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Abstract

Vigorous debates as to the evolutionary origins of culture remain unresolved due to an absence of methods for identifying learning mechanisms in natural populations. While laboratory experiments on captive animals have revealed evidence for a number of mechanisms, these may not necessarily reflect the processes typically operating in nature. We developed a novel method that allows social and asocial learning mechanisms to be determined in animal groups from the patterns of interaction with, and solving of, a task. We deployed it to analyse learning in groups of wild meerkats (*Suricata suricatta*) presented with a novel foraging apparatus. We identify nine separate learning processes underlying the meerkats' foraging behaviour, in each case precisely quantifying their strength and duration, including local enhancement, emulation, and a hitherto unrecognized form of social learning, which we term 'observational perseverance'. Our analysis suggests a key factor underlying the stability of behavioural traditions is a high ratio of specific to generalized social learning effects. The approach has widespread potential as an ecologically valid tool to investigate learning mechanisms in natural groups of animals, including humans.

Introduction

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37 It is widely agreed that scientific endeavours to understand the evolutionary roots of human
38 culture require knowledge of the extent to which the social transmission of information in
39 human and non-human societies relies on homologous mechanisms [1,2,3]. Laboratory
40 experiments can pinpoint the operation of specific mechanisms in captive animals, but cannot
41 generate evidence that the same mechanisms operate in natural social groups, subject to all
42 the stressors of life in the wild. Conversely, observations of natural behaviour alone cannot
43 discriminate between alternative social (or asocial) learning mechanisms. Here we present a
44 novel analytical tool that allows investigation of learning mechanisms in natural groups of
45 animals (including humans) and apply it to a new dataset from groups of wild meerkats. Our
46 methodology allows us to determine for the first time the social and asocial learning
47 mechanisms operating in the wild, but the methods could also be applied to captive groups.

48 Traditional social learning experiments involve presenting a set of subjects, or
49 “observers”, with the opportunity to observe one or more “demonstrator” animals that have
50 been trained to perform target behaviour, usually the solution to a foraging task. The subjects’
51 performance is then assessed in a subsequent test phase, in which they are given access to the
52 task, to ascertain whether acquisition of the behaviour has been improved as a result of the
53 observational experience, compared to control subjects. This traditional social learning
54 experiment design (henceforth ‘traditional approach’) has been modified in various ways to
55 isolate different social learning mechanisms, taking advantage of the fact that the
56 experimenter has a high degree of control over what social cues are available to the observers
57 [4].

58 The traditional approach has been fruitful in establishing that certain species have a
59 capacity for specific types of social learning [4]. However, the high level of experimental
60 control comes at the cost of decreased ecological validity: the traditional approach does not

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61 allow the level of social interaction that would occur in freely interacting groups of animals.
62 Consequently, the traditional approach can tell us little about the relative importance of
63 different social learning mechanisms in such situations, or the role each one has in promoting
64 or inhibiting the emergence and stability of traditions under natural conditions [5,6]. For
65 example, keas (*Nestor notabilis*) have been shown to use observational conditioning in
66 captivity [7] but failed to do so in the wild [8]. Furthermore, whilst laboratory experiments on
67 chimpanzees (*Pan troglodytes*) suggest an important role for imitation in tool use tasks [9],
68 some field researchers [10] suggest local enhancement plays a dominant role in the
69 acquisition of tool use in the wild. Similarly, social learning appears to be primarily restricted
70 to the juvenile period in wild chimpanzees [10] but not restricted in this way for captive
71 chimpanzees[9]. It is also conceivable that some species may not exhibit evidence of a
72 capacity for a specific type of social learning unless presented with naturalistic social
73 interactions. Finally many species are not amenable to study in the laboratory, and though
74 approaches similar to the traditional approach are sometimes possible in the field [11,12], this
75 will not always be the case. This is a severe limitation if one's goal is to obtain a picture of
76 the taxonomic distribution of social learning mechanisms or understand the selection
77 pressures driving their evolution.

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Such concerns have recently led researchers to devise experiments and observational studies of the diffusion of innovations through groups of freely interacting animals [11,13,14]. These range from initiated diffusions (where groups are presented with a novel task) in captive and wild groups, to natural diffusions of spontaneously arising innovations. It has been noted that whilst ecological validity and the potential for understanding the factors affecting culture increases with increased naturalism, the potential for understanding social learning processes decreases [15]. Further experimental control is possible in initiated diffusions by “seeding” groups with demonstrators trained to solve the task using one of two

86 or more different options: the researcher can then test whether the groups tend to adopt the
87 same option as their demonstrator. However, in all diffusion experiments, the experimenter
88 has, at best, very limited control over the social cues received by each individual, so
89 information on these must be gathered as observational data [16]. Such data, collected on a
90 fine temporal scale, is likely to contain statistical patterns indicative of different social and
91 asocial learning mechanisms, but the analytical tools required to extract these patterns have,
92 to date, been lacking.

93 Here we present a conceptual framework for the analysis of detailed observational
94 data from seeded or unseeded diffusion studies (or indeed other social learning experiments)
95 and present methods for detecting the presence of different mechanisms and quantifying their
96 effects. We deploy a novel statistical approach. We call this a ‘stochastic mechanism-fitting
97 model’ (henceforth ‘SMFM’) since it formulates hypothetical mechanisms as stochastic
98 models, allowing us to assess the evidence for their presence and estimate the size and
99 duration of their effects.

100 We applied the SMFM to data from a specially-designed initiated social diffusion
101 experiment on wild meerkats. Meerkats are cooperatively breeding mongooses that have been
102 the subjects of extensive studies of social learning under natural conditions [17]. However,
103 the mechanisms by which information spreads through meerkat groups (or indeed social
104 groups in any species) are unknown.

105 Demonstrator animals (subordinate adult male meerkats) were trained, out of sight of
106 others, to obtain food from an experimental apparatus (hereafter a ‘Box’) using one of two
107 ‘option-types’ (henceforth ‘Flap’ and ‘Tube’) positioned on opposite sides of a clear plastic
108 box (Fig. 1A and B). The demonstrators then reliably performed their trained behaviour in
109 front of a group of conspecifics over eight sessions, during which two identical Boxes were
110 positioned 30cm apart, facing opposite directions (Fig. 1A), giving four possible ‘options’ for

111 solving the task. Three meerkat groups were exposed to Flap-solver demonstrators, three to
112 Tube-solvers, and a further three had no demonstrators (controls). We recorded the duration
113 of all bouts of observation or interaction with the Boxes, noting the identity of the individuals
114 involved, whether an individual observed another interacting with a Flap or Tube, whether it
115 witnessed successful entry into a Box, whether food was obtained, and other relevant
116 variables (see Materials and Methods for details). The two-Box design allowed us to
117 distinguish between local enhancement effects (attraction to a particular location [18]) and
118 stimulus enhancement (attraction to a particular stimulus type, such as black flaps or white
119 tubes [19]), while other aspects of the method allow alternative learning mechanisms to be
120 isolated (see below).

121 Historically, researchers have assumed that imitation and teaching may be necessary
122 for stable cultural traditions [2,20,21], a view conflicting with recent empirical and
123 theoretical work suggesting that stimulus and local enhancement can result in the formation
124 of traditions [22,23,24,25,26]. Here we utilise a method that can be used to study these and
125 other learning mechanisms in a natural context, and allow us to investigate, empirically, the
126 relationship between learning mechanisms and the emergence of behavioural traditions.

127 We fitted stochastic models (see Methods and Materials) to the data, modelling
128 individuals' rates of transition between states of not interacting and interacting with each
129 specified Box and Option (Fig. 1B). We modelled the rate at which an individual, i , initiated
130 a bout of interaction with each Flap and Tube as a function of (i) individual differences in
131 rate, (ii) i 's past successes using Flap and/or Tube (asocial learning), (iii) the observed
132 number of entries by others to the Box using each option (direct social learning), and (iv) the
133 latency since i observed another individual interacting with each option (transient social
134 effects). We then used a stochastic model of the rate of interaction with the task in continuous
135 time, in which the rate of interaction with each option was specified at a given time. Learning

136 effects were modelled using an approximation to the Rescorla-Wagner learning rule, where
137 association of an option-type with food increased to a maximum strength with repeated
138 rewards. We derived a likelihood function and used Markov Chain Monte Carlo (MCMC) to
139 generate posterior samples for the parameters in the model. We summarise the posterior
140 sample using the median and 95% highest posterior density intervals (denoted as “95%
141 HPD”), giving the range of probable parameter values. Where relevant we also provide
142 posterior probabilities for statements regarding inequalities of parameters: for example
143 $p(s_{In} \leq s_R) = 0.019$ means that, conditional on the model, there is only a 1.9% probability that
144 s_R is less than or equal to s_{In} . To explore factors affecting the rates of task solving and task
145 abandonment we used Cox models, which have the advantage that they make no specific
146 assumptions about the shape of latency distributions underlying the model [27]. We used a
147 model averaging procedure to estimate effects, based on Akaike’s Information Criterion
148 (AIC), and present back-transformed 95% unconditional confidence intervals (denoted “95%
149 UCI”) [28]. Full details of the models and model selection procedure are given in the
150 Supporting Information.

