

1. INTRODUCTION

9 High fidelity social learning and innovation are considered crucial processes un-
10 derpinning cumulative cultural evolution, enabling individuals to acquire and mod-
11 ify knowledge that exceeds that which any single individual could invent alone [1]
12 [2]. However, social learning is not usually perfect [3]; copying errors may affect
13 the fidelity of transmission, causing the accumulation of copying error observed in
14 material culture [4].

15 It is plausible that most social learning errors are non-random, biased by anatom-
16 ical, cognitive and environmental features [5]. For example, experimental evidence
17 suggests that ‘reductive’ mutation of an artefact results in greater population-level
18 variation than ‘additive’ mutation [7], and that perceptual bias of whether an ob-
19 ject must be increased or decreased in size to match a model object size can result
20 in a respective decrease or increase in the population mean size over simulated
21 generations [6]. Also, learners attempting to imitate can perform the mirror image
22 of a demonstrated action [8] [9] because they are vulnerable to the correspondence
23 problem, which requires mapping between the perspective of the demonstrator and
24 the observer [10]. This can be particularly challenging when these perspectives dif-
25 fer, that is they are perpetually opaque [11]. Some social learning errors can result
26 from embodied cognition through interaction of the brain and anatomical features.
27 For instance, cultural and genetic propensity for a cognitive bias towards right-
28 handedness has interacted with the asymmetric position of the hand’s opposable
29 thumb to affect a wide range of technology, including cooking and writing imple-
30 ments, construction tools and musical instruments. Social learning biases have also
31 been shown to affect cultural evolution in domains besides technology, including
32 language [12], art [13] and narrative [14].

33 Following seminal works by Cavalli-Sforza and Feldman, and Boyd and Richer-
34 son [15] [16], models of within-population cultural evolutionary dynamics typically
35 parameterise the effects of mutation, transmission and selection but neglect the
36 effects of non-random error during social learning as a source of cultural variation
37 [16][3]. Typically, cultural variation is assumed to result from random mutation
38 or directed individual modification following, but not during, the process of so-
39 cial transmission, called ‘guided variation’ [3]. Cultural variants are subject to
40 selection via differential adoption of a trait based on: characteristics of the model
41 demonstrating the variant (e.g. a preference to copy a successful individual); the
42 frequency of the variant (e.g. a preference to copy a popular variant); or an intrin-
43 sic preference for the variant (e.g. a preference to learn, recall and transmit social
44 over technical information). These selective processes alter the relative frequencies
45 of extant variants but are not sources of variation.

46 A distinct approach to modelling cultural evolution, called cultural attraction
47 theory, highlights ‘factors-of-attraction’ as non-random causes of change in cul-
48 tural variant frequencies, including cognitive factors affecting the construction of

49 information during the social learning process [17][18]. Claidiere et al. [5] for-
50 malize this approach using a parameter-free model where the linear effect of a
51 transition matrix is used to predict the change in frequency of cultural variants
52 between generations and includes the combined effects of any factors-of-attraction.

53 Our study draws upon both approaches by developing a parametric model of
54 within-population cultural evolutionary dynamics to explore the combined effects
55 of the three classes of cognitive factors which may affect the production of cul-
56 tural variation during social transmission. First, variation may be caused by an
57 (absolute) learning bias towards an un-observed cultural variant; for instance, a
58 learner may observe a left-handed technique but adopt the right-handed equivalent
59 form. Second, a learner may generate a new variant by adopting a consistent (rel-
60 ative) transformation of the observed cultural variant; for instance, by adopting
61 the mirror image of what they observed. Finally, when a behavioural sequence,
62 or chaine-operatoire, is learned in chunks [19][?], a propensity to repeat previous
63 chunks, or not, can affect sequence variation measured across the population.

64 As a case study, we consider the social transmission of micro-structures in knot
65 tying, focusing on variation in the composition of two trefoil knots, known com-
66 monly as granny and reef knots. Originating 300kbp [20] and preserved from 5500
67 bp [21], simple knots are an ancient technology and remain relatively ubiquitous
68 [22]. The simplest knot, the trefoil or overhand knot, can take either a left (L)
69 or right (R) handed form, and the composite of two such trefoils are both granny
70 knots, formed of two left- or two right-handed trefoils (LL or RR), or reef knots,
71 formed of a left- and a right-handed trefoil (LR or RL) (Figure 1a). These knots
72 are typically used to tie shoelaces, by forming an overhand knot and then forming
73 a slipped overhand knot on top.

74 Shoelaces are commonly tied using a granny knot and, more generally, analysis
75 of the Ashley Book of Knots [22] revealed that from the composition of two trefoils,
76 the granny knot appears in 75% of cases (reef in 25%) [23]. An analysis of impact
77 in integrity of knot structure shows that the reef knot is less liable to come undone,
78 suggesting that non-functional biases may be required to explain the prevalence of
79 the granny [24][25].

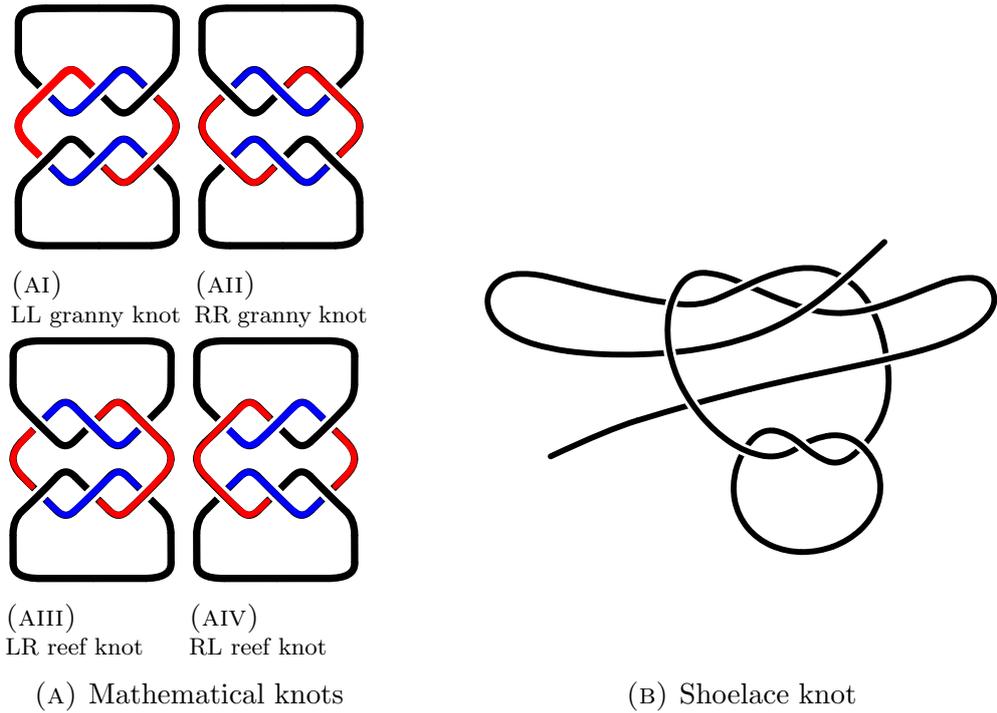


FIGURE 1. Figure 1a shows all possible mathematical granny and reef knots. Figure 1b illustrates a shoelace knot tied using a RL reef knot.

80 Mathematically, a knot is a 3-dimensional closed curve, where the string is over
 81 and under itself in some way with the ends glued together. The left- and right-
 82 handed versions of the trefoil are mirror images of one another and are mathe-
 83 matically distinct as they cannot be transformed into each other by Reidemeister
 84 moves [26] (a set of moves on the strands of a knot used to determine if two di-
 85 agrams relate to the same knot); the only way to change the left handed trefoil
 86 to the right handed trefoil is to cut the knot open and retie it. The granny and
 87 reef knots are distinct knots, and can be identified as such by knot invariants [27].
 88 Knot invariants will give the same result when two knots are the same, and differ-
 89 ent results when they are distinct. The Jones polynomial [28] is one such invariant,
 90 which assigns a polynomial to each knot and gives us some information about the
 91 crossings of that knot. The Jones polynomial is given for the left handed granny
 92 knot in Equation 1, the right handed granny knot in Equation 2 and both reef
 93 knots by Equation 3. We can see that the Jones polynomial for the left handed
 94 granny knot differs right handed granny knot by the sign of the exponents in the
 95 polynomial, the exponents for the left handed granny knot are all negative whilst
 96 they are positive for the right handed granny knot. This is the only difference

97 between the two polynomials and shows that the left handed and right handed
 98 granny knot are mirror images of one another. Both versions of the reef knot have
 99 the same Jones polynomial which contains both positive and negative values for
 100 the exponents showing that there is no difference between the two versions of this
 101 knot. These polynomials show that the granny knots are distinct from each other
 102 and both reef knots, but the two reef knots are not distinct, which can be seen
 103 by rotating one reef knot to match the other; no such rotation is possible for the
 104 granny knots (See Figure 1a).

$$105 \quad (1) \quad V_{LL}(t) = t^{-2} + 2t^{-4} - 2t^{-5} + t^{-6} - 2t^{-7} + t^{-8}$$

$$106 \quad (2) \quad V_{RR}(t) = t^2 + 2t^4 - 2t^5 + t^6 - 2t^7 + t^8$$

$$(3) \quad V_{reef}(t) = -t^3 + t^2 - t + 3 - t^{-1} + t^{-2} - t^{-3}$$

107 We apply experimental and modelling approaches to identify evidence for non-
 108 random error affecting the social transmission of all forms of granny (LL, RR) and
 109 reef knot (LR, RL). We use the models to predict their effects on the evolution of
 110 knot diversity in this closed system.

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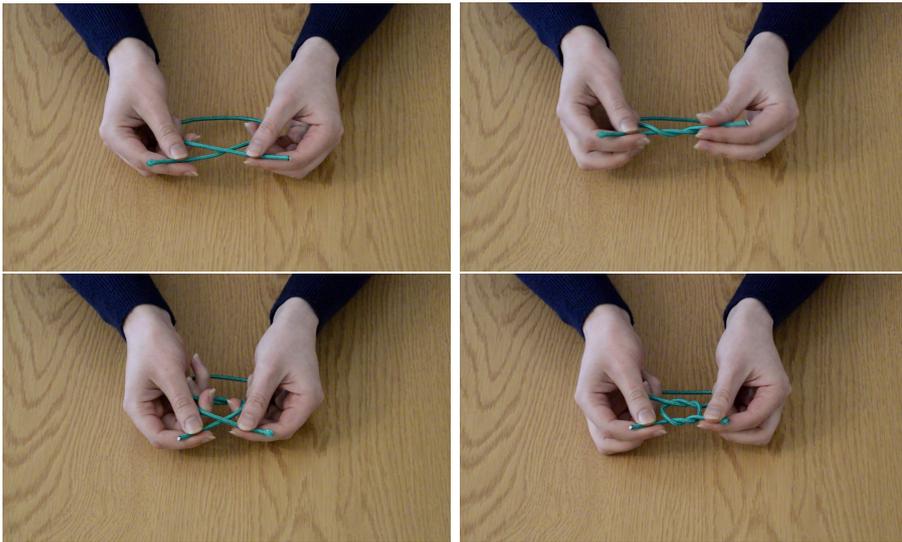
2. SOCIAL TRANSMISSION EXPERIMENT

112 The experiment consisted of two stages. The first stage established trefoil hand-
113 edness bias among participants in the absence of a social demonstration. The
114 second stage established social transmission fidelity of the granny and reef knots
115 (LL, RR, LR and RL). Participants were recruited from the student population
116 of Durham University. They were rewarded with a £4 food voucher for their par-
117 ticipation. In total 101 people took part in the experiment with 36 male. The
118 experiment took place in a lecture theatre, with batches of up to 10 participants
119 at a time. We treated between-participant effects as independent by spacing par-
120 ticipants widely across the lecture theatre and requiring each participant to tie
121 their knots within a modified cardboard box which prevented between-participant
122 observation.

