

1 **Enhancing student comprehension of paternity assignment in molecular primatology: a**  
2 **pilot study using a Shiny web application in Kenya**

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12 Running title: Teaching paternity inference with Shiny

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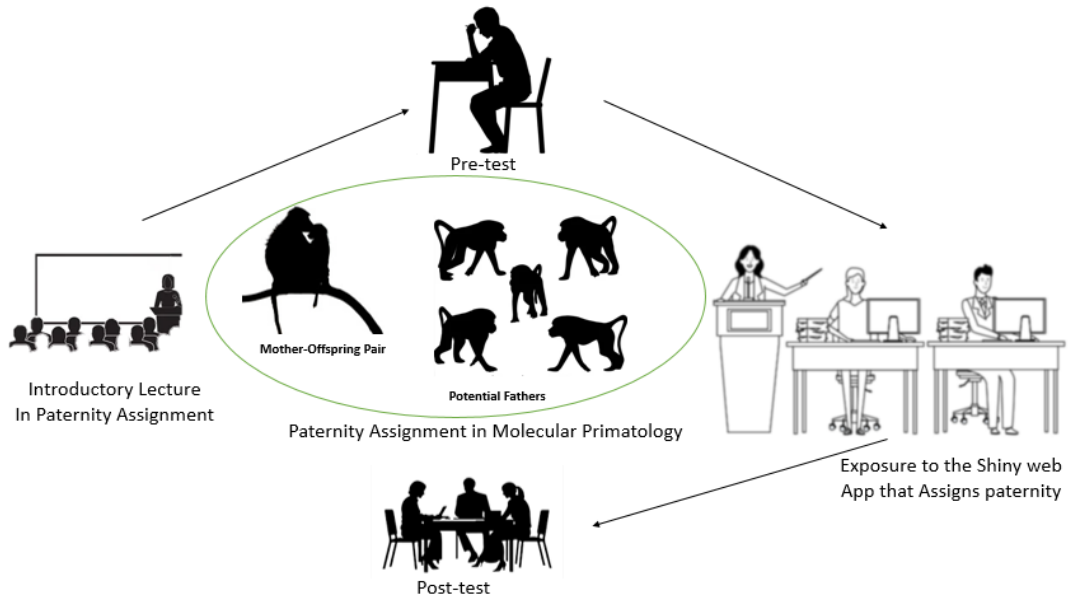
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22 **Graphical Abstract**

23 \*Images in the graphical abstract are courtesy of publicdomainpictures.net



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26

27 **Abstract**

28 Kinship is a major determinant of affiliative and mating behavior in primates. In field studies,  
29 identifying kin typically relies in part on genetic analysis, especially for discriminating  
30 paternal relationships. Such analyses assume knowledge of Mendelian inheritance,  
31 genotyping technologies, and basic statistical inference. Consequently, they can be difficult  
32 for students to grasp, particularly through traditional lecture formats. Here, we investigate  
33 whether integrating an additional active learning approach—interaction with a Shiny web  
34 application, *DadApp*, which implements a popular paternity inference approach in an  
35 accessible graphical user interface—improves student understanding of genetic kinship  
36 analysis in molecular primatology. We do so in the context of a non-traditional learning  
37 environment in Kenya, a developing nation in which students have limited access to  
38 technology, and where the efficacy of educational Shiny apps has never been assessed.  
39 Twenty-eight (28) participants with diverse educational backgrounds attended an  
40 introductory lecture on genetics and paternity inference, completed a pre-test, interacted  
41 with *DadApp* via a structured set of exercises and questions, and then completed a post-test  
42 and survey about their experience and subjective understanding. Post-test scores  
43 significantly improved relative to pre-test scores ( $p$ -value= $3.75 \times 10^{-6}$ ). Further, student  
44 interest and confidence in the subject matter significantly increased after the practical  
45 session with *DadApp*. Our results suggest that Shiny web app-based active learning  
46 approaches have potential benefits in communicating complex topics in molecular  
47 primatology, including in resource-limited settings where such methods have not yet  
48 experienced high penetrance.

49 **Keywords:** Shiny web app, active learning, paternity inference, molecular primatology

50

51

## 52 **Introduction**

53 Kinship is one of the most important determinants of social organization, social  
54 structure, and mating patterns in primates (Strier, 2008; Chapais & Berman, 2004; Kappeler  
55 & Van Schaik, 2002). For example, in many primates, close kin preferentially affiliate with  
56 one another, but scrupulously avoid mating (Dal Pesco et al., 2021; Guo et al., 2015;  
57 Chapais, 2001). Indeed, avoiding mating with close kin is thought to be one of the most  
58 important selective factors governing the evolution of sex-biased dispersal, which  
59 characterizes approximately 75% of group-living primates (Morrison et al., 2023; Wellens et  
60 al., 2022; Galezo et al., 2022; Pusey, 1990). Selective investment in kin has also been  
61 demonstrated in many primate species. Both maternal and paternal kin preferentially  
62 associate with multiple species, including female rhesus macaques (Widdig et al., 2001),  
63 female baboons (Archie et al., 2014), female white-faced capuchins (Perry et al., 2008), male  
64 chimpanzees (Mitani et al., 2000), and male Assamese macaques (De Moor et al., 2020).  
65 Additionally, the identification of genetic fathers shows that males of even polygynandrous  
66 species can exhibit prolonged paternal investment (Städele et al., 2016; Buchan et al., 2003).  
67 For instance, baboon males maintain social bonds with the mothers of their previous  
68 offspring and intervene in agonistic interactions in favor of their juvenile offspring (Städele  
69 et al., 2021; Nguyen et al., 2009; Buchan et al., 2003). Together, these findings underscore  
70 the fundamental importance of identifying kin for studies of primate behavior and genetic  
71 structure.