152 Results

153 Excluding the six trained demonstrators, 77/170 meerkats manipulated the task with a
154 total of 513 manipulations (mean= 6.7 per manipulator), 36 individuals were successful in
155 obtaining food (i.e. were “solvers”) with a total of 271 successful manipulations (mean= 7.5
156 per solver). The models identified nine separate processes underlying the successful foraging
157 behaviour of the meerkat groups, including three separate social learning processes and a
158 further six asocial learning processes (Fig 2, Table 1). In general, social factors played critical
159 roles in drawing meerkats to interact with the apparatus, and keeping them at the task, while
160 asocial learning processes dominated task acquisition.

161 Three factors were found to increase the rate of interaction with the box (Fig 2). The
162 first was operant conditioning (Process 1 in Fig 2, Table 1). The observed rate of interaction
163 with the box by a given individual was found to be positively associated with their number of
164 previous successful interactions, in an option-type specific manner. The estimated effect of
165 each successful manipulation for an average (median) subordinate meerkat was $\alpha = 0.051$;
166 95% HPD= [0.040, 0.063], where α is the parameter that quantifies the learning rate in the
167 Rescorla-Wagner model (see Eqn. 2). In contrast, dominant meerkats tended to be affected
168 very little by operant conditioning ($\alpha = 5.5E-12$; 95% HPD= [0, 9.9E-4]).

169 Second, we found that meerkats that observed a conspecific gain entry to the box
170 ($s_{in} = 0.0035$; 95% HPD=[0.0017, 0.0055]) themselves subsequently increased their rate of
171 interaction with the box (Process 2 in Fig 2, Table 1). Here and below, s'' terms can be
172 viewed as social equivalents to α . This observational effect was stronger than merely
173 observing an individual feeding inside the box ($s_{in} - s_R = 0.0028$; 95% HPD= [-5.1E-5,
174 0.0058]; $p(s_{in} \leq s_R) = 0.019$), and elevated relative to individuals who did not observe the
175 interaction at all ($s_{in} - s_{All} = 0.0028$; 95% HPD= [2.6E-5, 0.0054]; $p(s_{in} \leq s_{All}) < 0.001$; see Fig
176 S2). However, we found no evidence that the effect was stronger for individuals who
177 observed a conspecific both gaining entry to a box and receiving a reward ($s_{InR} - s_{InNR} = -$
178 $5.2E-4$; 95% HPD= [-0.0050, 0.0045]; $p(s_{InR} \leq s_{InNR}) = 0.583$), implying that observing a
179 conspecific gain entry to the box was necessary and sufficient for direct social learning to
180 occur. This effect generalised between option-types as observations of individuals gaining
181 entry via the flap increased rates of interaction with the tube, and vice versa (see Fig S1).
182 However, there was weak evidence that the effect was stronger on the same option-type
183 ($s - s_{cross} = 0.0022$; 95% HPD= [-1.1E-4, 0.0045]; $p(s \leq s_{cross}) = 0.027$; see Fig S1). These
184 observations rule out an interpretation of this form of observational learning in terms of local

185 or stimulus enhancement, observational conditioning, imitation or response facilitation, and
186 appear to be most consistent with the process of ‘emulation’ [29]. Broadly defined, emulation
187 occurs when after observing a demonstrator interacting with objects in its environment an
188 observer becomes more likely to perform any actions that bring about a similar effect on
189 those objects [4]. Here, the meerkats appear to have learned through observation that it was
190 possible to get into the box, and observation of others getting into the box makes them more
191 likely to try to do so themselves.

192 Third, we found that individuals were more likely to interact with all options on either
193 Box immediately after observing a conspecific interacting with any one of them (see Fig 3.
194 Process 3 in Fig 2, Table 1). We had allowed for the fact that observing others might
195 transiently increase an observer’s rate of interaction with the box, which could indirectly
196 result in social learning by influencing its asocial learning experience– for instance, through
197 ‘stimulus enhancement’ or ‘local enhancement’ [4]. This was detected by including a
198 component that was a function of the time since an individual had observed another
199 individual interacting with each other option, assuming such effects decay exponentially in
200 time (see Fig S2). There was strong evidence that the effect was larger for the specific option
201 and Box observed, indicating it was highly spatially-specific, and more pronounced in non-
202 adults than in adults (see Fig 3 and Table S1). This specific effect did not generalize to the
203 same option-type on the other Box, ruling out stimulus enhancement, and strongly indicating
204 an interpretation in terms of ‘local enhancement’. Local enhancement occurs when, after or
205 during a demonstrator’s presence, or interaction with objects at a particular location, an
206 observer is more likely to visit or interact with objects at that location [4,18].

207 Our model also enables us to estimate the duration of the local enhancement effect.
208 For an exponential model, this is intuitively captured by the half-life (time taken for the effect
209 to halve in magnitude), which we estimated to be 20s (95% HPD=[12, 29]). To our

210 knowledge this is the first precise estimate of the duration of local enhancement, although
211 experimental studies have determined that local enhancement effects persisted for greater
212 than a fixed interval¹[e.g. 30]. In addition, we can investigate the conditions under which
213 local enhancement occurred by fitting alternative models and comparing deviance
214 information criterion (DIC) values. We tested for transient effects conditional on observation
215 of a conspecific gaining entry to the box ($\Delta\text{DIC}=+168.2$), and observation of a conspecific
216 obtaining a reward ($\Delta\text{DIC}=+137.8$). We also fitted a model in which the transient effects
217 operated on all individuals present at an experimental session, regardless of whether they
218 were recorded as an observer ($\Delta\text{DIC}=+399.2$). All alternative models provide a worse fit to
219 the data, suggesting that observation of a conspecific interacting with an option was a
220 necessary and sufficient condition for the transient social effects to occur.

221 We estimated that meerkats that had previously solved the task subsequently solved it
222 at a 50% higher rate (Process 8 in Fig 2, Table 1: $x1.51$; 95% UCI= [1.00, 2.01]) and
223 abandoned the task at a third of the rate (Process 4 in Fig 2, Table 1: $x0.34$; 95% UCI= [0.23,
224 0.49]) during future manipulations of the same option-type. Counter-intuitively, the rate of
225 task abandonment increased with the number of further previous successes at either option-
226 type (Process 6 in Fig 2, Table 1: $x1.09$ each successful manipulation; 95% UCI= [1.04,
227 1.14]) perhaps due to decreased motivation, with the meerkats having become satiated. In
228 addition, the number of previous unsuccessful interactions was negatively associated with the
229 rate of abandonment (Process 5 in Fig 2, Table 1: $x0.84$ each unsuccessful manipulation; 95%
230 UCI= [0.74, 0.96]; option-type general) and positively associated with the rate of solving

¹ We suggest that determining whether a social effect persists for greater than a fixed interval is not a particularly good way of quantifying its duration. Whether or not we can detect an increase relative to baseline is as much a function of sample size as the nature of the process. If we had a very large sample size we might conclude that local enhancement lasts for a very long time: however, the estimated effect at this point would likely be so small as to be unimportant. It makes more sense to ask how fast the effect fades- the precision of this estimate is then a function of sample size.

231 (Process 9 in Fig 2, Table 1: $x1.12$ each successful manipulation; 95% UCI= [1.01, 1.25];
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2 232 option-type specific) suggesting individuals might acquire useful information from
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5 233 unsuccessful manipulations. This latter finding is consistent with findings that the ‘error’ can
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7 234 be crucially important to effective trial-and-error learning.
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10 235 While there was little evidence that observation of others directly affected the rate of
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12 236 solving the box task (see Table S5), an individual’s rate of task abandonment declined with
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14 237 the number of successes it had observed (Process 7 in Fig 2, Table 1: $x0.84$ each observation;
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17 238 95% UCI= [0.76, 0.94]), suggesting that observing the success of others decreased the rate at
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19 239 which individuals gave up on the task. There was strong evidence that this effect required
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22 240 observation of a conspecific both gaining entry to the box and obtaining a food reward and
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24 241 that the effect was not option-type specific (see Table S6). To our knowledge, this effect of
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27 242 social learning has not previously been detected in any previous human or animal experiment.
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29 243 As the effect of observing others’ successes appears primarily to encourage individuals to
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32 244 persist with the task, in the absence of a recognized label we have termed this process
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34 245 ‘observational perseverance’.
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36 246 Despite strong evidence of social learning processes affecting the learning of wild
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39 247 meerkats, the demonstrators’ techniques did not spread to form strong group-level traditions
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41 248 (see Fig 4, modified Option Bias test [31]; $P = 0.080$; see Supporting Information for details).
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44 249 We suggest that in this study the ratio of specific to generalized local enhancement effects
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46 250 was too low to promote the maintenance of the demonstrated option. Had the dominant social
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49 251 learning effects been more strongly option specific, rather than generalizing to other options,
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51 252 then traditions may have been detected. As a test of this hypothesis, we applied the SMFM
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54 253 method to experimental data reporting stronger evidence of group-level traditions in meerkat
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56 254 groups [5] and, as predicted, found the estimated transient effects were more specific to the
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58 255 observed option-type (Fig 5; see Supporting Information).
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Discussion