123 2.0.1. *Stage 1.* We asked participants to tie a “simple knot”. We then checked
124 that this was a trefoil knot. The knot was undone, then participants were asked
125 to tie a “simple knot” every 60s over a 10 minute period. Each knot was tied in
126 a separate 25cm length of string and the sealed in a small plastic bag. Over the
127 same period, participants were asked to complete a distraction task in between
128 tying each knot, requiring them to draw six concepts in order that another person
129 could match the concepts to the drawings at a later time. Both the plastic bag
130 containing the 10 knots and the paper with the drawings from the distraction task
131 were collected in at the end of this stage.

132 2.0.2. *Stage 2.* Participants were given 35cm length of string and shown a video
133 demonstrating the tying of either a LL granny knot (26 participants), a RR granny
134 knot (25 participants), a LR reef knot (25 participants) or a RL reef knot (25
135 participants), randomly assigned across batches (screenshots of the video and the
136 knots are shown in Figure 2). The video showed only hands tying a knot and
137 contained no audio. The video was recorded from the point of view of an observer
138 sitting across from the demonstrator. Participants were shown the video three
139 times, with a pause of 30 seconds between each showing. They were told they
140 could practice tying the knot whilst the video was being shown, and during the
141 pauses between the showings. After the final showing of the video, they were told
142 to untie any practice knots and asked to retie the knot shown in the video. This
143 delay effect was to reflect the process of learning from a demonstration.

144 2.0.3. *Questionnaire.* After both stages had been completed and all material col-
145 lected, participants were asked to complete a short questionnaire detailing their
146 name, gender, degree programme, handedness, hand usually used for writing, their
147 knot tying experience and whether they knew how to tie a granny or reef knot.
148 Details of the responses from the questionnaire can be found in Appendix A.



(A) Screenshots from video showing the tying of RR granny knot



(BI) LL granny knot (BII) RR granny knot



(BIII) LR reef knot (BIV) RL reef knot

(B) Tied granny and reef knots

FIGURE 2. Screenshots from a demonstration video used in the experiment and tied versions of all four knots used.

149 **2.1. Results.** For each participant in stage 1, we recorded knot handedness over
 150 the 10 trefoils as an estimate of knot handedness bias in the absence of a demon-
 151 stration. The frequency of right handed trefoils tied by each person is shown in
 152 Figure 3, where participants who tied no right handed trefoils tied all left handed
 153 trefoils. Two participants who tied knots which were not trefoils have not been
 154 included in these data.

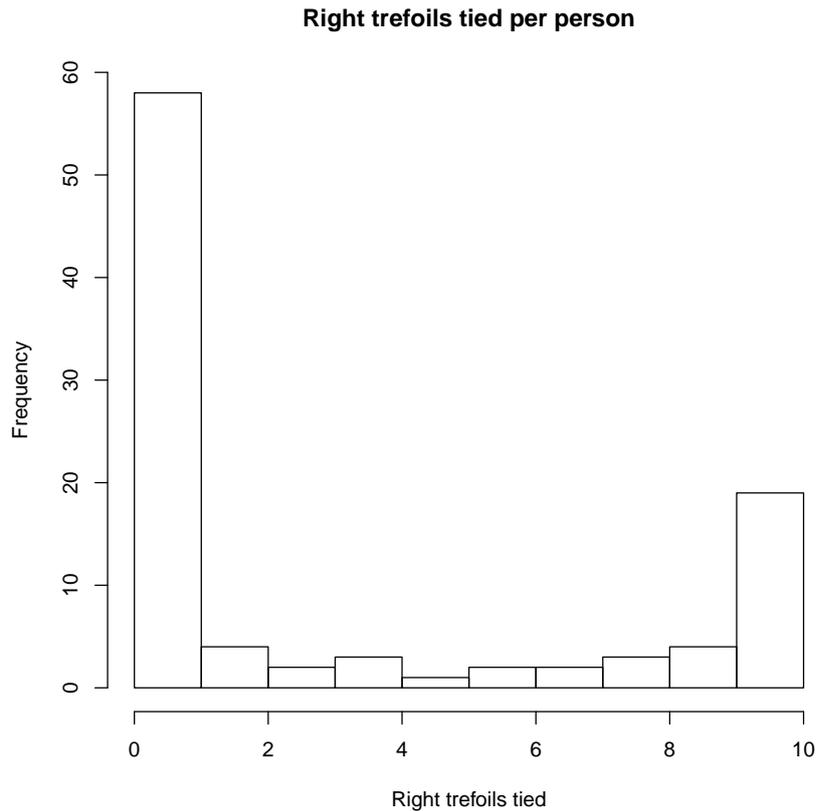


FIGURE 3. Frequency of right handed trefoils tied by participants, those who tied no right handed tied all left handed trefoils and vice versa

155 The majority of participants tied either all right handed or all left handed tre-
 156 foils, with a few tying a mixture of the two. Left handed trefoils were much more
 157 common than right handed trefoils. The mean proportion of right handed trefoils
 158 tied per person was 0.32. A Bayesian association analysis (see Figure 12) revealed
 159 weak evidence that individuals who typically write with their right hand are more

160 likely to tie a left-handed trefoil than those who write with their left, while those using
 161 their left hand to write are more likely to tie a right-handed trefoil than those who
 162 use their right.

163 Of the 101 knots tied after being shown the video, 100 of the knots were either
 164 LL, RR, LR or RL, and the remaining knot (a composition of the knot 5_1 and the
 165 knot 3_1) was excluded from the analysis.

		Knot tied by participants				
		LL	RR	LR	RL	Total
Demonstration	LL	14	9	1	2	26
	RR	9	15	0	1	25
	LR	4	4	8	8	24
	RL	6	1	6	12	25
Total		33	29	15	23	100

TABLE 1. Knots tied by participants given video shown in experiment, dashed lines delineate granny knots from reef knots

		Stage 2 knots tied by participants				
		LL	RR	LR	RL	Total
Stage 1 handedness bias	Left	25	20	12	11	68
	Right	6	9	2	12	29
Total		31	29	14	23	97

TABLE 2. Knot tied given handedness of trefoil tied by participants, dashed lines delineate granny knots from reef knots

166 Table 1 and Bayesian posterior distributions (see Appendix B, Figures -) for the
 167 probability of tying a knot given the knot shown both show that participants were
 168 most likely to tie the knot shown in the video, but that if a mistake was made,
 169 participants were most likely to tie the mirror image of the demonstrated knot over
 170 the other two variants. For example, more people tied the RR granny knot when
 171 shown LL, than tied either reef knot, LR or RL. Table 1 and Bayesian posterior
 172 distributions also indicate that granny knots were more likely to be tied than reef
 173 knots, suggesting that participants may exhibit a bias to repeat the handedness of
 174 the first trefoil they tie. Finally, participants that exhibited a handedness bias in
 175 stage 1, displayed the same bias in the first trefoil tied following the demonstration
 176 in stage 2, suggesting that knot handedness bias may affect social transmission

177 fidelity. For example, those who had a left-handed bias in stage 1 were more likely
 178 to begin their post-demonstration knot with L than R (see Appendix B Figure
 179 17).

180 Having identified preliminary evidence for imitation of the demonstrated knot,
 181 knot-handedness bias, mirroring and repetition, we develop a model that explores
 182 their effects on cultural evolutionary dynamics. We use the model to estimate
 183 their effect size in the experiment and consider the evolutionary trajectories that
 184 might result if experimental social transmission was iterated over many genera-
 185 tions. We contrast the predictions of this parametric approach with those of a
 186 non-parametric approach where transmission dynamics are determined by a tran-
 187 sition matrix calculated directly from the social transmission experimental data.

188 3. SOCIAL TRANSMISSION MODEL

189 **3.1. Assumptions.** We model the transmission of granny and reef knots within
 190 a population through oblique transmission [15] and assume a closed system such
 191 that when a granny or reef knot is demonstrated, the learned knot is always either
 192 a granny or a reef knot. Following the results of the experiment, we assume that
 193 four parameters can affect the fidelity of social transmission: the learner interprets
 194 the demonstrator's knot incorrectly as the knot's mirror image with a probability
 195 g ; the learner imitates each perceived form of trefoil with a probability s , where
 196 the perceived knot refers to the learner's interpretation of the demonstrated knot,
 197 which could either be the demonstrated knot or the mirror image of the demon-
 198 strated knot; the learner repeats the trefoil they tied for the first step of the knot
 199 with a probability r ; and the learner ties a right handed trefoil when they do not
 200 learn from the demonstration with a probability p .

201 Using these parameters, we can build a system of recurrence equations to de-
 202 scribe knot frequencies in the learner generation as a function of knot frequency
 203 in the demonstrator generation. We denote the proportion of knot ij tied in the
 204 demonstrating generation by f_{ij} where $ij \in \{RR, LL, RL, LR\}$, and the knots
 205 tied by the learner generation of the population after transmission as f'_{ij} where
 206 $f'_{RR} + f'_{LL} + f'_{RL} + f'_{LR} = 1$ with each f'_{ij} taking values in the interval $[0, 1]$. For
 207 example, take the granny knot formed by tying two right handed trefoils and de-
 208 note it by f_{RR} . This knot will be transmitted successfully if it is not mirrored and
 209 both trefoils that form it are accurately imitated by the next generation, denoted
 210 by $f_{RR}(s^2(1 - g))$. However, a right granny could also be formed by mirroring
 211 an LL with probability g and accurately imitating both trefoils of the perceived
 212 knot with probability s^2 , giving $f_{LL}(s^2g)$. A right granny could also be formed
 213 with no imitation at all, if the tyer has a bias towards tying right handed trefoils
 214 $f_{RR}((1 - s)^2p^2)$ or repeating the first knot tied, $f_{RR}((1 - s)^2(pr))$ and so we get the
 215 frequency of right grannies in the population as a function of grannies and reefs

216 already in the population and the probability parameters;

$$(4) \quad \begin{aligned} f'_{RR} = & f_{RR}(s^2(1-g)) + \dots + f_{RR}((1-s)^2p^2) + \dots \\ & + f_{RR}((1-s)^2(pr)) + \dots + f_{LL}(s^2g) + \dots \end{aligned}$$

217 It is important to think about how the parameters interact with each other. If
 218 a learner imitates the knot correctly then the learner's likelihood to repeat or tie
 219 a right handed trefoil does not matter. They will do what is shown regardless of
 220 their biases, and so we can discount repetition and right hand bias when the knot
 221 is accurately imitated. In the same way, when the learner simply repeats part of
 222 a knot their right hand bias does not matter, as they will repeat regardless of this
 223 bias. So we can discount right-hand bias when repetition takes place. Figure 4
 224 illustrates the effect of parameters on the transmission of knot RR in the order
 225 of mirroring, accuracy, repetition then handedness bias, but the order does not
 226 actually matter as the parameters commute and will cancel with each other (see
 227 Appendix C, for the recursions for all four knots).

