Anthropol 43:693–722 939
- Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Philos Trans R Soc B 941 364:2405–2415 942
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. In: Proceedings of the sixth international congress of genetics, vol 1. pp 356–366
  945
- Yamamoto S, Humle T, Tanaka M (2013) Basis for cumulative cultural 946
   evolution in chimpanzees: social learning of a more efficient tooluse technique. PLoS One 8:e55768 948

[AU1]