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Groups of wild meerkats were found to solve a novel foraging task through an interwoven complex of nine separate processes, including three types of operant conditioning and three separate forms of social learning. With respect to the latter, we found that observation of others interacting with and solving the task made meerkats more likely to succeed in a given bout of interaction with the task. This is unlikely to be a result of imitation (copying a motor pattern), since observing successful manipulations did not raise observers' solving rate disproportionately when using the same option type, nor did it improve the rate at which they solved the task during a bout of interaction. Rather, observation of others' successes caused individuals to interact with the task at higher rates and to persist for longer once they had begun a bout of interaction, with attention being transiently drawn to specific variant solutions. The dominant social influence was a specific local enhancement effect, which attracted individuals to the exact option and Box with which they observed another individual interacting, but emulation and observational perseverance also played a role. While it is known that influences on perseverance may in turn affect learning (e.g. [32]) the role of social observation in mediating perseverance and hence the acquisition of new skills has not previously been described. Moreover, although stimulus and local enhancement are commonly thought of as cognitively unsophisticated, an understanding of simple mechanisms is central to our understanding of cognitive evolution [33]. Laboratory studies commonly infer local and stimulus enhancement when evidence for imitation is lacking, but seldom discriminate between them, examine the magnitude or duration of these effects, specify the conditions under which they occur, or describe how they interact with other asocial and social learning processes. Nor, unlike the SMFM approach, do established social learning methodologies typically identify multiple learning processes underlying a particular bout of

281 behaviour. Accordingly, the insights gained from this study go significantly beyond
282 conventional studies of social learning, or the detection of local enhancement in the
283 laboratory.

284 Fig. 2 and Table 1 provide a summary of the effects found, and our causal
285 interpretation. Whilst not all effects detected map easily onto existing terminology for social
286 learning mechanisms, this terminology is based primarily on the study of animals in artificial
287 (i.e. laboratory) contexts, and existing classification schemes are widely thought to be
288 incomplete, with overlapping and non-hierarchical categories, and with evidence for several
289 processes contentious (e.g. [4,34]). The processes isolated here have the advantage that they
290 are known to be deployed in a natural context by wild animals. We are also able to infer the
291 conditions for each effect to occur, and the consequences this has for an individual's future
292 behaviour. As such, our SMFM approach might yield important insights into the limitations
293 of primarily laboratory-based terminology (e.g. [4,35]) for describing those learning
294 mechanisms actually deployed by animals in a natural social and ecological context. Perhaps
295 more importantly, the SMFM framework allows for the fact that information transmission in
296 animal groups might reflect a composition of multiple mechanisms, and provides a means for
297 disentangling and quantifying the mechanisms' individual effects in both laboratory and field
298 studies.

299 Moreover, our SMFM analysis detects strong evidence for social learning processes
300 affecting the learning of wild meerkats, despite the fact that demonstrators' techniques did
301 not spread to form group-level traditions. This has two important implications. First,
302 researchers deploying conventional tools reliant on finding between-group differences in
303 behaviour to infer social learning are probably failing to detect many instances of social
304 learning in natural animal populations. This is consistent with recent empirical findings
305 suggesting that, contrary to common assumption [31], social learning need not lead to within-

306 group homogeneity [5,12,36]. The SMFM approach has the advantage that it detects social
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2 307 influences on learning regardless of whether they result in population differences in
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5 308 behaviour. Second, by linking mechanisms to social behaviour, the SMFM approach is able
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7 309 to explain why, in this instance, traditions did not form. We suggest that in this study the ratio
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10 310 of specific to generalized local enhancement effects was too low to promote the maintenance
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12 311 of the demonstrated option. Had the dominant social learning effects been more strongly
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15 312 option-type specific, rather than generalizing to other option-types, then traditions may have
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17 313 been detected.

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19 314 While it is possible that the operation of mechanisms such as imitation may allow
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22 315 greater fidelity in the transmission of information [2], our analysis suggests that other factors
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24 316 are potentially important, consistent with recent experiments on humans, which suggest that
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27 317 faithful transmission and cumulative cultural change may occur in the absence of imitation
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29 318 [37]. Our analysis implies that the persistence of traditions is more dependent on whether the
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32 319 social learning processes deployed are highly option specific, thereby failing to generalize to
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34 320 other solutions to the task in hand, rather than on the mechanism through which social
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37 321 learning occurs. Researchers have frequently assumed that the occurrence, persistence and
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39 322 complexity of behavioural traditions in different species reflect alternative underlying
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41 323 learning mechanisms [1,2], yet hitherto it has not been possible to test this. It is also widely
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44 324 assumed that human cultural traditions are maintained through imitation and teaching
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46 325 [2,20,21], and that the greater stability of human traditions compared to those of other
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49 326 animals reflects a reliance on different learning mechanisms, but these assumptions are also
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51 327 virtually never tested. Our findings raise the possibility that human cumulative culture may
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54 328 require mechanisms that promote specificity in the solution adopted, such as conformity and
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56 329 punishment of violators of social norms [38], rather than, or as well as, high fidelity of
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58 330 information transmission. We suggest that the analytical tools presented here provide the
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1 331 means to meet these challenges and thus to develop a fuller understanding of the relationship
2 332 between human and animal culture.

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5 333 We note that application of SMFM to different task designs would allow researchers
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7 334 to distinguish between further mechanisms. For example, imitation and emulation could be
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9 335 distinguished if two options involved different motor patterns, but resulted in the same
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11 336 movements of the task (a ‘two-action test’ [39]). The SMFM would detect whether social
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13 337 influences are option-specific (indicating imitation), as well as providing additional
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15 338 information about which transitions are influenced, the time course of the effect, and the
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17 339 conditions under which it arises. The approach could also be generalized to apply to natural,
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19 340 rather than experimentally induced, traditions in animals, with particular utility where
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21 341 multiple options are observed (e.g. alternative ant-dipping methods by chimpanzees, *Pan*
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23 342 *troglydytes* [40], or variant tools used by New Caledonian crows, *Corvus moneduloides* [41].

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29 343 Whilst existing approaches allow inferences to be made about the way in which
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31 344 individuals use social information to solve a task, to our knowledge none do so at a sufficient
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33 345 level of detail to allow specific psychological mechanisms to be identified. For instance,
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35 346 Kendal et al [42] provide a method for quantifying the extent to which social learning
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37 347 influences the rate at which individuals approach and subsequently solve novel tasks.
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39 348 However as this method is applied at the level of the group, it cannot take into account the
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41 349 dynamic nature of skill acquisition, whereby an individual’s competence changes over time
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43 350 in relation to its specific previous experience. In contrast, McElreath et al [43] model
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45 351 individuals’ choices between alternative options as a function of their previous observations
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47 352 of others’ choices and the reward obtained, thus allowing inference about the social learning
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49 353 strategies being employed. However, this approach is only able to detect learning
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51 354 mechanisms that influence option choice, and not those that influence rate of interaction,
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53 355 success or task abandonment. Our approach also differs from the recent use of multistate
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356 Markov chain models to model animal behaviour [44] since the rates of transition between
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2 357 states are a function of each individual's past experience. Nonetheless, all of these studies
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5 358 share with SMFM the strategy of formulating hypotheses about behavioural mechanisms as
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7 359 stochastic models, which can be fitted to, and evaluated by time-structured data. We feel this
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10 360 under-used approach is likely to prove particularly fruitful in the study of animal behaviour
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12 361 [45].
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14 362 A stochastic modelling approach could allow researchers to study mechanisms of
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17 363 behaviour in the wild, including in species that are not amenable to experimental
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19 364 manipulation. This would allow comparisons to be made across a wide range of species, not
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22 365 just convenient laboratory models or species for which field experiments are feasible. This
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24 366 approach could be of particular utility for the study of all aspects of social behaviour (e.g.
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26 367 communication, grouping, social networks, agonistic and affiliative encounters), where it can
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29 368 be difficult to manipulate the social cues received by an individual experimentally, in either
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32 369 the lab or the field. There is also considerable potential for applying similar techniques to
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34 370 analyze aspects of human behaviour within the social sciences. Thus the approach has
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36 371 widespread potential as an ecologically valid analytical tool with which to investigate
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39 372 learning mechanisms in natural groups of animals, including humans.
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43 374 **Materials and Methods**

45 375 46 376 *Ethics Statement*

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49 377 All data collection was carried out following Association for the Study of Animal Behaviour
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51 378 guidelines, with ethics approval from the Universities of Cambridge and Pretoria, under
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56 379 Northern Cape Conservation Authority Permit ODB 2575/2009.
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381 ***Study site and meerkat population***

382 Experiments were conducted between January and May 2009 on nine groups of 12-24 free-
383 living meerkats (176 total) in the Kuruman River Reserve in northern South Africa. All
384 individuals were habituated to close observation (<1m) and could be recognised through
385 unique marks of hair dye on their fur. Groups were located by radio-tracking one collared
386 individual in each group. Whilst the meerkat population is habituated to human observers, it
387 is entirely wild and thus subject to intense predation and food restriction [46,47], and unlike
388 captive groups, the meerkats exhibit natural social dynamics including dispersal, eviction,
389 inter-group encounters and infanticide [48]. Crumbs of egg are used to attract meerkats onto
390 scales for weighing as part of a long-term study, but these crumbs are <1g (typically less than
391 0.15% of body weight). Rates of predator attack may be lower while researchers are present,
392 but observers are not present continuously and survival rates are still lower than in related
393 species [46].