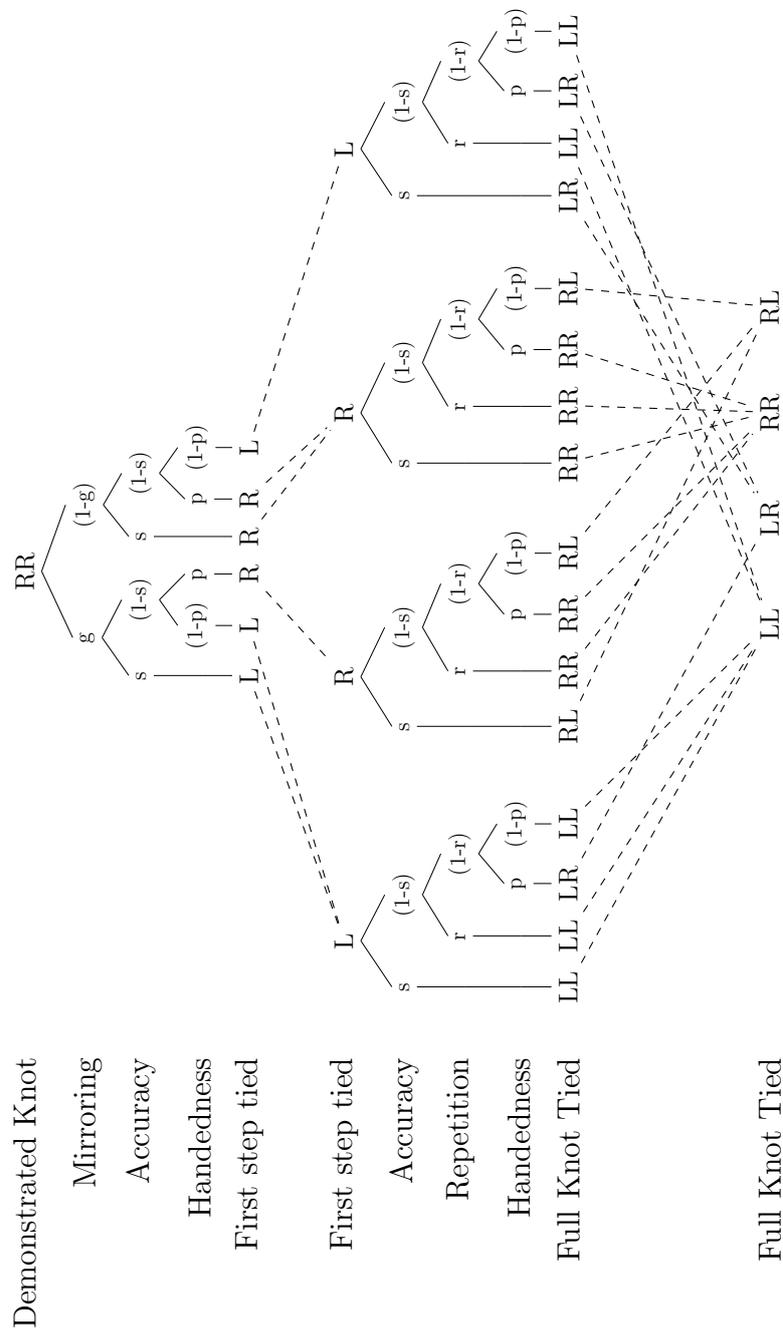


FIGURE 4. Decision tree showing the effect of parameters on the transmission of knot RR

228 **3.2. Evolutionary Dynamics.** Each set of parameter values $0 \leq (s, g, r, p) \leq$
 229 1, determines the evolutionary trajectory and a single equilibrium point, where
 230 $f_{ij} = f'_{ij} = \hat{f}_{ij}$, (expressions for equilibrium states are given in Appendix D).
 231 If $s = 0$, the system jumps to a stable equilibrium point determined by the p
 232 and r and is unaffected by starting values of f_{ij} . By contrast, if imitation is
 233 always accurate, $s = 1$, and mirroring never occurs, $g = 0$ ($0 \leq r \leq 1$), the
 234 population does not evolve from starting frequencies, so if a small perturbation in
 235 frequencies is induced, the population remains at the new frequencies. If there is
 236 some imitation, $0 < s < 1$, the population evolves to a stable equilibrium, such
 237 that the population returns to the original equilibrium state following a small
 238 perturbation in frequencies.

239 Figure 5 illustrates the effect of imitation accuracy and mirroring on equilibrium
 240 frequencies. In Figure 5a, the value of s is set lower than in 5b, resulting in only
 241 a slight change in the values of \hat{f}_{RR} , \hat{f}_{LL} and \hat{f}_{RL} and \hat{f}_{LR} . This is compared
 242 with the higher value of s in 5b and the curved lines representing the frequencies.
 243 This shows that imitation needs to be highly probable for mirroring to affect the
 244 proportion of knots tied in the population. We notice that the two reef knot
 245 frequencies, f_{LR} and f_{RL} , are always equal at equilibria. This is consistent with
 246 the fact that LR and RL represent the same knot mathematically, as shown by
 247 their Jones polynomial in Equation 3.

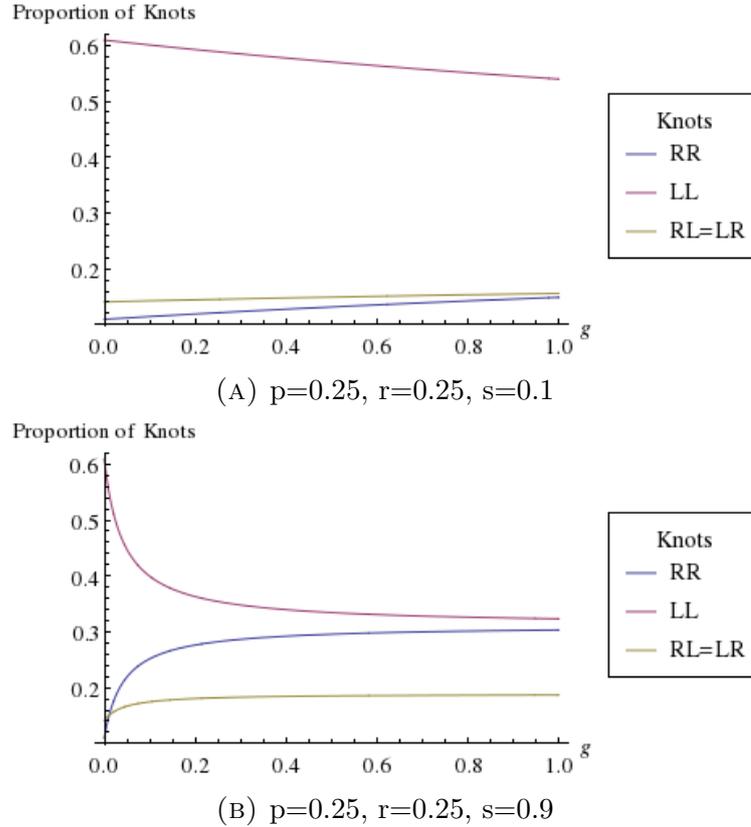


FIGURE 5. Line plots showing the proportion of knots at equilibria when the imitation coefficient is (A) low, and (B) high. The values of \hat{f}_{LR} and \hat{f}_{RL} are equal so these are represented by the same line on the graph, while \hat{f}_{RR} and \hat{f}_{LL} are represented by separate lines.

248 Prior to reaching an equilibrium state, evolutionary dynamics typically follow
 249 a smooth trajectory (assuming $0 < s < 1$), but a high probability of mirroring
 250 can cause oscillations in the trajectory when imitation accuracy is high. When
 251 mirroring is low (Figure 6a), we see the system evolve in a smooth curve to a
 252 point strongly affected by the handedness bias, p and repetition bias, r . The value
 253 of p causes the point to be closer to the corner f_{RR} than f_{LL} but the value of
 254 r does not cause the point to be as close to the $f_{RL} + f_{LR} = 1$ boundary as we
 255 may expect. In 6b, mirroring is likely to occur. Coupled with the high imitation
 256 accuracy, the system evolves to a similar equilibrium point as shown in 6a, but the
 257 high probability of mirroring causes the path to oscillate to the point rather than
 258 evolve in a smooth trajectory.

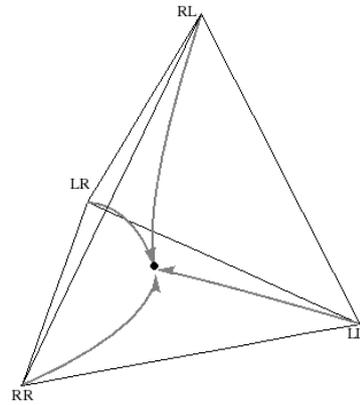
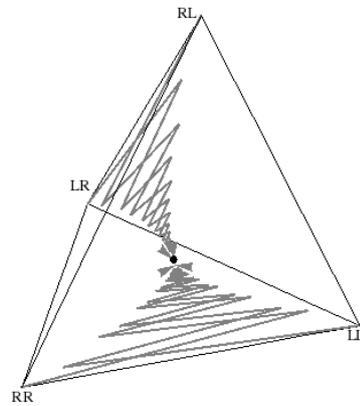
(A) $p=0.75, g=0.1, r=0.25, s=0.9$ (B) $p=0.75, g=0.9, r=0.25, s=0.9$

FIGURE 6. Evolutionary plots showing the change in frequency of knots. Each arrow represents the change in frequency of each type of knot in the population, starting from sole existence in each corner to a mixture of different knots. The solid disk is the equilibrium state which is evolved towards no matter the starting frequencies. Frequencies are plotted in tetrahedral space using barycentric coordinates (see Appendix F).

259 Most combinations of parameter values result in an excess of granny knots over
 260 reef knots at equilibrium. As noted above, any repetition bias will favour the
 261 granny knot, but even when repetition never occurs, the population is still more
 262 likely to tie granny knots than reef knots if there is any handedness bias. Figure
 263 7 illustrates the predominance of granny knots at equilibrium, taking the case
 264 where there is no repetition in the absence of guidance, $r = 0$, and intermediate
 265 mirroring, $g = 1/2$. The bias towards granny knots is strongest when handedness

266 bias, p , is either high or low and the imitation coefficient, s , is low; in other words,
 267 when individuals consistently tie with the same handedness rather than imitating
 268 a different knot.

269 There are only two cases where the equilibrium proportion of granny and reef
 270 knots is equal ($\hat{f}_{RR} + \hat{f}_{LL} = \hat{f}_{RL} + \hat{f}_{LR}$). The first case is when imitation is not
 271 perfect, $0 \leq s < 1$, the first knot is never repeated, $r = 0$, and there is no
 272 handedness bias, $p = 1/2$, where $0 \leq g \leq 1$. The absence of repetition bias
 273 prevents predominance of granny knots, and the lack of handedness bias prevents
 274 the prevalence of either granny knot. The second case is when imitation always
 275 occurs, $s = 1$, individuals never repeat the first knot tied, $r = 0$, and there is
 276 some mirroring $0 < g \leq 1$, where $0 \leq p \leq 1$. Again, the absence of repetition bias
 277 prevents predominance of granny knots, *perceived* imitation is always perfect, but
 278 mirroring causes knots to be copied incorrectly. Both these cases are illustrated in
 279 Figure 7. Finally, we note that reef knots can only be more prevalent than granny
 280 knots if this is exhibited in their starting frequencies and when the system does
 281 not evolve ($s = 1$ and $g = 0$; discussed above).