72           While in some cases, kin relationships can be identified or reliably inferred through  
73   observational data alone, in most cases, at least some kin ties must be confirmed through  
74   genetic analysis (Städele & Vigilant, 2016). Studies in unhabituated animals, for instance,  
75   preclude observation of even close maternal kin (Masi et al., 2021). Additionally, even in  
76   highly habituated social groups, fertile females may mate with multiple partners in a  
77   conceptive cycle, leading to uncertainty about paternity and relationships among paternal  
78   kin (Rosenbaum & Silk, 2022; Platak & Shackelford, 2006). Consequently, many primate field  
79   studies infer relatedness by first using genetic data to reconstruct pedigrees that represent  
80   lineal descent, and then identify kin relationships based on the completed pedigree (as  
81   inferring non-parent-offspring kin classes directly from genotype data is typically quite  
82   noisy: (Van Horn et al., 2008)). Paternity (and/or maternity) inference is the crucial first step  
83   in this process.

84           Though methods for pedigree reconstruction and paternity inference in natural  
85   populations are well developed (Rentof et al., 2024; Petty et al., 2021; Sard et al., 2021),  
86   their application involves understanding several complex concepts. Students interested in  
87   pedigree inference in molecular primatology must, for instance, understand how alleles are  
88   transmitted through Mendelian inheritance. They also must understand how the accuracy of  
89   paternity assignment depends on both the quantity of genetic data available and the  
90   information content per genotyped locus, which in turn depends on genetic diversity in the  
91   species or population of interest. Additionally, students should understand how this  
92   information is used to then infer pedigree links. Doing so draws on concepts in both genetics  
93   and statistics, a combination that students can find challenging as they may not be covered

94 together in one course or in relation to practical application in primatology (Fawcett &  
95 Higginson, 2012). Consequently, interested researchers or students may have only an  
96 abstract understanding of pedigree reconstruction using genetic data.

97       Such problems are not uncommon in ecology and evolutionary biology (Shou et al.,  
98 2015; Marquet et al., 2014). However, recent studies suggest that incorporating interactive  
99 learning tools can help students independently explore modelling and inference problems in  
100 biology and can help enhance student interest and confidence (Andrews et al., 2017; Haak  
101 et al., 2011; Nelson, 2008). For example, computer simulations can help improve student  
102 understanding of the mathematical underpinnings of population genetics (Hoban et al.,  
103 2012). Classroom exercises where students use simulated populations have also proven to  
104 be beneficial (Speth et al., 2010; Soderberg & Price, 2003; Winterer, 2001). In one study, for  
105 instance, active learning with population-level Punnett squares was shown to increase  
106 understanding and calculation proficiency in high-anxiety students, particularly for  
107 understanding Hardy-Weinberg equilibrium (Williams et al., 2021). Incorporation of games,  
108 clicker questions, and peer discussion or instruction can also help engage students more  
109 deeply in their learning materials (Subhash & Cudney, 2018; Smith & Wood, 2016; Kober,  
110 2015; Vickrey et al., 2015). The common thread in these approaches is that they encourage  
111 students to become active participants rather than passive observers (Bernardo, 2017;  
112 Hague, 2011), allowing them to better understand and retain complex concepts in ecology  
113 and evolutionary biology.

114           One efficient and accessible method for developing active learning tools relies on the  
115 Shiny package (Kasprzak et al., 2021; Wang et al., 2021; Fawcett, 2018; Doi et al., 2016), an  
116 approach for web-based app development that builds on the popular R statistical  
117 programming language (Chang et al., 2015). R-based Shiny apps have become popular as  
118 teaching and data visualization tools in life sciences: as of 2022, more than 470 biological  
119 web applications have been developed and made accessible through online platforms such  
120 as shinyapps.io, CRAN, Github, or institutional websites and custom domains (Jia et al.,  
121 2022; Kasprzak et al., 2021). Their efficacy for instruction has been assessed in several ways.  
122 For example, González et al (2018) conducted a qualitative study where they evaluated the  
123 efficacy of Shiny apps based on student feedback. They concluded that students perceived  
124 Shiny apps as a useful educational tool for understanding probability, statistical inference,  
125 hypothesis testing, and modelling. Neyhard and Watkins (2020) also reported increased  
126 interest in and confidence with concepts in statistical genetics after interaction with Shiny  
127 simulations. Moore et al (2022) observed increased familiarity with ecological forecasting in  
128 undergraduate students after interacting with an interactive online module, built with R  
129 Shiny, which served as a visualization tool. These studies indicate that Shiny apps can  
130 provide useful practical experience for learning concepts in genetics, statistics, ecology, and  
131 evolution.