394

395 ***Experimental apparatus***

396 All experiments used identical “Box” apparatus (Fig. 1 a, Fig S3). A Box consisted of a
397 rectangular plastic box 37.5 cm long, 26.5 cm wide and 15 cm high. One face of the box had
398 a black cat flap, hinged at the top, while the opposite face had a plastic tube which led into
399 the box and protruded 2 cm from the face diametrically opposite to the flap. The tube was
400 lined with a baggy, white fabric sleeve that blocked visual access to the inside of the box.
401 Meerkats could either go through the flap to obtain food (crumbs of hard-boiled egg and
402 pieces of freshly-killed scorpion) from a clear plastic pot (“Flap technique”) or push through
403 the sleeve into the tube and rip apart a kitchen paper lid to access food from another pot
404 (“Tube technique”). Boxes were made of clear plastic with perforations to allow individuals
405 to see and smell the contents.

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2 407 ***Training demonstrators***
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5 408 One demonstrator in three groups was trained on the Flap technique, and one demonstrator in
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7 409 another three groups was trained on the Tube technique. A further three control groups had
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9 410 no demonstrators. All demonstrators were subordinate adult males. We ensured that only
10
11 411 demonstrators were exposed to training by conducting training sessions when demonstrators
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13 412 were foraging out of sight of the rest of the group or when demonstrators were babysitting
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15 413 pups that were underground at the breeding burrow while the rest of the group was foraging
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17 414 elsewhere. Demonstrators typically required five days of training to reach proficiency in
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19 415 either technique (4-9 training trials per demonstrator). Once demonstrators were fully trained
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21 416 (successful completion on five subsequent presentations), we conducted one training trial
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23 417 with two identical boxes, facing opposite directions. In all cases, demonstrators successfully
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25 418 obtained food from both boxes using their trained technique.
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32 419 *Flap training:* we began by propping open the flap and leaving a trail of food leading into the
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34 420 box. We then incrementally closed the flap so that the individual had to push against it to
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36 421 enter the flap. Training ended once individuals reliably approached the box, pushed through
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38 422 the flap to obtain food from the pot inside and subsequently exited the box.
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41 423 *Tube training:* We trained demonstrators on the Tube technique by first enticing them to go
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43 424 through the tube (with no sleeve) and obtain food from the pot inside. We then attached the
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45 425 sleeve and made it increasingly baggy until the sleeve obscured the view into the tube and the
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47 426 demonstrator had to push through it to go through the tube. Once demonstrators were reliably
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49 427 going through the tube in this manner, we began affixing a kitchen paper lid to the pot
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51 428 containing rewards. Initially, the lid was loosely attached on one side, so that the individual
52
53 429 could put its paw under the paper to scoop out food. As individual grew more competent at
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55 430 this technique, we began to attach the paper more securely on all sides so that paper had to be
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1
2 431 ripped to access the food. Training ceased once demonstrators reliably approached the box,
3 432 pushed through the tube, broke the paper lid and consumed food.

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7 434 *Control groups:* to ensure that individuals in control groups were not afraid of the Boxes, we
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9 435 conducted a session prior to the group phase where the two boxes were placed on the floor
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11 436 and could be seen by all group members. No meerkats displayed mobbing behaviour,
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13 437 produced alarm calls or showed any fearful response to the Boxes, and no individuals
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15 438 attempted to enter the boxes.

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22 440 ***Group phase***

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24 441 Once demonstrators were trained, group sessions were conducted during the morning period
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26 442 when all group members were present at the sleeping burrow before setting out to forage.
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28 443 Meerkats do not eat during the night, so motivation to obtain food should be comparable for
29
30 444 all individuals. Two identical boxes, 30cm apart and facing opposite directions were placed
31
32 445 adjacent to the sleeping burrow, visible to and approximately equidistant from all group
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34 446 members. Sessions lasted 3 – 35 mins (mean = 19 mins \pm 0.9), depending on how long the
35
36 447 group spent at the burrow, with sessions ending once the first individual moved more than 20
37
38 448 m from the burrow. We conducted eight sessions at each group, with sessions spaced at least
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40 449 three days apart (mean days between sessions = 11 \pm 0.5). For one group, MM, we conducted
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42 450 an additional ninth session so that the total duration of all sessions was comparable (within 20
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44 451 mins) at all groups. In all experimental groups the trained animals successfully demonstrated
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46 452 the target behaviour proficiently.

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56 454 Sessions were videorecorded using a Panasonic NV-GS80 camcorder (Panasonic
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58 455 Corporation, Kadoma, Japan). From the videos, the duration of all bouts where an individual

1 456 interacted with a box or observed another meerkat interacting with a box were later
2
3 457 transcribed by AT and JS. Bouts of interaction and observation could be coded
4
5 458 unambiguously, and independent coding of the first five group sessions by AT and JS showed
6
7 459 interobserver reliability of >95%. An interaction bout refers to a discrete period spent
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9 460 interacting with the apparatus (scratching, pushing or otherwise manipulating it). Interaction
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11 461 bouts commenced when a meerkat made physical contact with the apparatus and ended when
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13 462 the animal moved away from the apparatus. During interaction bouts, we noted which part of
14
15 463 which box the individual interacted with (flap, tube or other), whether it entered the box and
16
17 464 whether it obtained food. We recorded an individual as solving the task when it gained access
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19 465 to food inside the box, and we refer to the bout of interaction leading to this as a successful
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21 466 interaction. Observation bouts were defined as occurring when a meerkat was within 1m of,
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23 467 and had its head oriented towards, another individual that was interacting with the box.
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25 468 During observation bouts, we noted whether an individual observed another interacting with
26
27 469 a flap or tube and whether it witnessed successful entry into the box and/or acquisition of
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29 470 food. Whenever an individual ripped a paper lid or consumed the majority of the food in a
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31 471 box, we waited for it to leave and then rapidly removed the box (< 10 secs), affixed a pre-
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33 472 prepared replacement paper lid and replenished the food before placing the box back in its
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35 473 original position.
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50 *Data Analysis*

51 477 Full details of the model, model selection procedure and causal interpretation of the model
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53 478 can be found in the Supporting Information. Here we give a brief overview of the stochastic
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55 479 mechanism-fitting model. In sum, we derived a likelihood function and used Markov Chain
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57 480 Monte Carlo (MCMC) to generate posterior samples for the parameters in the model, using
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481 WinBUGS 1.4 [49], which were analysed using the coda [50] package in the R statistical
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 2 482 environment [51].
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 7 484 *Stochastic model of interaction with the task:* We modelled the rate at which individuals
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 9 485 initiated bouts of interaction with option-type k (flap=1, tube=2), on box l (left=1, right=2)
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 11 486 for individual i in group j at time t in session s as:
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$$487 \lambda_{ijkl}(t) = \exp(\mu_k + I_{ij}) + \omega V_{ijks}(t) + T_{ijkl}(t), \quad 1$$

17 488 where μ_k determines the rate of interaction for option-type k, I_{ij} is a linear function of time-
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 19
 20 489 constant variables influencing i's baseline rate of interaction with the task (age-class, sex,
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 22 490 dominance and individual and group-level random effects), $V_{ijks}(t)$ is i's association of
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 24 491 option-type k with reward, which is a function of past asocial and direct social learning (see
 25
 26 492 below), $\omega \geq 0$ is a parameter determining the relative influence of learning, and $T_{ijkl}(t)$ is a
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 28 493 function describing transient social effects on i's rate of interaction with option-type k, on
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 30 494 box l at time t during session s (see below).
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34 495 Learning in the model was based on the established Rescorla-Wagner learning rule [52],
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 36 496 where a rewarded interaction with k by individual i in group j, increments its association with
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 38 497 that option-type as follows:
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$$498 \Delta V_{ijks} = \alpha (1 - V_{ijks}) \quad 2$$

46 499 where α is a parameter controlling how quickly the maximum association is attained. This
 47
 48 500 can be approximated, and extended to include the direct effects of observation as follows:
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 50

$$501 V_{ijks}(t) = 1 - \exp(-\alpha R_{ijks}(t) - s O_{ijks}(t)) \quad 3$$

54 502 where $R_{ijks}(t)$ is the number of times i has been rewarded for interacting with k prior to time t
 55
 56
 57 503 in session s and all previous sessions. $O_{ijks}(t)$ is the number of observations by i of
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 59 504 interactions with k prior to time t in session s and in all previous sessions and s controls the
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505 strength the social learning in a manner analogous to α . This means that inferences regarding
 506 s assess the evidence that observation of another individual solving the task exerts a
 507 permanent influence on the observer's future rate of interaction with the flap and tube, as
 508 oppose to a transient effect (see below). We further generalised learning to investigate the
 509 conditions under which direct social learning occurred, by distinguishing different types of
 510 observation events, and allowing the rate of social learning to vary between them (e.g. s_{In}
 511 denotes the effect of observing a conspecific gain entry to the box).