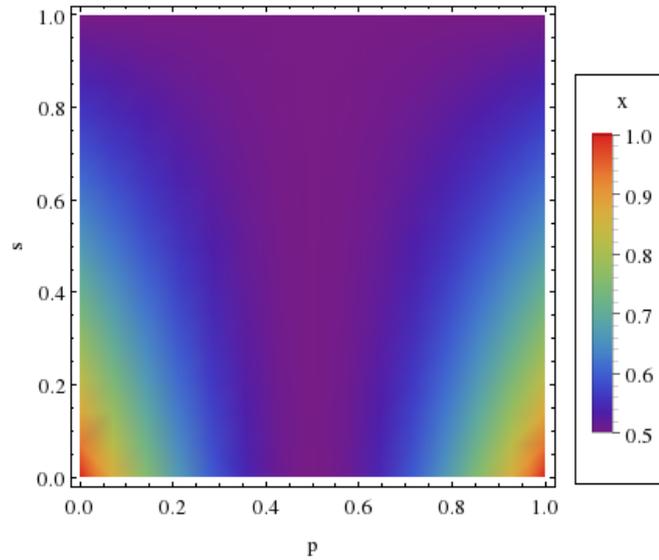


FIGURE 7. Density plots showing the proportion of granny knots at equilibrium, denoted by $x = \hat{f}_{RR} + \hat{f}_{LL}$, as a function of the handedness-bias, p and the imitation coefficient, s , where $g=1/2$ and $r=0$.

282 4. APPLYING THE PARAMETRIC MODEL TO EXPERIMENTAL RESULTS

283 Using Approximate Bayesian Computation (ABC) [29], we can use our model to
 284 estimate parameter values that predict the experimental data. ABC works on the
 285 same premise as Bayes' theorem, relating conditional probability of parameters θ ,
 286 to data D by the rule

$$(5) \quad p(\theta|D) = \frac{p(D|\theta)p(\theta)}{p(D)},$$

287 where $p(\theta|D)$ is referred to as the posterior, $p(\theta)$ represents the prior beliefs
 288 before any data is available, $p(D|\theta)$ the likelihood of data D occurring given the
 289 prior and $p(D)$ the evidence [30]. With this rule, we can calculate the posterior by
 290 taking the product of prior beliefs with the likelihood of data occurring, divided
 291 by the evidence observed. To obtain the probability of data D given parameter θ ,
 292 we use our model to simulate data for a given parameter set and decide whether it
 293 fits the observed data. We construct a metric to describe our observed data such
 294 that we can accept or reject the simulated parameter set depending on whether
 295 it generated data within a tolerated degree of proximity from the observed. The
 296 retained parameter distributions give us $p(\theta|D)$.

297 Taking our observed data from Table 1 as a 4×4 matrix O and simulating data
 298 of the same form using our model to give a 4×4 matrix S , we compare these two
 299 sets of data using the metric;

$$(6) \quad d(O, S) = \sum_{i,j} a_{ij}^2,$$

300 where a_{ij} are the entries of the matrix $O - S$. This metric is proportional to finding
 301 the Euclidean distance between the points in the two matrices.

302 We use grid approximation and simulate data for values of each parameter p, g, r
 303 and s between 0 and 1 with intervals of 0.01. The simulations match the experi-
 304 mental conditions by starting with even frequency states, $f_{ij} = 1/4$, and running
 305 the simulation over a single generation. The metric in Equation 6 is calculated for
 306 all 101^4 simulations.

307 **4.1. ABC results.** Figure 8 shows the parameter distributions from the 204 sim-
 308 ulations that resulted in a metric value, $d(O, S) = \sum_{i,j} a_{ij}^2 \leq 0.04$. We see from
 309 these plots that the value of the parameters can almost be stated explicitly. Tak-
 310 ing the mean value at 2 decimal places for each parameter, which is equal to the
 311 median and the mode, we note a non-random, right-handed trefoil bias ($\bar{p} = 0.35$),
 312 predicting that more left handed trefoil knots are tied by the population when
 313 given no guidance than right handed trefoils. This value is similar to our experi-
 314 mental (stage 1) mean handedness bias, 0.32. The model predicts that individuals
 315 mirror fairly frequently ($\bar{g} = 0.39$) but that knots are mirrored less often than they
 316 are correctly interpreted. Also, individuals are more likely to repeat the first part
 317 of the knot tied than not ($\bar{r} = 0.61$). Finally, there is a relatively high accuracy of

318 imitation ($\bar{s} = 0.79$). These results are concordant with our interpretation of the
 319 descriptive statistics from the experiment (see Table 1).

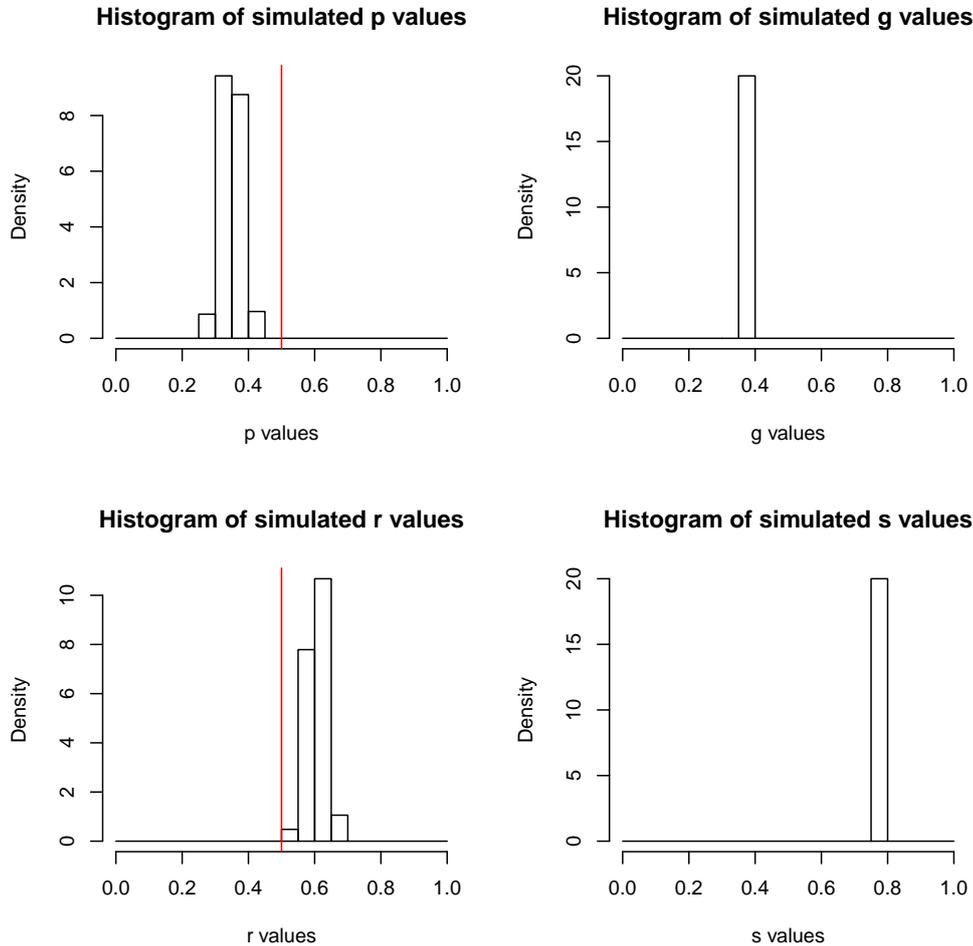


FIGURE 8. Histograms of parameter values from the the 204 simulations retained within acceptance interval $d(O, S) \leq 0.04$. Red lines indicate unbiased parameter values, $p = 1/2$ and $r = 1/2$, giving equal probability of tying right- and left-handed trefoils and equal probability of repeating the previous knot as not, respectively.

320 We can establish what effect our posterior parameter estimates would have on
 321 the cultural evolution of granny and reef knots by plugging these values into the
 322 model. Figure 9 shows how the population evolves towards a single polymorphic
 323 equilibrium state, no matter the starting distribution (grey arrows leading to black
 324 disc). The effect of the high posterior imitation value, $\bar{s} = 0.79$, is shown by

325 comparing this equilibrium state against the expected equilibrium frequencies in
 326 the absence of social learning ($s = 0$, red disc).

327 We can see the effect of learning biases by comparing against trajectories where
 328 these biases are absent ($p = 0.5, r = 0.5, g = 0$; blue arrows leading to blue disc).
 329 Although imitation is a relatively high value, $\bar{s} = 0.79$, granny knots evolve to be
 330 more common than reef knots, caused by the repetition bias, while left-handed
 331 granny knots are more common than right, caused by the handedness bias. Given
 332 the high posterior mean imitation value, the posterior mean mirroring value is
 333 not large enough to cause the characteristic oscillating dynamics shown in Figure
 334 6b and has negligible effect on the relative equilibrium frequency of left- to right-
 335 handed granny knots.

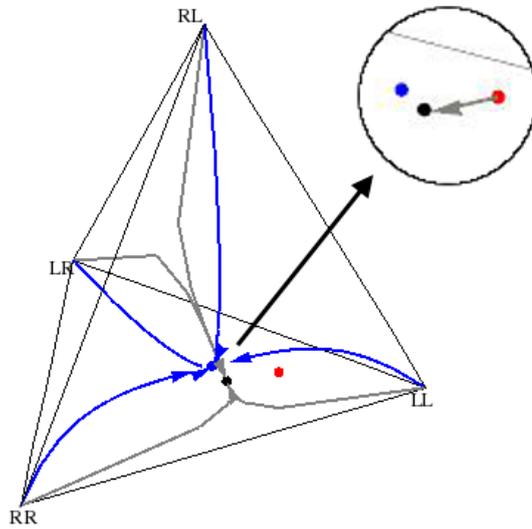


FIGURE 9. Evolutionary trajectories of the four knot forms, where $f_{ij} = 1$ in each corner and frequencies are equal at the centre of the tetrahedron, plotted by converting frequencies to Barycentric coordinates. Trajectories using the mean posterior parameter values are shown by the grey arrows and black disc, $\hat{f}_{LL} = 0.4241, \hat{f}_{RR} = 0.3835, \hat{f}_{LR} = \hat{f}_{RL} = 0.0962$. In the absence of social learning, the expected knot frequencies are shown by the red disc $\hat{f}_{LL} = 0.5613, \hat{f}_{RR} = 0.2613, \hat{f}_{LR} = \hat{f}_{RL} = 0.0887$, and are governed by the degree of repetition and handedness. The blue arrows and disc, $\hat{f}_{LL} = 0.375, \hat{f}_{RR} = 0.375, \hat{f}_{LR} = \hat{f}_{RL} = 0.125$, show the trajectories in the absence of learning biases and mirroring, $p = 0.5, r = 0.5, g = 0$, where $\bar{s} = 0.79$.

336 Finally, we note that the absence of learning biases does not necessarily lead to
 337 equal knot frequencies of cultural variants (i.e. the blue disc is not in the centre of
 338 the tetrahedron), rather that granny knots are expected in higher frequency than
 339 reef knots. This occurs because of the non-independent relationships between the
 340 parameters. Consider for instance the case where there is no social learning in the
 341 absence of both handedness or repetition biases and mirroring $p = 0.5, r = 0.5, g =$
 342 $0, s = 0$. Figure 10 shows that the probability of tying each knot is $P(LL) = \frac{3}{8}$
 343 and $P(RR) = \frac{3}{8}$, and $P(RL) = \frac{1}{8}$ and $P(LR) = \frac{1}{8}$.