132           Shiny apps are accessible with minimal technological infrastructure: access to a  
133 computer, or, in some cases, a mobile device (Kasprzak et al., 2021). They also provide  
134 approaches for student interaction and inquiry that do not require wet lab facilities or  
135 reagents. These properties make them a particularly interesting avenue to consider in



136 resource-limited settings, such as learning environments in developing nations. However, to  
137 date, studies that investigate the utility or efficacy of Shiny apps for life sciences education  
138 have focused on university settings in wealthy developed nations (e.g., Jia et al., 2022;  
139 Fawcett, 2018; Doi et al., 2016). Their potential as active learning tools for more diverse  
140 audiences, particularly in settings with more limited pedagogical and/or technological  
141 resources, has not been well-assessed.

142         To address this gap, we conducted a pilot study to test whether interaction with a  
143 Shiny web app, as a complement to a traditional lecture-based approach, improved student  
144 conceptual understanding of pedigree reconstruction in molecular primatology. Participants  
145 in the study were students and researchers with an interest in primate studies, but no  
146 specific background in genetic analysis or genetic paternity inference. First, we describe  
147 development of the app itself, *DadApp*, which implements the basic analytical algorithm in  
148 the program *CERVUS*, a standard tool for paternity inference in molecular ecology  
149 (Kalinowski et al., 2007; Slate et al., 2000; Marshall et al., 1998). *DadApp* allows users to  
150 provide biallelic genotype data and to calculate the relative log-odds (LOD scores) that a  
151 candidate individual is the parent of a given offspring of interest, given a set of possible  
152 candidates (Mwaura et al., 2023). We confirmed that *DadApp* correctly assigns paternity  
153 using data from a wild baboon population in the Amboseli region of Kenya (Alberts &  
154 Altmann, 2012). Second, we used a pre-test/post-test approach to assess the effectiveness  
155 of *DadApp* as an active learning tool outside of a university setting. Here, we gauged both its  
156 ability to increase student interest and engagement and its effect on improving conceptual  
157 understanding.

158

## 159 **Materials and Methods**

### 160 *Application Development*

161 We developed *DadApp* in R, one of the most common programming languages for  
162 biological data analysis and visualization (<https://www.R-project.org/>) (R Core Team, 2018),  
163 using the *shiny* package (Chang et al., 2017). *DadApp* is made up of two functional parts:  
164 ui.R, which specifies the user interface, and server.R, which specifies the calculations made  
165 on user-provided data and the resulting graphical representation of the results (Mwaura et  
166 al., 2023). To run, *DadApp* requires R version 3.4.0 or higher on a Microsoft Windows, Apple  
167 macOS, or Linux operating system, and can be run for data sets of up to 100 individuals and  
168 200 loci using <1 Mb of storage space and <100 Mb of RAM. Upon execution, the application  
169 is launched in the user's default web browser (e.g., Chrome, Firefox, Internet Explorer, or  
170 Safari), without requiring an internet connection.

171 *DadApp* operates under the simplifying assumption that the input data are biallelic  
172 genotypes, as in typical single nucleotide polymorphism data sets. Following convention, it  
173 represents homozygous reference genotypes as 0, heterozygous genotypes as 1, and  
174 homozygous alternate genotypes as 2. Following the approach described by Marshall et al.,  
175 (1998), *DadApp* uses these data to determine locus-specific allele frequencies and then uses  
176 the rules of Mendelian inheritance to calculate the likelihood that a candidate parent is the  
177 true parent of a given focal offspring (i.e., the probability of the observed genotype data,  
178 under the hypothesis that the candidate is a true parent), relative to the likelihood that a

179 random individual from the population is the true parent (i.e., the probability of the  
180 observed genotype data, given a model/hypothesis where the parent's genotype is drawn  
181 randomly from the study population) (Kalinowski et al., 2010, 2007). This "background"  
182 likelihood is based on the allele frequencies in the population as a whole, which are  
183 calculated from the genotype data provided for the full, user-supplied data set. Values for  
184 each locus are combined across loci, under the assumption that each typed locus provides  
185 independent information (i.e., is unlinked).

186 If genotype data from a known parent are available, this information can also be  
187 provided to improve the accuracy of inference. Users can therefore provide these data by  
188 using the upload widget of the app. In primate studies, if one parent is known, it is typically  
189 the mother (Buchan et al., 2003). Therefore, in the scenarios we discuss below and *DadApp*  
190 itself, we refer to genotype data from the known parent as data from the mother, and treat  
191 the father as the unknown parent. However, the logic of the approach is identical if this  
192 scenario were reversed.