512 We modelled transient social effects these effects by taking $T_{ijkl}(t)$ to be a function of the
 513 time since the times since another individual had last interacted with each option at each box
 514 within that session. We assumed that each of these effects would be strongest while a
 515 conspecific was interacting with the option in question, and fade away to baseline levels as
 516 time went on. For example, we modelled the effect of observation of a conspecific at the
 517 same option-type on the same box (SOSB) effect as follows:

$$T_{ijkl}(t) = \theta_{SOSB} \exp(-\beta x_{ijkl}(t)), \quad 4$$

518 where $x_{ijkl}(t)$ is the time since the last observation of a manipulation by individual i in group
 519 j , during session s of option-type k on box l , excluding manipulations by i , with $x_{ijkl}(0) = \infty$,
 520 $\theta_{SOSB} \geq 0$ gives the strength of the SOSB effect, and $\beta \geq 0$ is the rate at which transient social
 521 effects die away, with $H = \ln(2)/\beta$ giving the half-life of the effects. We expanded the
 522 model to include transient effects operating across options and used the contrasts between
 523 these effects to distinguish local and stimulus enhancement. For example, stimulus
 524 enhancement would be inferred if observation increased interaction with the same option-
 525 type on a different box (SODB) more than the different option-type on the different box
 526 (DODB), i.e. $\theta_{SODB} > \theta_{DODB}$. We further expanded the model to include interactions of asocial
 527 learning, direct social learning, and transient effects with age-class, sex and dominance.
 528

529 Details of the final model are given in Table S1. In the results we give 95% highest posterior
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2 530 density (HPD) intervals for parameters and contrasts of interest, taken from the final model or
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5 531 from a model with unimportant effects added back in.
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10 533 *Modelling probability of successful manipulation:* To model the probability that an individual
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12 534 would be successful (i.e. obtain food) in a given bout of manipulation with the task we used a
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14 535 GLMM with a binomial error structure and logit link function, with nested random effects for
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17 536 group and individual. We allowed for a difference in difficulty between flap and tube and
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19 537 tested for between-individual differences in the probability of success between males and
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22 538 females, pups, juveniles, sub-adults, subordinate adults and dominant adults. We also tested
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24 539 for how probability of success depended on an individual's prior experience. As before, we
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26 540 assumed that potential influences could be *a*) an individual's own history of manipulations,
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29 541 i.e. the cumulative number of successful interactions and number of unsuccessful interactions
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31 542 at the option being manipulated; *b*) direct social learning: a permanent effect resulting from
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34 543 observation, i.e. the cumulative number of observed successful manipulations at each option,
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36 544 and *c*) transient social influence, i.e. the time since another individual last interacted with the
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39 545 same option at the same box².
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41 546 Models were fitted using the lmer function in the lme4 package [53] of the R statistical
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43 547 environment [51], using the Laplace approximation. We fitted models including every
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46 548 combination of fixed effects, using R code that fitted each model and recorded the AIC
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49 549 (Akaike's Information Criterion) in each case. This allowed us to judge the evidence for each
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51 550 behavioural mechanism based on its total Akaike weight, and provide model-averaged
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53 551 estimates for supported effects (see Supporting Material for details) [28].
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59 ² This particular transient effect was chosen as the most likely to be in operation in light of its
60 dominant effect on the rate of interaction.
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552 Changes in the probability of success in a bout could logically be the result of only two
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2 553 factors: *a*) changes in the rate at which individuals terminate a bout of interaction
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5 554 unsuccessfully, henceforth ‘task abandonment’; or *b*) changes in the rate at which individual
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7 555 terminate a bout successfully, henceforth ‘rate of solving’. To investigate how each variable
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10 556 operated, we fitted a separate model of each process, using a Cox Proportional Hazards
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12 557 survival analysis model [27]. For *a*), the time of ‘death’ is the time since initiating a bout at
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15 558 which an individual terminates a bout without gaining a reward. Those individuals who gain
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17 559 a reward are considered to be ‘censored’, equivalent to surviving the course of a survival
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19 560 analysis. Conversely, for *b*) the time of ‘death’ is the time since initiating a bout at which an
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22 561 individual terminates a bout by gaining a reward. In this case, those individuals who do not
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24 562 gain a reward are ‘censored’. The models were fitted using the `coxme` function in the `coxme`
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27 563 package [54] in the R statistical environment [51]. For each of *a*) and *b*) we used the same
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29 564 model averaging procedure as above, calculating AIC using the integrated likelihood. In the
30
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32 565 results we report 95% unconditional confidence intervals for parameters of interest, allowing
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34 566 for model selection uncertainty across all other variables.

36 567

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- 579
1 580
2 581 1. Galef BGJ (1992) The question of animal culture. *Human Nature* 3:157-178.
3 582 2. Tomasello M (1994) *The Question of Chimpanzee Cultures*. Chimpanzee Cultures.
4 Cambridge: Harvard University Press. pp. 301-317.
5 583
6 584 3. Laland KN, Galef BGJ, editors (2009) *The Question of Animal Culture*. Cambridge:
7 Harvard University Press.
8 585
9 586 4. Hoppitt W, Laland KN (2008) Social processes influencing learning in animals: A
10 587 review of the evidence. *Advances in the Study of Behavior*, Vol 38: 105-165.
11 588 5. Thornton A, Malapert A (2009) Experimental evidence for social transmission of food
12 589 acquisition techniques in wild meerkats. *Animal Behaviour* 78:255-264.
13 590 6. Thornton A, Malapert A (2009) The rise and fall of an arbitrary tradition: an
14 591 experiment with wild meerkats. *Proceedings of the Royal Society B Biological
15 592 Sciences* 276:1269-1276.
16 592
17 593 7. Huber L, Rechberger S, Taborsky M (2001) Social learning affects object exploration
18 594 and manipulation in keas, *Nestor notabilis*. *Animal Behaviour* 62:945-954.
19 595 8. Gajdon GK, Fijn N, Huber L (2004) Testing social learning in a wild mountain parrot,
20 596 the kea (*Nestor notabilis*). *Learning & Behavior* 32:62-71.
21 596
22 597 9. Whiten A, Horner I, Litchfield CA, Marshall P, Pescini S (2004) How do apes ape?
23 598 *Learning & Behavior* 32:36-52.
24 598
25 599 10. Inoue Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild
26 600 chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:159-
27 601 173.
28 602
29 603 11. Reader SM, Biro D (2010) Experimental identification of social learning in wild
30 603 animals. *Learning & Behavior* 38:265-283.
31 604 12. Muller CA, Cant MA (2010) Imitation and Traditions in Wild Banded Mongooses.
32 605 *Current Biology* 20:1171-1175.
33 606
34 606 13. Whiten A, Mesoudi A (2008) Establishing an experimental science of culture: animal
35 607 social diffusion experiments. *Philosophical Transactions of the Royal Society B
36 608 Biological Sciences* 363:3477-3488.
37 609 14. Galef BG (2004) Approaches to the study of traditional behaviors of free-living
38 610 animals. *Learning & Behavior* 32:53-61.
39 610
40 611 15. Kendal RL, Galef BG, van Schaik CP (2010) Social learning research outside the
41 612 laboratory: How and why? INTRODUCTION. *Learning & Behavior* 38:187-194.
42 613
43 614 16. Shipley B (2000) *Cause and correlation in biology: A user's guide to path analysis,
44 615 structural equations and causal inference*. Cambridge: Cambridge University
45 615 Press.
46 616 17. Thornton A, Clutton-Brock T (2011) Social learning and the development of
47 617 individual and group behaviour in mammal societies. *Philosophical Transactions
48 618 of the Royal Society B Biological Sciences* 366:978-987.
49 618
50 619 18. Thorpe WH (1956) *Learning and Instinct in Animals*. London: Methuen.
51 620 19. Spence KW (1937) The differential response in an animal to stimuli varying with
52 621 within a single dimension. *Psychological Review* 44:430-444.
53 622 20. Laland K, Galef BG, editors (2009) *The question of animal culture*. Cambridge MA:
54 623 Harvard University Press.
55 623
56 624 21. Laland KN, Janik VM (2006) The animal cultures debate. *Trends in Ecology &
57 625 Evolution* 21:542-547.