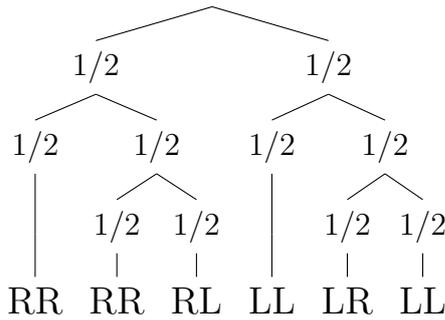


FIGURE 10. A decision tree showing knots tied in the absence of biases in handedness ($p = 0.5$; top layer decision) and repetition biases ($r = 0.5$; second layer decision).

344 **4.2. Comparing Parametric and Non-parametric Approaches.** We compare
 345 the equilibrium results of the parametric model, described above, with a
 346 non-parametric approach which predicts equilibrium frequencies from the trans-
 347 mission matrix which is taken directly from the experimental data (Table 1), and
 348 represents the probability of the change in knot types from those demonstrated to
 349 those learned. For example $x_{2,1} = P(LL|RR)$ is the probability of tying knot LL
 350 when shown RR.

$$(7) \quad X = \begin{bmatrix} \frac{14}{26} & \frac{9}{26} & \frac{1}{26} & \frac{2}{26} \\ \frac{9}{25} & \frac{15}{25} & 0 & \frac{1}{25} \\ \frac{4}{24} & \frac{4}{24} & \frac{8}{24} & \frac{8}{24} \\ \frac{6}{25} & \frac{1}{25} & \frac{6}{25} & \frac{12}{25} \end{bmatrix}$$

351 X is a right stochastic matrix representing the frequency of change in knots
 352 tied given by the experimental data. We can simulate social transmission of these
 353 knots within future generations by taking powers of this matrix, basing future
 354 generations solely on the present state. This approach treats any cognitive fac-
 355 tors affecting change in cultural variant frequency as implicit, linear effects in the

356 transition matrix. After 20 generations we have stability in transmission such that
 357 the probability of tying any given knot remains constant (measured to 3 decimal
 358 places).

Knot	Parametric Approach	Non-parametric Approach
LL	42.41%	40.1%
RR	38.35%	39.1%
LR	9.62%	7.2%
RL	9.62%	13.6%

TABLE 3. Percentage of each type of knot in the population at equilibrium, calculated using the parametric and non-parametric models.

359 Table 3 shows that both the parametric and non-parametric models predict
 360 a prevalence of granny over reef knots at equilibrium, but the parametric ap-
 361 proach predicts a higher left- to right-handed bias in granny knots and, unlike the
 362 non-parametric approach, gives equal frequencies of both reef knots. The non-
 363 parametric approach makes no theoretical assumptions over how cognitive factors
 364 interact so it is unsurprising to find unequal reef knot frequencies. The parametric
 365 model behaviour is, by definition, determined by the probabilistic interactions of
 366 proposed cognitive factors (s, g, r, p) but the model does not assume that individ-
 367 uals recognise or treat the two reef knots to be mathematically the same.

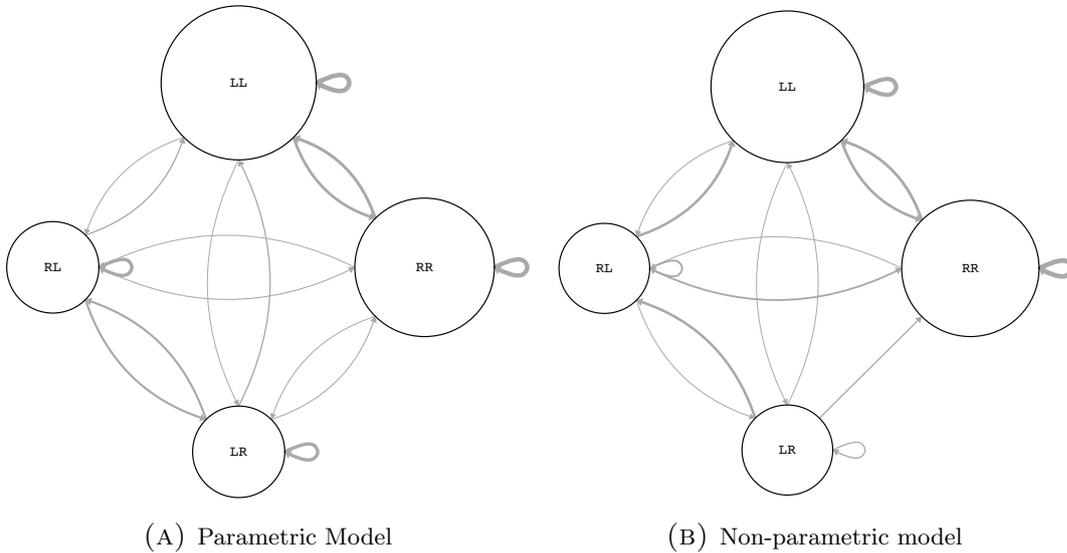


FIGURE 11. Weighted graph demonstrating the transmission of each knot under (A) a parametric approach and (B) a non-parametric approach

368 Figure 11b shows the transmission of each knot type from the transition matrix.
 369 We observe the absence of knot transitions from RR to LR as none did so in the
 370 experimental data. Occurrences like this lack of transition can affect the expected
 371 equilibria under the non-parametric approach, causing lower frequencies of knot
 372 LR to be expected, as seen in Table 3 but are not seen under the parametric
 373 approach shown in Figure 11a.

374

5. DISCUSSION

375 In this paper we have combined an experiment and model to investigate the
 376 effects of non-random learning errors on the evolution of granny and reef knots.
 377 Using experimental data we have seen that granny knots are more commonly
 378 correctly transmitted than reef knots. Using ABC, we predict that participants
 379 in the experiment were less likely to mirror than not to mirror the demonstrated
 380 knot but likely to imitate the perceived knot. Also, on average, they were biased
 381 towards tying left handed trefoils and more likely than not to inadvertently repeat
 382 the first knot tied.

383 The estimate of mirroring suggests that faithful cultural transmission is vulner-
 384 able to the correspondence problem [11] in which case this effect might be reduced
 385 if observers and demonstrators sit side-by-side, taking a similar visual perspective.
 386 The average bias towards left-handed knots may be a relatively asocial phenom-
 387 enon as this was observed in both the asocial stage (1) and demonstration state
 388 (2), and was strongly correlated with the handedness of the individual. While
 389 complex skills can be honed by repetition, our study suggests that a tendency for
 390 inadvertent repetition of task chunks can reduce within-sequence variation over
 391 evolutionary time, in this case promoting granny over reef knots.

392 Our results suggest that errors in attempts to faithfully reproduce demonstrated
 393 knots are unlikely to be random, and can affect cultural evolutionary trajectories
 394 even when transmission fidelity is relatively high, as the population evolves towards
 395 an equilibrium characterised by a prevalence of left- over right-handed granny
 396 knots and a preponderance of granny knots over reef knots. Even if the proposed
 397 cognitive factors were unbiased in their effects, their interactions do not produce
 398 an even distribution of knot forms because of their conditional, or nested, effects.
 399 Thus empirical evidence for granny over reef knots does not necessary result from
 400 a knot preference (although it may) but from the interaction of cognitive factors
 401 that affect their construction.

402 We contrast the equilibrium states that result from the parametric and non-
 403 parametric approaches and note that only the parametric model predicts equal
 404 frequencies of the two reef knot frequencies. While there is no assumption in the
 405 model that individuals recognise both forms of reef knot to be equivalent, the
 406 proposed cognitive factors result in an equilibrium state that is consistent with
 407 our mathematical understanding that these two forms (LR and RL) are actually
 408 the same knot. This result is caused (in an evolving population) by any degree of

409 imperfect imitation (i.e. $0 \leq s \leq 1$), which increases variation in cultural forms by
410 driving the population toward equal frequencies of all knot forms; this only holds
411 where individuals tie some form of trefoil knot, rather than abstaining from the
412 knot-tying behaviour if they fail to imitate. Mirroring also pushes the population
413 toward equal frequencies of knot forms because it is most likely, by chance, to
414 reverse the handedness of the most common trefoil. Thus the effect of these two
415 factors accounts for the parity of reef knot forms at equilibrium but, on their own,
416 would also have a similar effect on forms of granny knot, even though these are
417 not mathematically identical. The parity of reef knot forms at equilibrium should
418 not be used as confirmation of a ‘good’ model; rather, cognitive factors act in a
419 way that results in variation that is consistent with mathematical classification of
420 knots.

421 Cladiere et al. ([5], p.5, Table 1 and Eq.4.1) use a non-parametric transition
422 matrix, which they label an “evolutionary causal matrix” (p.5), to illustrate evolu-
423 tionarily causal relations between variants, highlighting Markovian and frequency-
424 dependent properties of evolutionary processes, although they indicate that their
425 use of a non-parametric transition matrix was not intended as an “adequate formal
426 modelling tool” ([5], p.7). Our transition matrix (Equation 7) exhibits relatively
427 high values along the leading diagonal, which is consistent with “homo-impact”
428 [5], such that the frequency of variants are more strongly affected by their own
429 prior frequency than by others’, such as caused by imitation. But our diago-
430 nal values are higher for the granny knots than for the reef knots, and indeed
431 the reef knot diagonal values are not dissimilar to the off-diagonal elements; this
432 is consistent with what Cladiere et al call “hetero-impact”, or between-variant
433 frequency-dependent effects such as caused by mirroring. These observations in-
434 dicate that different factors may be affecting granny and reef knot frequencies.
435 If these factors were variant-specific (e.g. a bias for either LL, RR, LR or RL),
436 a non-parametric transition matrix would suffice, but our analysis suggests that
437 cognitive factors affect learning of particular knot properties or relations, so it is
438 best to employ a parametric approach to account for the non-linear interactions
439 between these factors.

440 The use of ABC illustrates how cross-generation data can be used to estimate
441 the influence of the proposed cognitive factors. The narrow posterior distributions
442 and the matching of the posterior handedness estimate to the experiment stage
443 one results are encouraging signals of their explanatory value but of course we
444 cannot rule out the influence of other factors not considered in our model. Using
445 our mathematical model of the cultural evolutionary dynamic, ABC has the ob-
446 vious advantage over a generalized linear regression approach in that it accounts
447 for non-linear interactions between cognitive factors as structured in the social
448 learning process. Although we are estimating the effects of individual-level prop-
449 erties of learning by comparing simulated and observed population-level measures

450 of cultural variation, our task is made easier by having individual-level data; i.e.
451 we know what each individual observed and which knot they tied.