193 By rotating through the set of candidate fathers, each potential father is assigned a  
194 log-transformed likelihood ratio (LOD score). A positive LOD score indicates that the  
195 candidate's genotype is more compatible with the genotype of the real father than a  
196 random genotype drawn from the population, while a negative LOD score indicates that the  
197 candidate's genotype is less compatible with the genotype of the real father than a random  
198 genotype drawn from the population. The male with the highest LOD score is the  
199 algorithm's top candidate. *CERVUS* provides an approach for assessing the confidence of top

200 assignments (Slate et al., 2000; Marshall et al., 1998), but for simplicity here (and because  
201 the test data set used for the pedagogical analysis always included the true father), *DadApp*  
202 assigns paternity to the male with the highest LOD score. Following the approach in *CERVUS*,  
203 we also account for potential genotyping error by reassigning locus-specific likelihood values  
204 of 0, which can occur if a candidate father's genotype is incompatible with the offspring's  
205 genotype (Slate et al., 2000) (e.g., the father is CC but the offspring is TT), to a default value  
206 of 0.01. This approach avoids completely excluding candidate fathers based on a possible  
207 genotyping error, although incompatible values still considerably penalize the LOD score.  
208 This value can be changed by the user.

209

210 *Confirming accurate paternity assignments with pedigree and genetic data from wild*

211 *baboons*

212 To confirm that *DadApp* can make correct paternity assignments using genotypes  
213 and pedigree structures found in real populations, we drew on a subset of the data from  
214 Vilgalys et al., (2022), who analyzed whole genome resequencing data collected from a wild  
215 population of baboons in southern Kenya. This study population has been under continuous  
216 observation since 1971 (Alberts & Altmann, 2012), during which genetically assigned  
217 paternity has contributed to key insights about paternal care, reproductive skew, and  
218 inbreeding avoidance (Galezo et al., 2022; Alberts et al., 2006; Buchan et al., 2003). For the  
219 purposes of validating *DadApp* assignments, we subsampled local ancestry calls from 99  
220 unlinked loci (this population is composed of hybrids between the yellow baboon, *Papio*

221 *cynocephalus*, and the anubis baboon, *P. anubis*) and converted them to biallelic genotypes  
222 for all members of ten known pedigree trios (father, mother, and offspring). We then tested  
223 whether analyzing these data in *DadApp* resolved the correct father in each trio, within the  
224 full candidate set of all other males in the sample.

225

#### 226 *Assessment of DadApp as an educational tool*

227 Our primary goal was to assess whether an active learning component, here  
228 implemented using the *DadApp* interactive Shiny tool, improved student understanding of  
229 Mendelian inheritance, genetic data analysis, and paternity inference in the context of  
230 molecular primatology. To do so, we conducted a pre-test/post-test comparison of students  
231 and research staff at the Kenya Institute of Primate Research (KIPRE) in Nairobi, Kenya.  
232 KIPRE's mission is to study nonhuman primates as models for human health and behavior.  
233 Most of KIPRE's researchers do not primarily focus on genetics. Hence, participants in this  
234 study had a background in biology, but with limited formal training in genetics. Participants  
235 were recruited voluntarily into the study through direct outreach and referrals.

236 Participants (n=28) were given a one-hour introductory lecture on Mendelian  
237 inheritance, kinship, and genetic paternity. They then took an individual pre-test to assess  
238 their comprehension of these concepts (Supplementary Materials 1). After the pre-test,  
239 participants were asked to interact with *DadApp* to upload data, run analyses, and visualize  
240 results following a guided set of questions to explore alternative scenarios (e.g., data sets  
241 with or without maternal genotype data; data sets of differing size). The interaction phase

242 took place in groups of 3-6 participants, 1-2 days after the lecture and pre-test.  
243 Subsequently, participants answered the pre-test questions again in a post-test phase.  
244 Notably, unlike in the pre-test phase, in the post-test phase they were able to engage in  
245 discussion with other group members. Finally, participants completed a post-test  
246 engagement survey in which they provided feedback on their understanding of key concepts  
247 before and after the active learning component (Supplementary Material 2). The survey  
248 included 5-level Likert-scale questions to quantify both perceived level of understanding  
249 (e.g. 1 -Not Confident, 2 -Somewhat Confident, 3 -Don't Know, 4 -Confident, 5 -Extremely  
250 Confident) and interest/enthusiasm in the topic (e.g. 1 -Very Disinterested, 2 -Disinterested,  
251 3 -Neutral/No opinion, 4 -Interested, 5 -Very Interested).

252 To assess the change in pre-test to post-test scores, we used paired Wilcoxon signed-  
253 ranks test to evaluate within-individual changes in performance following the active learning  
254 component. To evaluate whether this effect differed depending on characteristics of the  
255 student, we also used linear regression models to ask whether educational background, self-  
256 reported confidence, or self-reported interest predicted the percent change in pre-test to  
257 post-test score. In this study, we categorized educational background into three levels:  
258 undergraduates (current undergraduate students or students who had completed their  
259 undergraduate studies but no post-graduate education), MSc-level students (students  
260 currently enrolled in a Master's program or students who had completed an MSc but no  
261 further education) and PhD-level students (students currently enrolled in a PhD program or  
262 who had completed a PhD). Finally, to assess whether the active learning component

263 increased student interest in the topic, we analysed the feedback received from participants  
264 through their survey responses (Supplementary Material 3).