58
59
60
61
62
63
64
65

- 626 22. Franz M, Matthews LJ (2010) Social enhancement can create adaptive, arbitrary and
1 627 maladaptive cultural traditions. *Proceedings of the Royal Society B Biological
2 628 Sciences* 277:3363-3372.
- 3 629 23. Laland KN, Plotkin HC (1991) Excretory Deposits Surrounding Food Sites Facilitate
4 630 Social Learning of Food Preferences in Norway Rats. *Animal Behaviour* 41:997-
5 631 1005.
- 6 632 24. Galef BG, Allen C (1995) A New Model System for Studying Behavioral Traditions in
7 633 Animals. *Animal Behaviour* 50:705-717.
- 8 634 25. Laland KN, Williams K (1997) Shoaling generates social learning of foraging
9 635 information in puppies. *Animal Behaviour* 53:1161-1169.
- 10 636 26. Vander Post DJ, Hogeweg P (2008) Diet traditions and cumulative cultural
11 637 processes as side effects of grouping. *Animal Behaviour* 75:1330-1344.
- 12 638 27. Therneau TM, Grambsch PM (2000) *Modeling Survival Data: Extending the Cox
13 639 Model*. New York: Springer.
- 14 640 28. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A
15 641 Practical Information-Theoretic Approach*. New York: Springer.
- 16 642 29. Tomasello M (1990) Cultural transmission in the tool use and communicatory
17 643 signalling of chimpanzees? In: Parker ST, Gibson KR, editors. 'Language' and
18 644 Intelligence in Monkeys and Apes: Comparative Developmental Perspectives.
19 645 Cambridge: Cambridge University Press. pp. 274-311.
- 20 646 30. McQuoid LM, Galef BG (1992) Social influences on feeding site selection by Burmese
21 647 Fowl (*Gallus gallus*). *Journal of Comparative Psychology* 106:1370-141.
- 22 648 31. Kendal RL, Kendal JR, Hoppitt W, Laland KN (2009) Identifying social learning in
23 649 animal populations: a new 'option-bias' method. *Plos One* 4:e6541.
- 24 650 32. Tebbich S, Stankewitz S, Teschke I (2012) The Relationship Between Foraging,
25 651 Learning Abilities and Neophobia in Two Species of Darwin's Finches. *Ethology*
26 652 118:135-146.
- 27 653 33. Shettleworth SJ (2010) Clever animals and killjoy explanations in comparative
28 654 psychology. *Trends in Cognitive Sciences* 14:477-481.
- 29 655 34. Byrne RW (2002) Imitation of novel complex actions: what does the evidence from
30 656 animals mean? *Advances in the Study of Behavior* 31:77-105.
- 31 657 35. Heyes CM (1994) Social Learning in Animals: Categories and Mechanisms.
32 658 *Biological Reviews of the Cambridge Philosophical Society* 69:207-231.
- 33 659 36. Sargeant BL, Mann J (2009) Acquiring Culture: Individual Variation and Behavioural
34 660 Development in Bottlenose Dolphins. In: Laland KN, Galef BG, editors. *The
35 661 Question of Animal Culture*. Cambridge: Harvard University Press. pp. 152-173.
- 36 662 37. Caldwell CA, Millen AE (2009) Social Learning Mechanisms and Cumulative Cultural
37 663 Evolution: Is Imitation Necessary? *Psychological Science* 20:1478-1483.
- 38 664 38. Boyd R, Richerson P (1985) *Culture and the Evolutionary Process*. Chicago: Chicago
39 665 University Press.
- 40 666 39. Heyes CM, E. D. R. (2000) What is the significance of imitation in animals? *Advances
41 667 in the Study of Behavior* 29:215-245.
- 42 668 40. McGrew WC, Schoning C, Humle T, Mobius Y (2008) The nature of culture:
43 669 Technological variation in chimpanzee predation on army ants revisited. *Journal
44 670 of Human Evolution* 55:480-59.
- 45 671 41. Hunt GR, Gray RD (2003) Diversification and cumulative evolution in New
46 672 Caledonian crow tool manufacture. *Proceedings of the Royal Society of London
47 673 Series B Biological Sciences* 270:867-874.

674 42. Kendal JR, Kendal RL, Laland KN (2007) Quantifying and modelling social learning
1 675 processes in monkey populations. *International Journal of Psychology and*
2 676 *Psychological Therapy* 7:123-138.

3 677 43. McElreath R, Bell A, Efferson C, Lubell M, Richerson P, et al. (2008) Beyond existence
4 678 and aiming outside the laboratory: estimating frequency-dependent and payoff-
5 679 biased social learning strategies. *Philosophical Transactions of the Royal Society*
6 680 *B Biological Sciences* 363:3515-3528.

7 681 44. Harcourt JL, Sweetman G, Manica A, Johnstone RA (2010) Pairs of Fish Resolve
8 682 Conflict over Coordinated Movement by Taking Turns. *Current Biology* 20:1560
9 683 160.

10 684 45. Haccou P, Meelis E (1992) *Statistical Analysis of Behavioural Data: An Approach*
11 685 *Based on Time-Structured Models*. New York: Oxford University Press.

12 686 46. Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, et al. (1999)
13 687 Predation, group size and mortality in a cooperative mongoose, *Suricata*
14 688 *suricata*. *Journal of Animal Ecology* 68:672-682.

15 689 47. Hodges J, Thornton A, Power P, Clutton-Brock TH (2009) Food limitation
16 690 increases aggression in juvenile meerkats. *Behavioral Ecology* 20:930-935.

17 691 48. Clutton-Brock TH, Brotherton PNM, Smith R, McIlrath GM, Kansky R, et al. (1998)
18 692 Infanticide and expulsion of females in a cooperative mammal. *Proceedings of*
19 693 *the Royal Society of London Series B Biological Sciences* 265:2291-2295.

20 694 49. Spiegelhalter D, Thomas A, Best N, Lunn D (2003) *WinBUGS User Manual Version*
21 695 *1.4*. MRC Biostatistics Unit.

22 696 50. Plummer M, Best N, Cowles K, Vines K (2010) coda: Output analysis and diagnostics
23 697 for MCMC. R package version 0.1402.

24 698 51. Team RDC (2008) *R: A Language and Environment for Statistical Computing*. Vienna:
25 699 *R Foundation for Statistical Computing*.

26 700 52. Rescorla SM, Wagner AR (1972) A theory of Pavlovian conditioning: Variations in
27 701 the effectiveness of reinforcement and nonreinforcement. In: Black AH, Prokasy
28 702 WF, editors. *Classical conditioning II: Current research and theory*. New York:
29 703 *Appleton-Century-Crofts*. pp. 64-99.

30 704 53. Bates D, Maechler M, Dai B (2008) lme4: Linear mixed-effects models using Eigen
31 705 and Eigenfaces. R package version 0.999375028 ed.

32 706 54. Therneau T (2009) coxme: Mixed Effects Cox Models. R package version 2.0 ed.

33 707
34 708
35 709
36
37
38
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710 **Figure legends**

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712 **Fig. 1.** a) A “Box”. The “Flap” technique involved going through a black cat flap to obtain
713 food from a pot; the “Tube” technique involved pushing through a fabric sleeve on the tube
714 and breaking a paper lid to obtain food; b) experimental layout of the two identical Boxes; c)
715 diagrammatic representation of the stochastic mechanism-fitting model (SMFM) showing the
716 three rates of transition that were modelled. In reality ‘rate of interaction’ involved modelling
717 four ‘competing’ transition rates, to each of the four options available: left Flap, right Flap,
718 left Tube and right Tube. We recorded an individual as solving the task when it gained access
719 to food inside the box, and as abandoning the task when it terminated a bout of interaction
720 without gaining access to food inside the box.

721

722 **Fig. 2.** Diagrammatic representation of all effects found. Each effect is described and
723 interpreted in Table 1. The positioning of the arrow for each effect represents the transition
724 rate affected. Green arrows mean a rate of transition was found to be a function of an
725 individual’s previous manipulations of the task, interpreted as asocial learning or changes in
726 motivation. Red arrows mean a rate of transition was found to be a function of the number of
727 previous observations, interpreted as direct social learning. The blue arrow indicates the rate
728 of interaction was found to be a function of the time since last observation at each option,
729 interpreted as a transient local enhancement effect. + or - indicates whether the transition rate
730 was positively or negatively associated with the variable in question.

731

732 **Fig. 3.** a) Estimated size of the transient increase in rate of interaction at each option
733 immediately following observation, for different age classes of meerkats (taken from the final
734 model). These effects are decomposed into b) box-level local enhancement, influencing rate

735 of interaction with both options at the manipulated box; and c) specific local enhancement,
1
2 736 further influencing rate of interaction with the manipulated option. Estimates are the median
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5 737 of the posterior distribution, scaled relative to the estimated median baseline rate of
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7 738 interaction with the flap option. Error bars give the 95% highest posterior density (HPD)
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10 739 interval. Green points and error bars give the estimates of the difference in effect size
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12 740 between different age classes, where A=adult; J/SA= juveniles and sub-adults; P=pups.