452 We restricted our analysis to a small closed set of cultural variants so social
453 learning errors, or mutations, are a source of population-level variation even though
454 the mutation may often not be novel to the population. In the open set of knots
455 collated by Ashley [22], knot variation is likely to be constrained by technical prop-
456 erties, social function and aesthetic qualities. Nonetheless, it is possible that the
457 cognitive factors we have investigated may affect the distribution of pairs of tre-
458 foils within composite knots (i.e. microstructure). Of the composite knots within
459 Ashley, the proportion of granny to reef knots exactly matches the 3 to 1 ratio pre-
460 dicted by our parametric model at equilibrium in the absence of non-random error
461 and mirroring and is similar to that predicted using the posterior estimates from
462 the experiment (approx. 81% granny knots) [22] [23]. We resist drawing strong
463 conclusions from the similarity between our results and the single population-level
464 estimate of granny and reef knot frequencies found in Ashley’s corpus but the cor-
465 relation indicates that our modelling treatments of the experimental sample may
466 be worth developing further, for instance, to consider micro-structure variation
467 that may be redundant in relation to function (i.e. synonymous mutation). Anal-
468 ysis of experimental and real-world data should allow us to unpick the cognitive,
469 ecological and social factors affecting the evolution of cultural variation.

470

APPENDIX A. QUESTIONNAIRE INFORMATION

471 As part of the experiment described in Section 2 the participants were asked to
 472 complete a questionnaire detailing their name, gender, degree programme, hand-
 473 edness and hand usually written with, their knot tying experience and whether
 474 they knew how to tie a reef or granny knot. The questionnaire was filled in by
 475 participants at the end of the experiment, when all materials had been collected.

476 Participants recorded the hand they usually write with.

		Trefoil Tied		Total
		Right	Left	
Hand usually written with	Right	25	62	87
	Left	4	6	10
Self reported handedness	Right	23	58	81
	Left	4	5	9
	Ambidextrous	2	5	7
Total		29	68	97

TABLE 4. Handedness of trefoils tied given hand usually written with

477 The majority of participants usually wrote with their right hand and tied a
 478 majority of left trefoils. Using a Bayesian analysis to test proportions [30] shown
 479 in Figure 12 we see there is a larger probability of tying a left handed trefoil
 480 by participants who usually wrote with their right hand than those who wrote
 481 with their left. Similarly there is a larger probability of tying a right handed
 482 trefoil by those who usually wrote with their left hand. However, the percentage
 483 of participants who usually wrote with their left hand is quite low so might not
 484 be wholly representative. The same result can be found using the self reported
 485 handedness data with those reporting as ambidextrous having a larger probability
 486 of tying a left trefoil. However, as most of those reporting as ambidextrous usually
 487 wrote with their right hand, this fits with the test of proportions for hand written
 488 with and trefoil tied.

489 Participants were asked to record their gender in a free-form box.

		Tied correct knot		Total
		Y	N	
Gender	Male	19	17	36
	Female	28	33	61
	Other	2	1	3
Total		49	51	100

TABLE 5. Performance in experiment given gender

490 Table 5 shows the proportion of participants who tied the knot shown in the
 491 video given their gender. It is clear to see that their gender had no bearing on
 492 their performance in the experiment.

493 Participants were asked to rate their experience in knot tying on a scale of one to
 494 five, with one meaning they considered themselves a beginner and five an expert.
 495 They then had the opportunity to give details in a free-form box.

		Tied correct knot		
		Y	N	Total
Experience	1	18	19	37
	2	10	11	21
	3	14	14	28
	4	7	6	13
	5	0	1	1
Total		49	51	100

TABLE 6. Performance in experiment given knot tying experience

496 Table 6 shows the proportion of participants who tied the knot shown in the
 497 video given the experience rated on the questionnaire. It is clear to see that the
 498 self rated experience had no bearing on the performance in the experiment.

499 Participants were also asked whether they knew how to tie a granny and a reef
 500 knot.

		Knot tied		
		Granny	Reef	Total
Knew how to tie a granny knot	Yes	17	13	30
	No	45	25	70
Total		62	38	100

TABLE 7. Performance in experiment given knowledge of granny knots

		Knot tied		
		Granny	Reef	Total
Knew how to tie a reef knot	Yes	17	17	34
	No	45	21	66
Total		62	38	100

TABLE 8. Performance in experiment given knowledge of reef knots

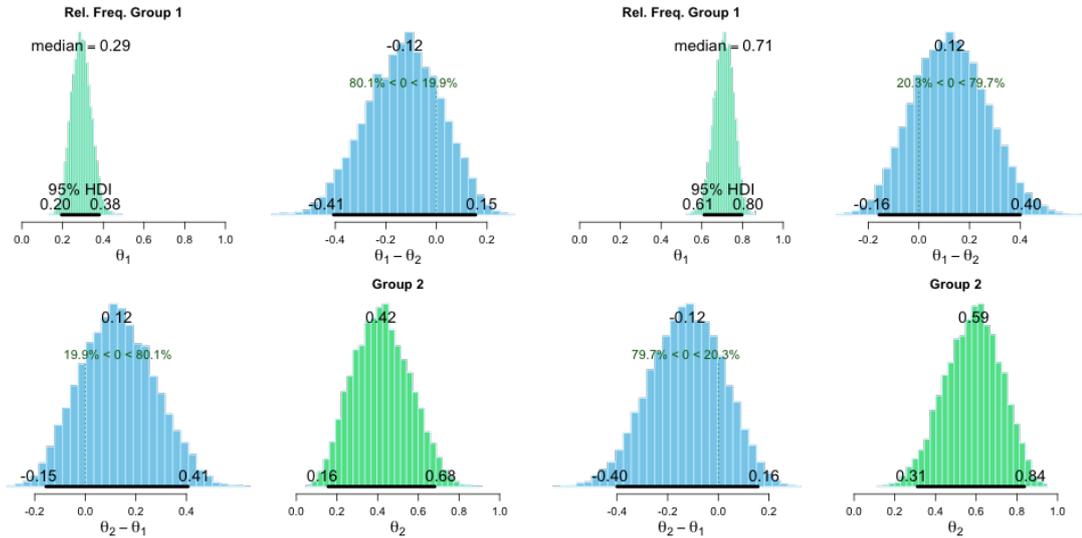
501 Tables 7 and 8 show the proportion of participants who tied granny and reef
 502 knots given the knowledge rated on the questionnaire. It is clear to see that the

503 self rated knowledge also had no bearing on the knots tied in the experiment. It
504 is interesting to note that more participants knew how to tie the reef knot than
505 the granny. This could be due to the belief that the reef knot is superior to the
506 granny and so more likely to be taught.

507

APPENDIX B. POSTERIOR SIMULATIONS

508 Posterior simulations of the test of proportions generated using R package
 509 Bayesian First Aid [31]. The test of proportions assumes flat priors constructed
 510 as a Beta(1,1) distribution.



(A) Posterior simulation of right trefoils tied (B) Posterior simulation of left trefoils tied

FIGURE 12. Figure 12a shows the simulations of tying right handed trefoils by those who wrote with either hand. θ_1 refers to those who wrote with their right hand and tied a right trefoil whilst θ_2 refers to those who wrote with their left hand and tied a right trefoil, the differences $\theta_1 - \theta_2$ and $\theta_2 - \theta_1$ refer to the difference between these groups. We see there is a larger probability of those who write with their left hand tying a right handed trefoil than those who wrote with their right hand. Figure 12b shows the simulations of tying left handed trefoils by those who wrote with either hand. θ_1 refers to those who wrote with their right hand and tied a left trefoil whilst θ_2 refers to those who wrote with their left hand and tied a left trefoil, the differences $\theta_1 - \theta_2$ and $\theta_2 - \theta_1$ refer to the difference between these groups. We see there is a larger probability of those who write with their right hand tying a left handed trefoil than those who wrote with their left hand. However if we look at both Figures 12a and 12b we see those who wrote with their left hand were slightly more likely to tie a left handed trefoil than a right handed as the left handed trefoil was the most common amongst both groups and there were relatively few people reporting as writing with their left hand.

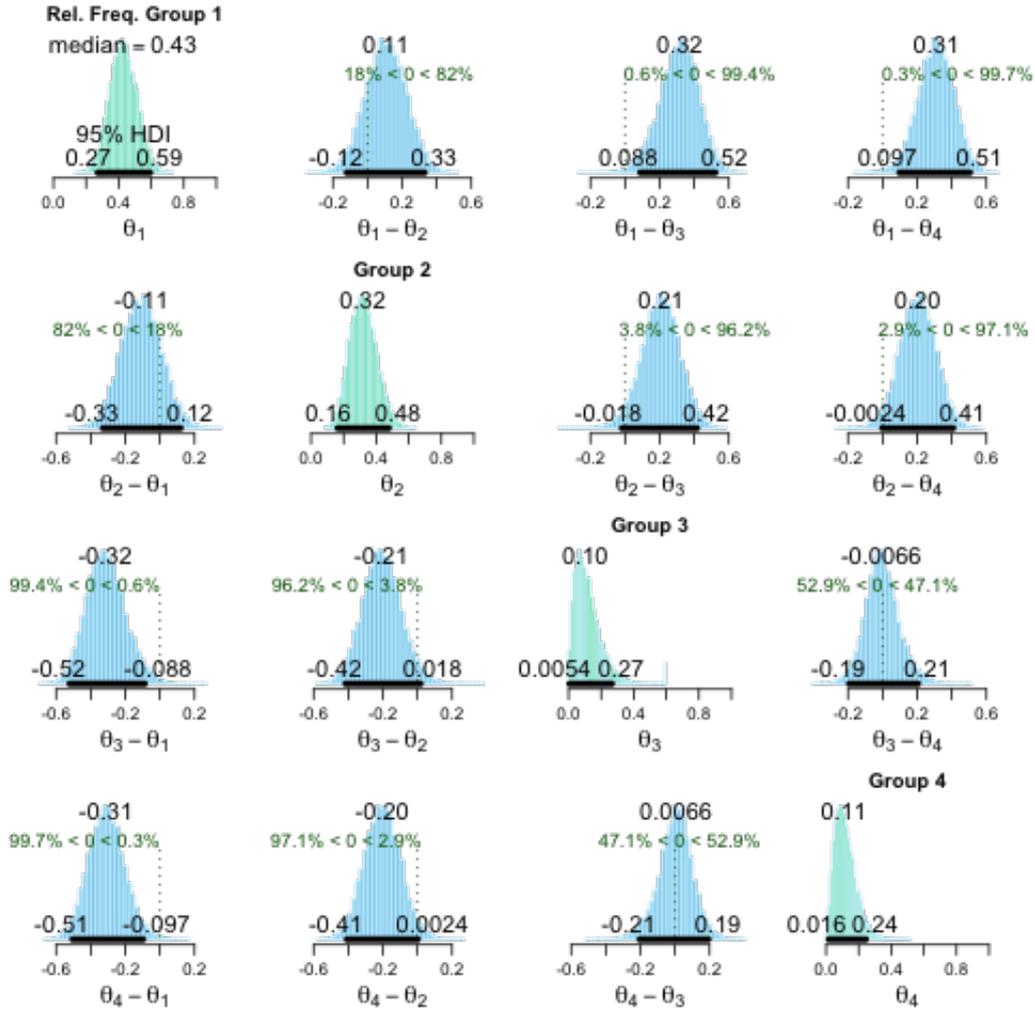


FIGURE 13. Posterior simulation of LL knots tied given demonstration knot. θ_1 refers to those who were shown the knot LL and tied LL, θ_2 those who were shown RR and tied LL, θ_3 those who were shown LR and tied LL and θ_4 those who were shown RL and tied LL with $\theta_i - \theta_j$, ($i, j \in \{1, 2, 3, 4\}, i \neq j$) referring to the difference between groups. We see a larger probability for those who were shown either LL or RR tying LL than LR or RL, with those shown LL having the largest probability.