265 Ethical clearance for this work was granted through the Kenyatta National Hospital-  
266 University of Nairobi Ethics and Research Committee protocol no. P689/09/2023.

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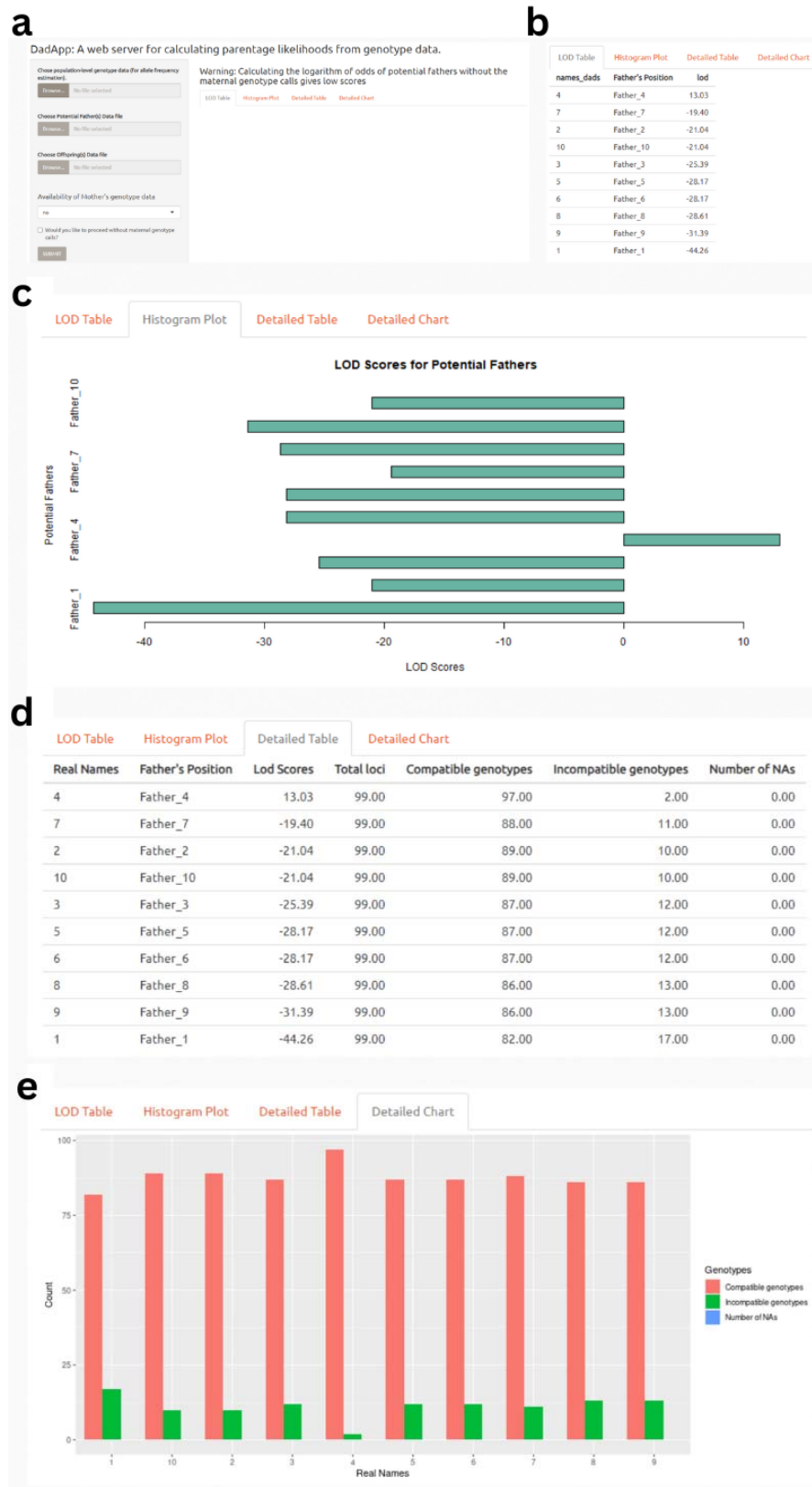
## 268 **Results**

269 *Implementation of DadApp: an R Shiny package for exploring paternity inference and*  
270 *pedigree analysis*

271 *DadApp* is freely available through Posit's shinyapps.io platform at <https://kiragu->  
272 [mwaura.shinyapps.io/dadapp/](https://kiragu-mwaura.shinyapps.io/dadapp/), with additional annotated source code and instructions for  
273 installation and execution at <https://github.com/KIRAGU->  
274 [MWAURA/DadApp\\_Shiny\\_Web\\_App](https://github.com/KIRAGU-MWAURA/DadApp_Shiny_Web_App).

275 Examples of its user interface and outputs are shown in Figure 1, and example  
276 genotype data are available at <https://github.com/KIRAGU->  
277 [MWAURA/DadApp\\_Shiny\\_Web\\_App](https://github.com/KIRAGU-MWAURA/DadApp_Shiny_Web_App) and the Supplementary Materials 4.