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16 742 **Fig. 4.** Group differences in i) the number of manipulations of the flap and tube; ii) the
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18 743 number of successful manipulations of the flap and tube; iii) the proportion of individuals that
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20 744 manipulated the flap and tube; and iv) the proportion of individuals solving the task using the
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22 745 flap and tube. Trained demonstrators are not included in all cases. Letter codes refer to
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24 746 different groups.

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28 748 **Fig. 5.** Specificity of the transient social effect for different age classes for the current study
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30 749 and the previous experiment by Thornton and Malapert [21]. Specificity quantifies the
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32 750 probability a naive observer will use the same option-type it has observed, given that it
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34 751 manipulates one of them immediately after observation. The mean of the posterior sample is
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36 752 shown in each case, with the 95% central interval. * Indicates that the 95% central interval
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38 753 for the difference between the two studies did not include zero, whereas NS signifies that it
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40 754 did.

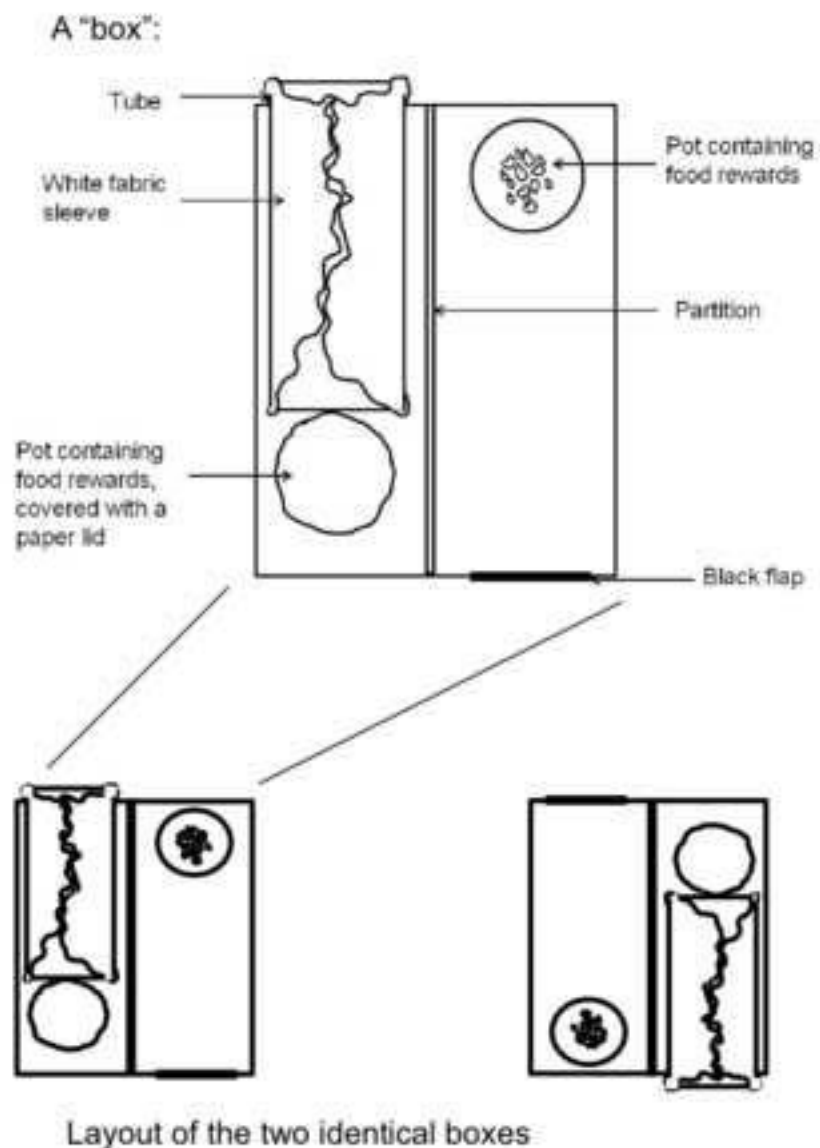
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757 **Table captions**

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48 759 **Table 1** Summary of effects found on meerkats' task solving behaviour, and our
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50 interpretation. See also Fig 2.

Figure 1
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a) Experimental setup



b) Stochastic mechanism-fitting model

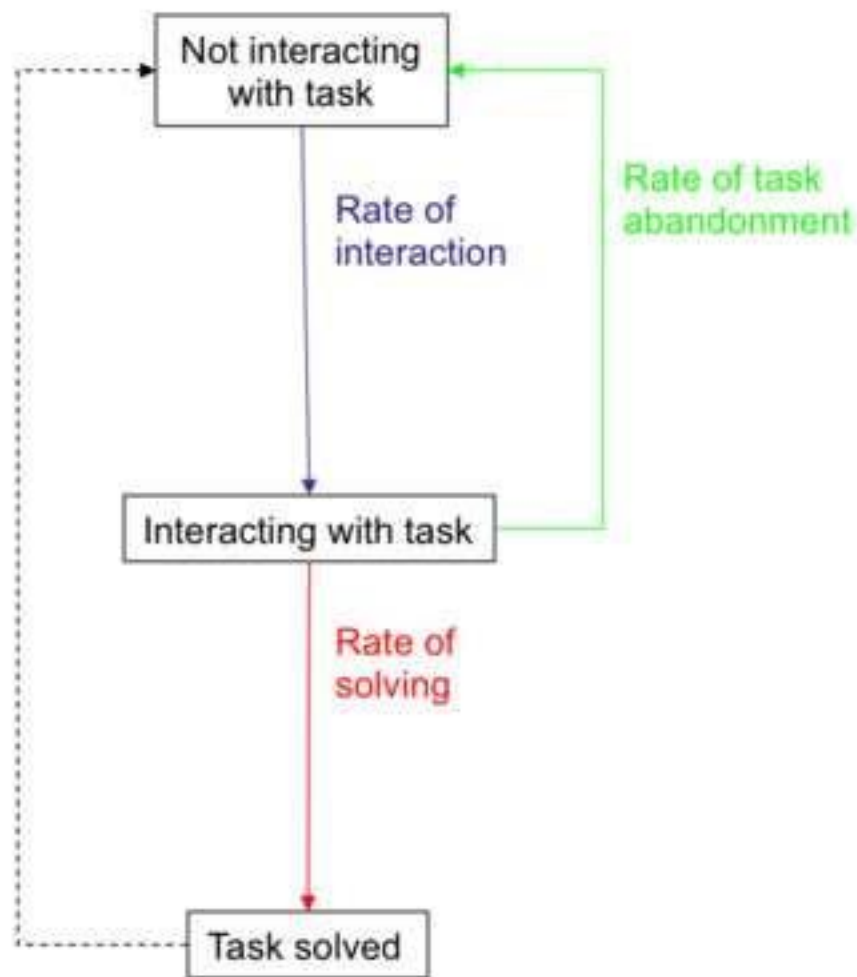
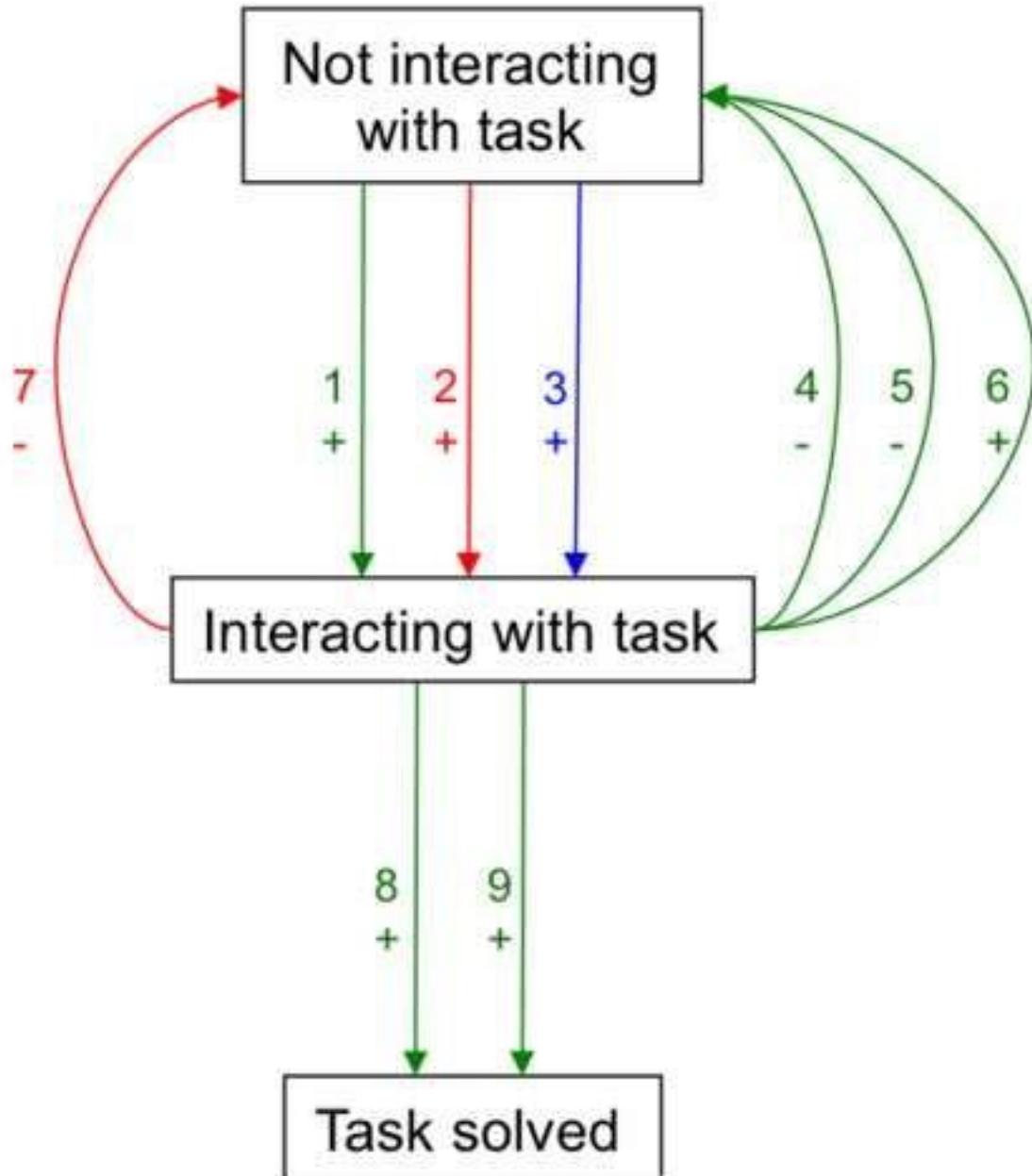