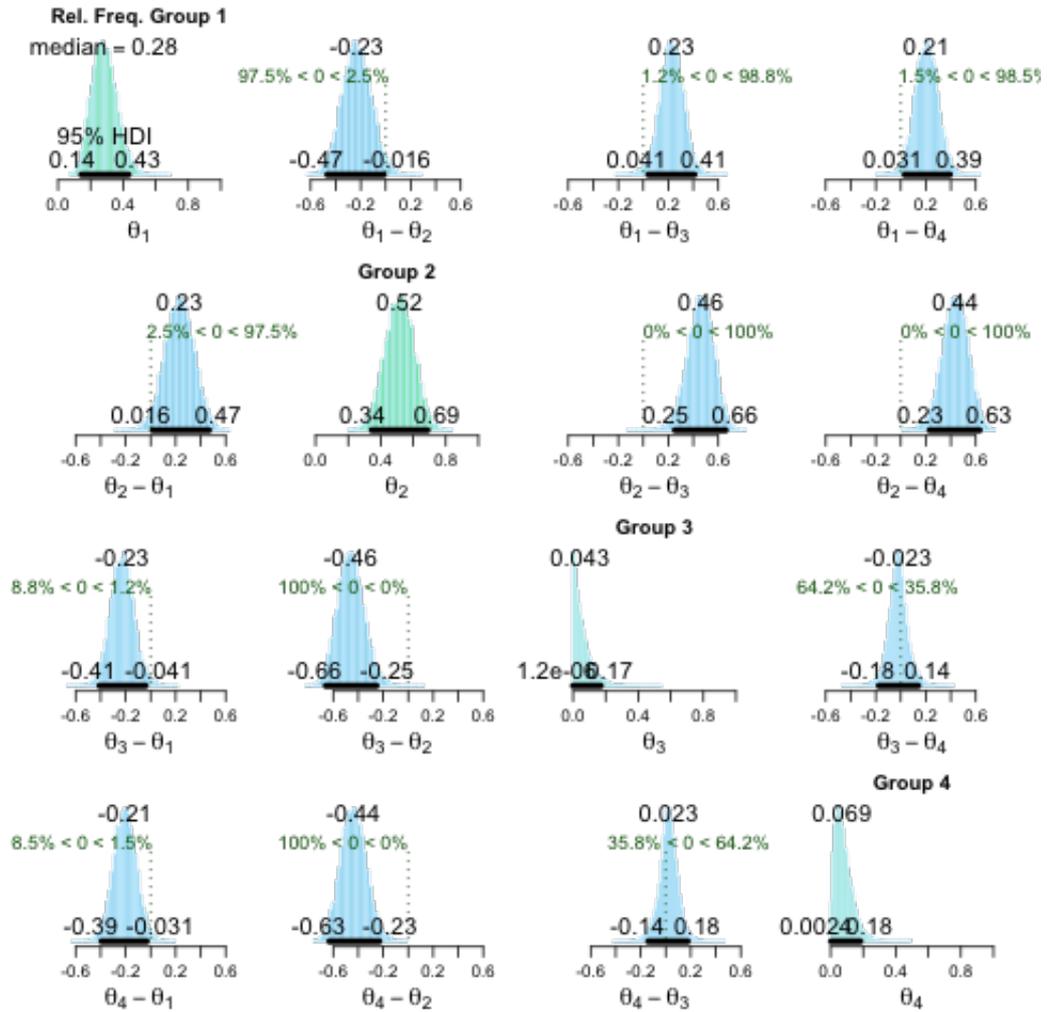


FIGURE 14. Posterior simulation of RR knots tied given demonstration knot. θ_1 refers to those who were shown the knot LL and tied RR, θ_2 those who were shown RR and tied RR, θ_3 those who were shown LR and tied RR and θ_4 those who were shown RL and tied RR with $\theta_i - \theta_j$, ($i, j \in \{1, 2, 3, 4\}, i \neq j$) referring to the difference between groups. We see a larger probability for those who were shown either LL or RR tying RR than LR or RL, with those shown RR having the largest probability.

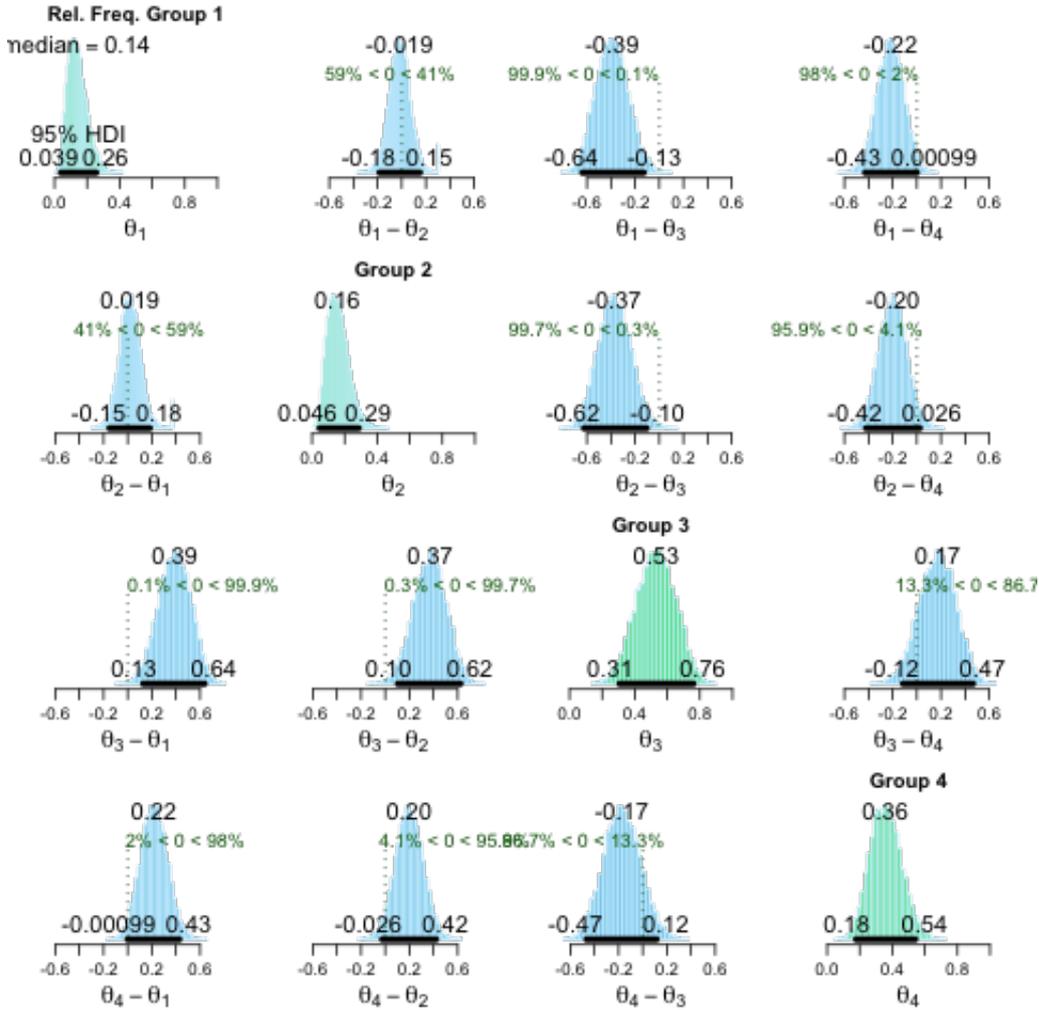


FIGURE 15. Posterior simulation of LR knots tied given demonstration knot. θ_1 refers to those who were shown the knot LL and tied LR, θ_2 those who were shown RR and tied LR, θ_3 those who were shown LR and tied LR and θ_4 those who were shown RL and tied LR with $\theta_i - \theta_j$, ($i, j \in \{1, 2, 3, 4\}, i \neq j$) referring to the difference between groups. We see a larger probability for those who were shown either LR or RL tying LR than LL or RR, with those shown LR having the largest probability.

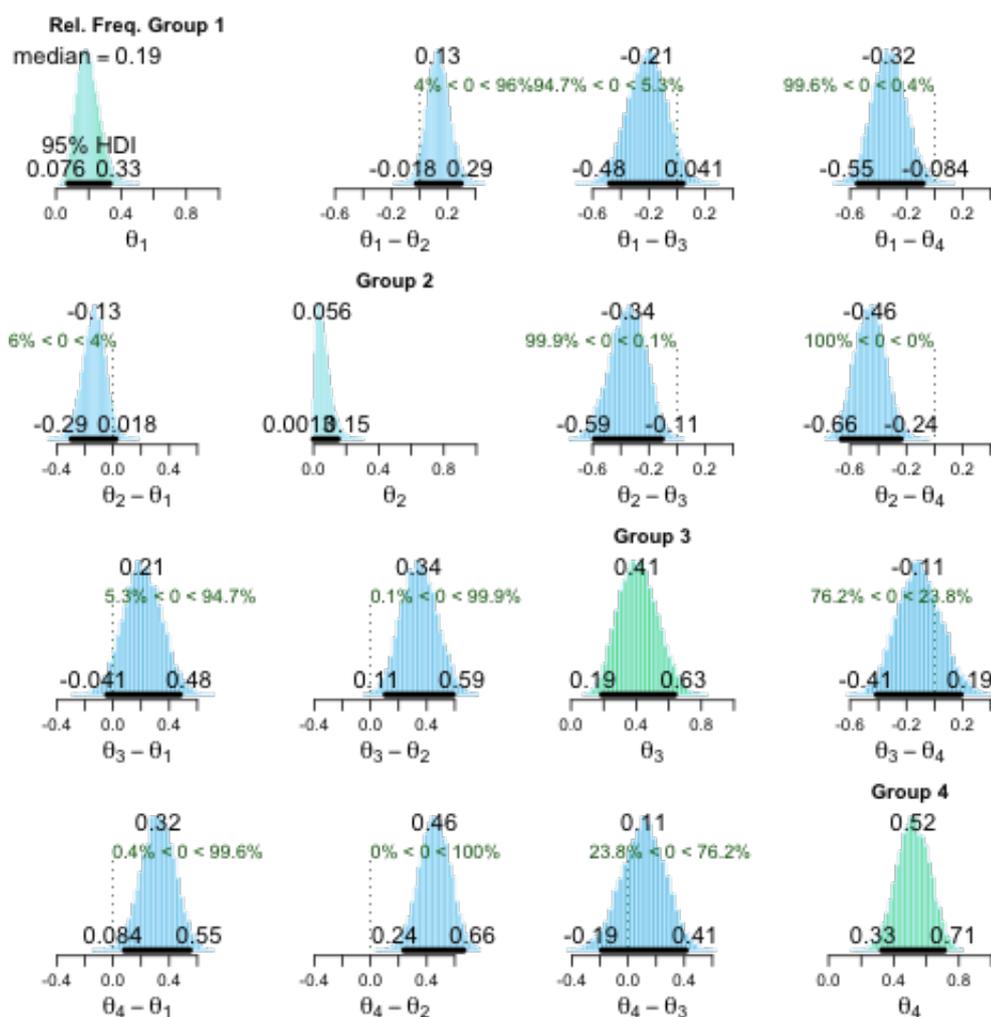
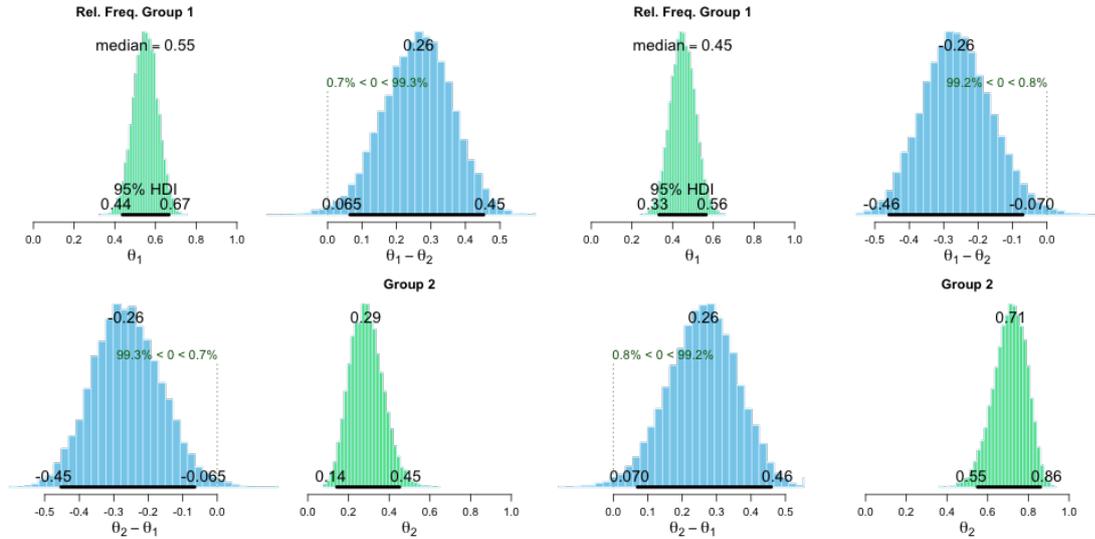