278





280 **Figure 1: The *DadApp* user interface.** a) The *DadApp* default user interface upon start up; b)  
281 Tabular representation of the app output, showing candidate fathers and their associated  
282 LOD scores; c) Barplot representation of candidate father LOD scores d) Detailed tabular  
283 representation of LOD scores for candidate fathers, including the total number of loci used  
284 to calculate the LOD score, number of compatible genotypes, number of incompatible  
285 genotypes, and number of loci with missing data; e) A barplot output showing the number  
286 of compatible genotypes, incompatible genotypes, and loci with missing data (denoted as  
287 NA) for each candidate father.

288

289 *DadApp correctly assigns paternity in trio data from wild baboons*

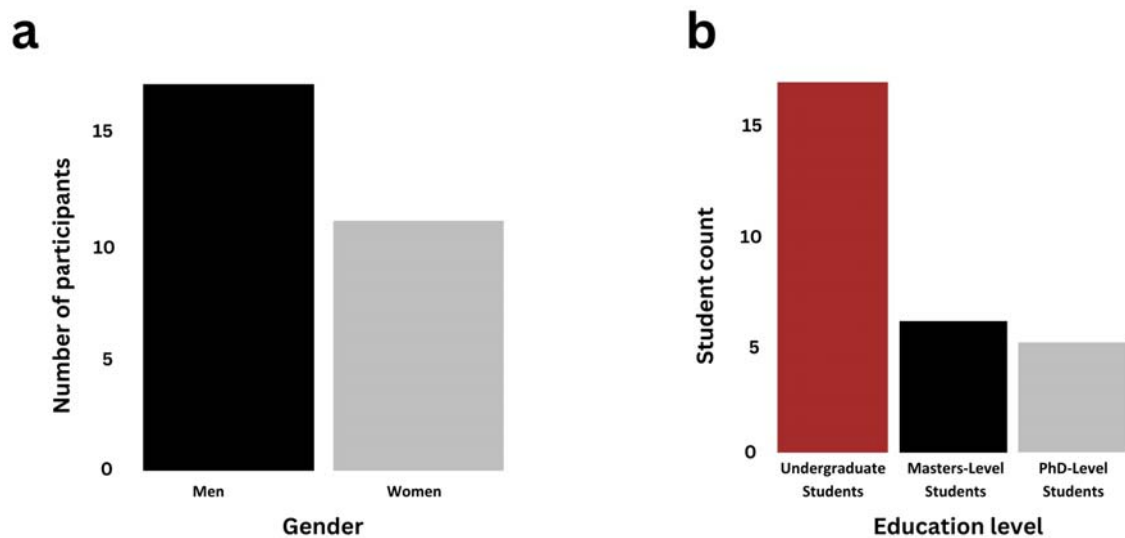
290 We tested *DadApp* on genotype data from 99 biallelic loci, for 30 individuals (10  
291 trios). In all cases, the highest LOD score candidate matched the independently assigned  
292 father in the Amboseli Baboon Research Project pedigree, where paternity assignment was  
293 based on genotyping data from 6 – 14 microsatellite loci (Alberts et al., 2006; Buchan et al.,  
294 2003). This result confirms that *DadApp* correctly implements the *CERVUS* algorithm in  
295 Shiny. It may therefore also be useful for basic paternity assignment in real data, provided  
296 the data types are compatible with *DadApp*'s capabilities.

297

298 *The utility of DadApp as an active learning tool*

299 We recruited 28 volunteer participants into our study. Demographic data on self-reported  
300 gender, and educational level are shown in Figure 2.

301



302

303 **Figure 2: Participant information.** Bar plot showing the distribution of participants by a)

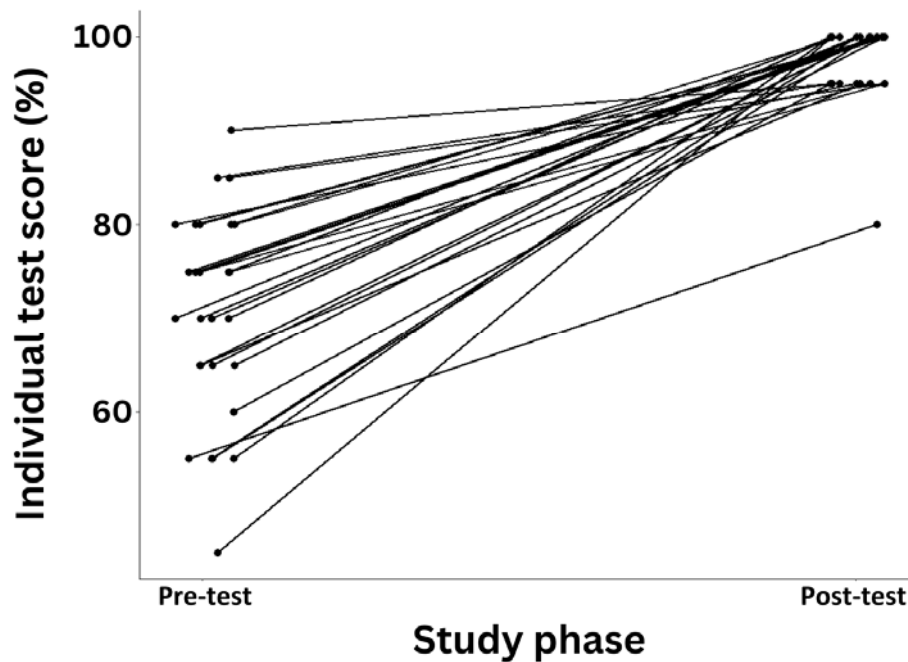
304 Self-identified gender and b) Self-reported education level.