Figure 2
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- Asocial learning/ motivation
- Direct social learning
- Transient local enhancement

Figure 3
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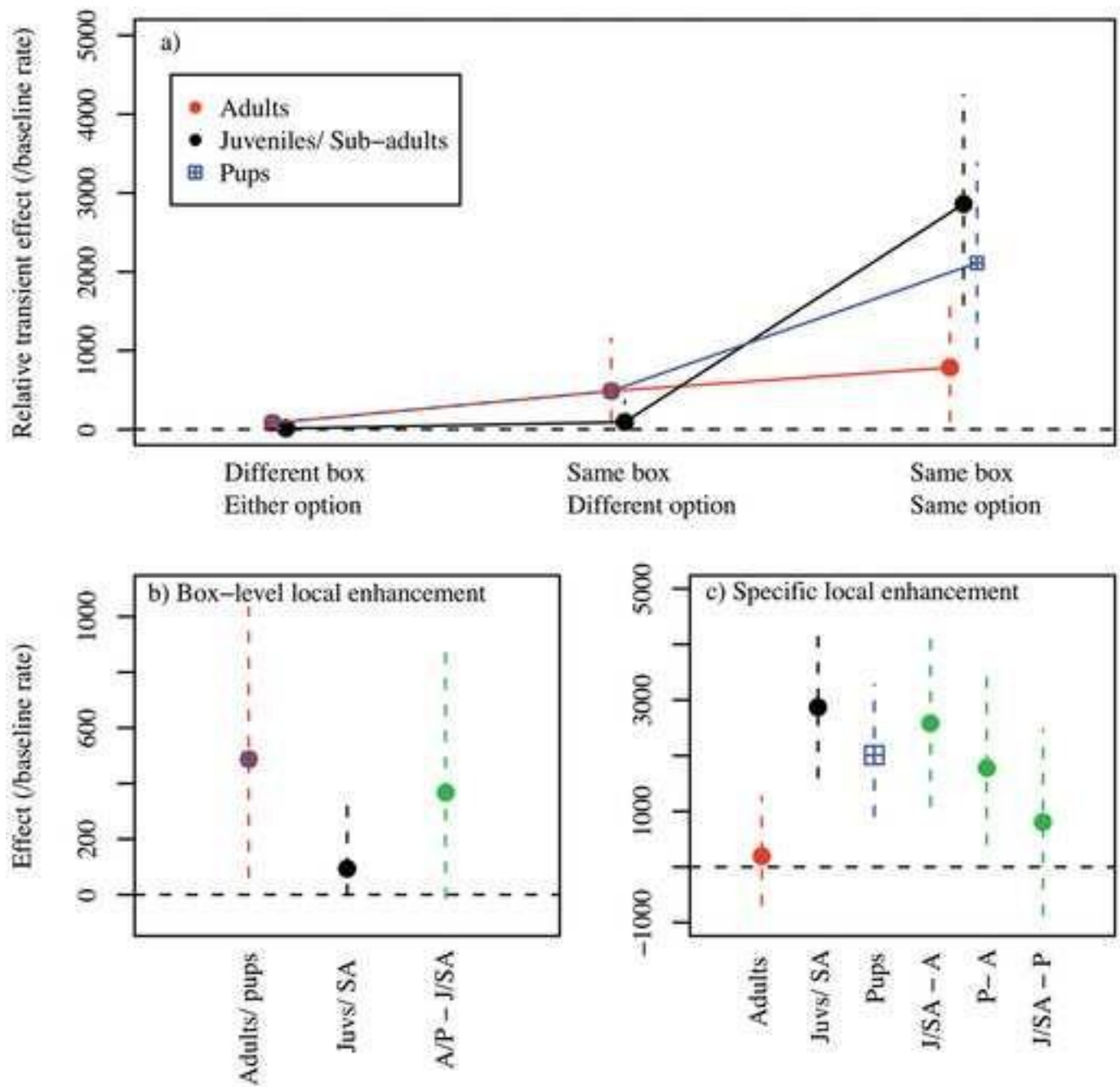


Figure 4
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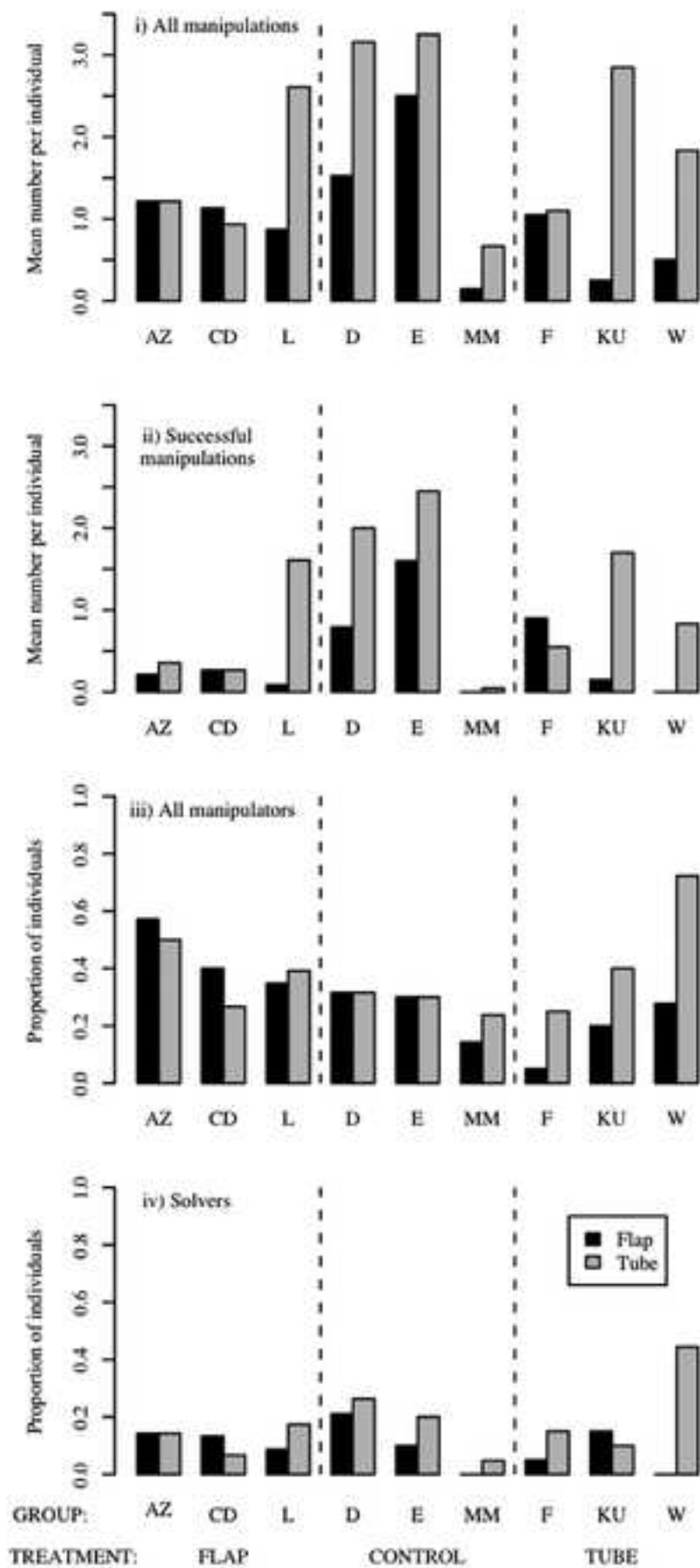


Figure 5
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