FIGURE 16. Posterior simulation of RL knots tied given demonstration knot. θ_1 refers to those who were shown the knot LL and tied RL, θ_2 those who were shown RR and tied RL, θ_3 those who were shown LR and tied RL and θ_4 those who were shown RL and tied RL with $\theta_i - \theta_j$, ($i, j \in \{1, 2, 3, 4\}, i \neq j$) referring to the difference between groups. We see a larger probability for those who were shown either LR or RL tying RL than LL or RR, with those shown RL having the largest probability.



(A) Posterior simulation of knots tied by those with a left hand bias in stage 1 (B) Posterior simulation of knots tied by those with a right hand bias in stage 1

FIGURE 17. Figure 17a shows the simulations of tying an L or R knot first post demonstration given a left hand bias in stage 1. θ_1 refers to those who had a left hand bias in stage 1 and tied an L knot first post demonstration, θ_2 those who had a left hand bias and tied an R knot first and $\theta_1 - \theta_2$ and $\theta_2 - \theta_1$ the difference between groups. We see there is a larger probability of those who had a left hand bias starting their post-demonstration knot with an L knot than an R. Figure 17b shows the simulations of tying an L or R knot first post demonstration given a right hand bias in stage 1. θ_1 refers to those who had a right hand bias in stage 1 and tied an L knot first post demonstration, θ_2 those who had a right hand bias and tied an R knot first and $\theta_1 - \theta_2$ and $\theta_2 - \theta_1$ the difference between groups. We see there is a larger probability of those who had a right hand bias starting their post-demonstration knot with an R knot than an L.

APPENDIX C. EQUATIONS

511

512 The equations are

$$\begin{aligned}
f'_{RR} = & f_{RR}((1-g)s^2 + (1-s)^2(1-r)p^2 + (1-s)^2rp + 2(1-g)s(1-s)r) \\
& + 2(1-g)s(1-s)(1-r)p \\
& + f_{LL}((1-s)^2(1-r)p^2 + (1-s)^2rp + gs^2 + 2gs(1-s)r) \\
& + 2gs(1-s)(1-r)p \\
& + (f_{RL} + f_{LR})((1-s)^2(1-r)p^2 + (1-s)^2rp + s(1-s)r) \\
& + s(1-s)(1-r)p
\end{aligned}
\tag{8}$$

513

$$\begin{aligned}
f'_{LL} = & f_{RR}(gs^2 + (1-s)^2(1-r)(1-p)^2 + (1-s)^2r(1-p) + 2gs(1-s)r) \\
& + 2gs(1-s)(1-r)(1-p) \\
& + f_{LL}((1-g)s^2 + (1-s)^2(1-r)(1-p)^2 + (1-s)^2r(1-p)) \\
& + 2(1-g)s(1-s)(1-r)(1-p) + 2(1-g)s(1-s)r) \\
& + (f_{RL} + f_{LR})((1-s)^2(1-r)(1-p)^2 + (1-s)^2r(1-p)) \\
& + s(1-s)(1-r)(1-p) + s(1-s)r)
\end{aligned}
\tag{9}$$

514

$$\begin{aligned}
f'_{RL} = & f_{RR}((1-s)^2(1-r)p(1-p) + (1-g)s(1-s)(1-r)(1-p)) \\
& + g(1-s)s(1-r)p) \\
& + f_{LL}((1-s)^2(1-r)p(1-p) + (1-g)(1-s)s(1-r)p) \\
& + gs(1-s)(1-r)(1-p)) \\
& + f_{RL}((1-g)s^2 + (1-s)^2(1-r)p(1-p) + (1-g)s(1-s)(1-r)) \\
& + f_{LR}(gs^2 + (1-s)^2(1-r)p(1-p) + gs(1-s)(1-r))
\end{aligned}
\tag{10}$$

515

$$\begin{aligned}
f'_{LR} = & f_{RR}((1-s)^2(1-r)(1-p)p + (1-g)(1-s)s(1-r)(1-p)) \\
& + gs(1-s)(1-r)p) \\
& + f_{LL}((1-s)^2(1-r)(1-p)p + (1-g)s(1-s)(1-r)p) \\
& + g(1-s)s(1-r)(1-p)) \\
& + f_{RL}(gs^2 + (1-s)^2(1-r)(1-p)p + gs(1-s)(1-r)) \\
& + f_{LR}((1-g)s^2 + (1-s)^2(1-r)(1-p)p + (1-g)s(1-s)(1-r))
\end{aligned}
\tag{11}$$

516

APPENDIX D. EQUILIBRIA EQUATIONS

Equilibria occur when

$$\hat{f}_{RR} = \frac{Q_1}{P}$$

where

(12)

$$Q_1 = -p^2(r-1)(s-1)(1+s(2g-1)(r-1) + rs^2(2g-1)) + gs(r(s^2-2) - s) \\ + p(s-1)(2gs + r^2s(2g-1)(1+s) + r(1+s-2gs(2-s)))$$

$$\hat{f}_{LL} = \frac{Q_2}{P}$$

where

$$(13) \quad Q_2 = s^2(1-g) - p^2(r-1)(s-1)(1+s(2g-1)(r-1) + rs^2(2g-1)) - 1 \\ + r(s(1-2g) + s^3(g-1)) + p(s-1)(r^2s(2g-1)(1+s) \\ + 2s(g-1) + rs(1+(3-4g) - 2s^2(g-1)) - 2)$$

$$\hat{f}_{LR} = \frac{Q_3}{P}$$

where

$$(14) \quad Q_3 = (r-1)(gs - p(s-1)(1+p^2(s-1))(1+(2g-1)(s(r-1) + rs^2)))$$

$$\hat{f}_{RL} = \frac{Q_4}{P}$$

where

$$(15) \quad Q_4 = (r-1)(gs - p(s-1)(1+p^2(s-1))(1+(2g-1)(s(r-1) + rs^2)))$$

517 and

$$(16) \quad P = (1+s)(s(2g-1)(rs - r - 1) - 1).$$

APPENDIX E. STABILITY

518

519 In this system, an equilibrium point is stable if no matter the starting values
 520 of f_{RR} , f_{LL} , f_{LR} , f_{RL} , the system comes to rest at the same point. If the point
 521 changes depending on these starting values then it is not stable.

522 To find the stable equilibrium points we set f_{ij} equal to the equilibria points
 523 determined by the equations, plus some small perturbation ϵ_{ij} . The equilibrium is
 524 stable if the value of f'_{ij} , moves towards the equilibria points given by the equations
 525 in Appendix D.

526 Let

$$(17) \quad f_{RR} = \frac{Q_1}{P} + \epsilon_{RR}$$

527

$$(18) \quad f_{LL} = \frac{Q_2}{P} + \epsilon_{LL}$$

528

$$(19) \quad f_{LR} = \frac{Q_3}{P} + \epsilon_{LR}$$

529

$$(20) \quad f_{RL} = \frac{Q_4}{P} + \epsilon_{RL}$$

530 where Q_i and P are as given in Appendix D, and

$$(21) \quad \epsilon_{RL} = -\epsilon_{RR} - \epsilon_{LL} - \epsilon_{LR}$$

531 to ensure f_{ij} sum to one.532 We then compute f'_{RR} , f'_{LL} , f'_{LR} , f'_{RL} and the distance:

$$(22) \quad d_{RR} = f'_{RR} - \frac{Q_1}{P}$$

533

$$(23) \quad d_{LL} = f'_{LL} - \frac{Q_2}{P}$$

534

$$(24) \quad d_{LR} = f'_{LR} - \frac{Q_3}{P}$$

535

$$(25) \quad d_{RL} = f'_{RL} - \frac{Q_4}{P}$$

536 We then have the following cases.

537 Case 1:

$$(26) \quad d_{ij} = 0$$

538 In this case the system jumps to an equilibrium point given by the parameters.
 539 The system then remains at this point for all generations. This occurs when there

540 is no accurate imitation, when $s = 0$. The system is not affected by starting values
541 of f_{ij} , the frequency of each type of knot is determined solely by the values of p
542 and r .

543 Case 2:

$$(27) \quad d_{ij} = \epsilon_{ij}$$

544 In this case there is no change in the system, meaning the system is currently at
545 equilibria, with the system remaining at this point for all generations. This occurs
546 when imitation is always accurate and mirroring never occurs, when $s = 1$ and
547 $g = 0$. The equilibrium state is determined by the starting values of f_{ij} and is
548 independent of the values of p and r . The frequency of each type of knot remains
549 constant across generations.

550 Case 3:

$$(28) \quad d_{ij} < \epsilon_{ij}$$

551 In this case the system moves towards the equilibrium point given by the parame-
552 ters. This occurs when $s < 1$, when imitation is not perfect and the system evolves
553 towards equilibria over generations.

554 Case 4:

$$(29) \quad d_{ij} > \epsilon_{ij}$$

555 In this case the system moves away from the equilibrium point given by the pa-
556 rameters. This never occurs for any equilibrium point in the system, meaning all
557 points are stable.

558

APPENDIX F. BARYCENTRIC COORDINATES

559 We plot a tetrahedron with vertices at the points $\begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}$, $\begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix}$, $\begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$ and $\begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$.

560 Taking values of f'_{ij} from our equations, we can represent the values of f'_{ij} as
 561 points \mathbf{p} inside the tetrahedron using the conversion

$$(30) \quad \mathbf{p} = \begin{pmatrix} f'_{RR} + f'_{RL} \\ f'_{LL} + f'_{RL} \\ f'_{LR} + f'_{RL} \end{pmatrix}$$

562

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