305

306 The participants underwent tests before and after their interaction with the *DadApp*  
307 to evaluate their understanding of Mendelian inheritance, kinship, and genetic paternity  
308 inference. The mean score of participants across all subjects, out of a maximum of 100%,  
309 was 70.54% in the pre-test stage (standard deviation= 10.92, range= 45% - 90%) and 97.86%  
310 in the post-test stage (standard deviation= 4.18, range= 80% - 100%). We observed a  
311 statistically significant within-individual increase from the pre-test to post-test scores  
312 (paired Wilcoxon Signed-Rank test  $p = 3.75 \times 10^{-6}$ ; Figure 3). Educational level did not affect

313 test performance in either the pre-test (ANOVA:  $df = 2$ ,  $F\text{-value} = 2.037$ ,  $p\text{-value} = 0.152$ ) or  
314 post-test stages ( $df = 2$ ,  $F\text{-value} = 0.584$ ,  $p\text{-value} = 0.565$ ). Self-reported confidence after the  
315 introductory lecture and self-reported interest at the beginning of the study did not  
316 significantly predict the percent change in the test score (linear regression:  $p\text{-value} = 0.652$   
317 and  $p\text{-value} = 0.9152$ , respectively).

318



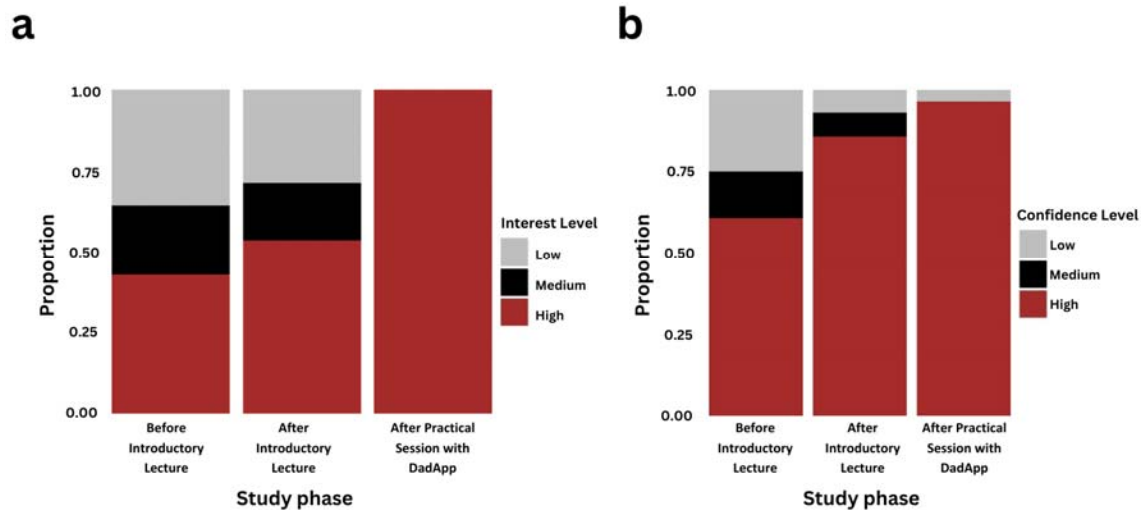
319

320 **Figure 3. Within-individual comparison of pre-test and post-test scores after interacting**  
321 **with *DadApp*.** Lines connect the scores for the same individual between pre-test and post-  
322 test stages. The grouping of post-test scores may reflect discussion among individuals taking  
323 the post-test at the same time. Overall, post-test scores improved over pre-test scores

324 (n=28, paired Wilcoxon Signed-Rank test  $p = 3.75 \times 10^{-6}$ ). Points are jittered within pre-test  
325 and post-test values to avoid overplotting.

326

327 Finally, the participants completed a post-engagement retrospective survey to  
328 provide feedback on their experience. Participants' ratings for most survey questions  
329 covered the entire 5-point scale. We observed no statistically significant difference in self-  
330 described interest based on the introductory lecture (mean rating provided retrospectively  
331 for interest before the lecture =  $3.046 \pm 1.48$  s.d. versus interest after the lecture =  $3.038 \pm$   
332  $1.40$  s.d.;  $p$ -value=0.6114; paired t-test). Conversely, we observed a highly significant  
333 difference ( $p$ -value =  $9.485 \times 10^{-5}$ ; paired t-test) in self-described interest when comparing  
334 the post-introductory lecture responses to responses after the practical session with  
335 *DadApp* (mean =  $4.746 \pm 0.489$  s.d.; Figure 4a). Similarly, we observed a statistically  
336 significant increase in participant confidence between the post-introductory lecture stage  
337 (mean= $4.038 \pm 0.958$  s.d.) and after the practical session with *DadApp* (mean =  $4.769 \pm$   
338  $0.815$  s.d.; paired t-test  $p = 8.103 \times 10^{-4}$ ) (Figure 4b).



339  
340

341 **Figure 4: Participant interest and confidence throughout the study.** Bar plot showing a)  
342 Change in participant interest levels across stages of the study. b) Change in participant  
343 confidence levels across stages of the study

344

## 345 Discussion

346 This study provides a first investigation of how Shiny apps can affect student learning  
347 and engagement in molecular primatology in a non-traditional classroom setting in the  
348 developing world. Our results show that Shiny apps can be effectively deployed in this  
349 context, where resources to support other forms of active learning (e.g., field courses, wet-  
350 lab practical) may be limited and non-traditional pedagogical approaches are not yet in wide  
351 use. And while we conducted this study at a suburban research institute, it is  
352 straightforward to envision using this or similar approaches even in field settings, where  
353 much of primate research is conducted in practice.

354 Exposure to *DadApp* as an instructional tool improved post-test performance  
355 compared to pre-test performance across educational levels. This result is consistent with  
356 work by Moore et al. (2020), who reported increased comprehension and interest in  
357 ecological modelling and forecasting for both undergraduate and graduate students when  
358 deploying an R Shiny application-based module. The use of technological enhancements and  
359 a collaborative learning environment has been repeatedly shown to improve student  
360 performance (Qureshi et al., 2023; Herrera-Pavo, 2021). Here, we generalize this finding, for  
361 the first time, to concepts in molecular primatology in a primate range country.

362 One of the most interesting results from our pilot is that, beyond test performance,  
363 student confidence and interest in kinship analysis and paternity inference increased  
364 significantly after interacting with *DadApp*. This finding also aligns with previous studies that  
365 reported enhanced engagement and student experience following exposure to interactive  
366 and application-based learning tools. For example, Neyhart & Watkins (2020) showed an  
367 encouraging increase in interest in statistical genetics after post-engagement with the  
368 *qshiny* Shiny app, which is designed to teach basic theory in quantitative and population  
369 genetics. Additionally, participant self-described confidence significantly improved after an  
370 active learning component in Moore et al. (2020), the R Shiny app-based ecological  
371 forecasting study. Overall, the literature suggests that interactive elements in educational  
372 software can foster deeper engagement and motivation among students (Clark & Mayer,  
373 2016). Beyond comprehension, user experience and engagement are often linked to the  
374 interactivity, user-friendliness of the design, and relevance of the learning tool to real-world  
375 applications (González et al., 2018; Zhang, 2005).

376           Finally, while promising, we note some important limitations to the current study.  
377   The most significant limitation is that participants were allowed to take the post-test in  
378   small groups of 3-6, which likely inflated and reduced variance in the post-test scores and,  
379   consequently, the estimated effect of the app. Group dynamics, such as peer pressure, can  
380   lead participants to defer to the most confident or knowledgeable member of the group.  
381   Such dynamics can affect the accuracy and reliability of the post-test results as a direct  
382   assessment of the educational tool itself, as they can conflate individual-level with group-  
383   level comprehension. In retrospect, a more direct study design would have been to conduct  
384   the post-test in the same setting as the pre-test. An interesting possibility raised by our  
385   findings, though, is that peer discussion and interaction can amplify the effects of other  
386   active learning tools, as suggested by Freeman et al (2014). This possibility could be directly  
387   assessed in future work. A second limitation is that all assessments in this study were short-  
388   term. Consequently, we do not know how our deployment of *DadApp* affects long-term  
389   retention of the subject matter or participant interest. Finally, a potential downside of using  
390   educational apps is the significant amount of instructional effort and preparation required,  
391   including the time and resources needed for app design (Hanč et al., 2020; Doi et al., 2016).  
392   These costs can make active learning approaches more demanding than delivering a  
393   traditional lecture. However, it is worth noting that many developers are actively creating  
394   interactive biological web apps (Jia et al., 2022) and lesson plans, which may alleviate the  
395   burden on educators by reducing the need for new, extensive class preparation or  
396   development.

397

398 **Conclusions**

399           Parentage analysis and pedigree reconstruction have become essential methods in  
400 molecular primatology. However, the concepts required to understand these methods can  
401 be difficult to teach. Our study suggests that incorporating active learning tools can help  
402 improve student understanding and, perhaps more importantly, student confidence and  
403 interest, even in non-traditional classroom settings in a developing nation context. Further,  
404 it shows that development of such tools using the Shiny platform is a feasible goal, and  
405 potentially another avenue for developing and learning skillsets important in modern  
406 primatology. Future studies should continue to evaluate the efficacy of these and other  
407 active learning approaches in diverse settings, with a diverse set of participants.

408

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415

416 **Conflict of Interest**

417           The authors declare no conflict of interest.



418

419 **Data Availability Statement**

420 The data required to reproduce the analyses in this manuscript are provided as part of the  
421 Supplementary Materials.

422

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