

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

3 **David K. Mwaura^{1,2}, Jordan A. Anderson³, Daniel M. Kiboi¹, Mercy Y. Akinyi², Jenny**
4 **Tung^{3,4*}**

5 ¹Department of Biochemistry, Jomo Kenyatta University of Agriculture and Technology,
6 Nairobi, Kenya

7 ²Department of Animal Sciences, Kenya Institute of Primate Research, Nairobi, Kenya

8 ³Department of Evolutionary Anthropology, Duke University, Durham, NC, USA

9 ⁴Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary
10 Anthropology, Leipzig, Germany

11

12 Running title: Teaching paternity inference with Shiny

13

14 *Correspondence to: Jenny Tung, Department of Primate Behavior and Evolution, Max
15 Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.

16 E-mail: jtung@eva.mpg.de

17 Phone: +49 341 3550 ext. 200

18

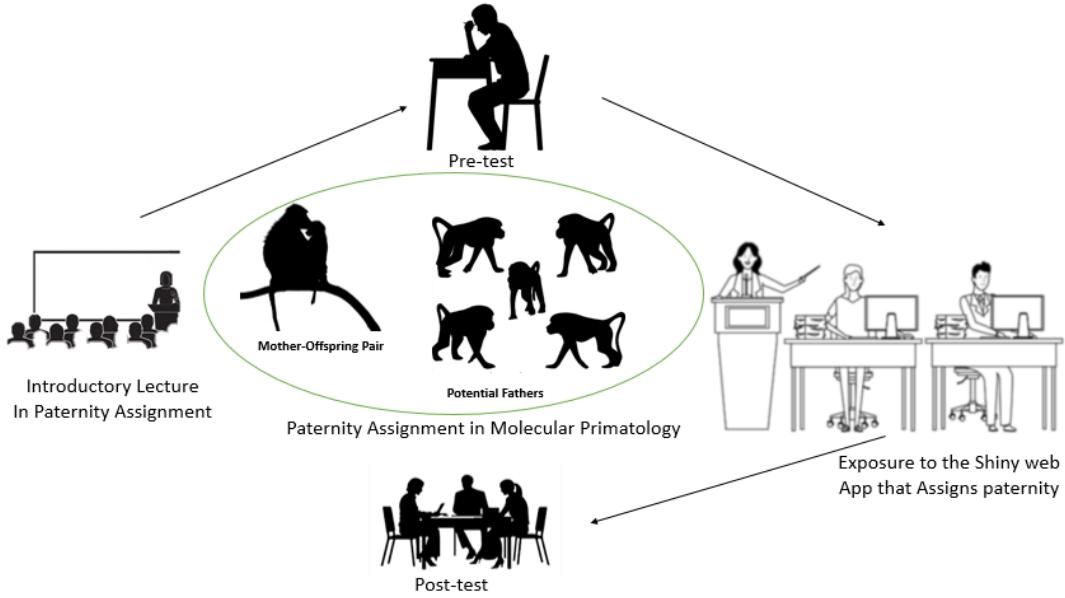
19

20

21

22 **Graphical Abstract**

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



24

25

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 ($p\text{-value}=3.75 \times 10^{-6}$). 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 conception cycle, leading to uncertainty about paternity and relationships among paternal
78 kin (Rosenbaum & Silk, 2022; Platek & 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.

267

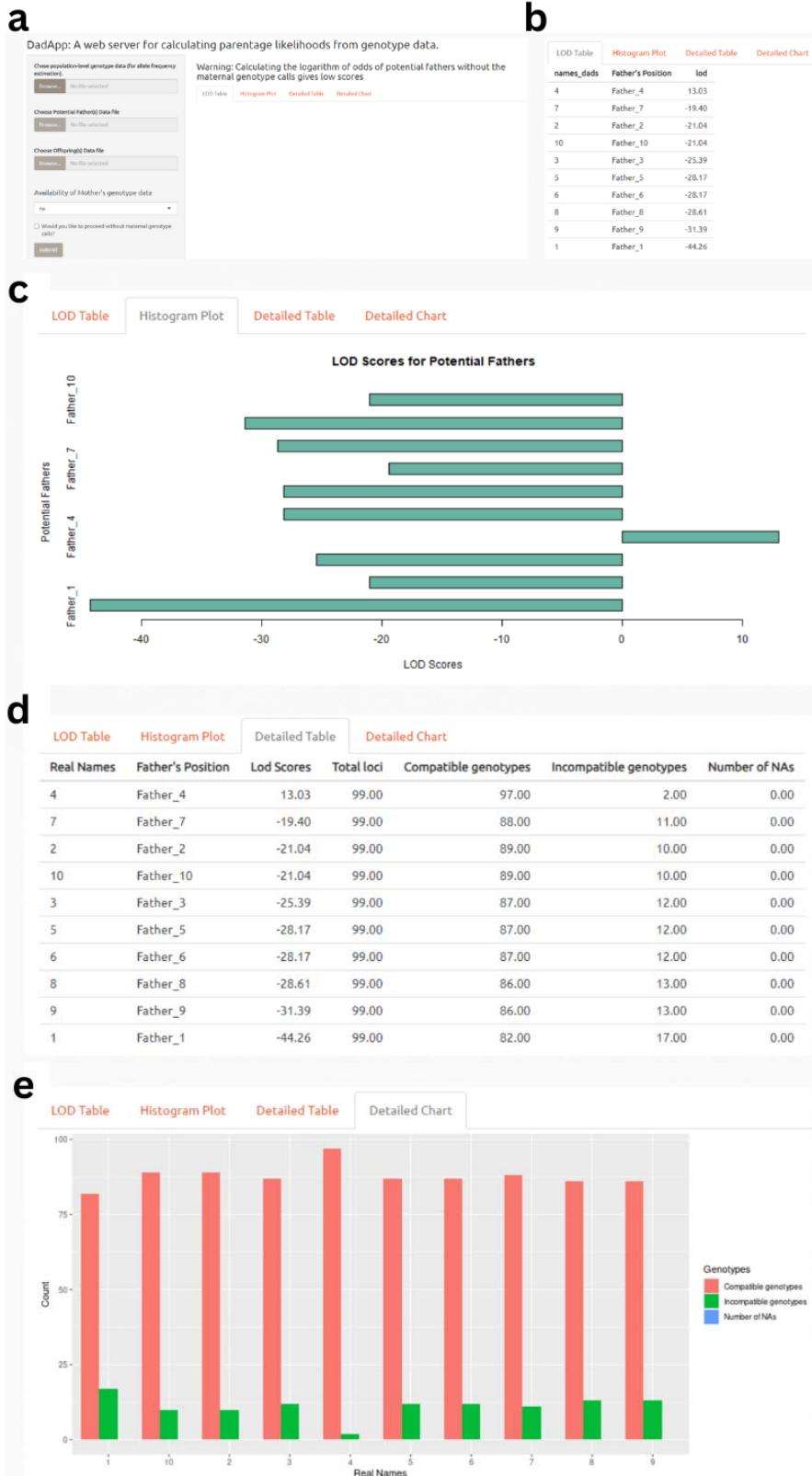
268 **Results**

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-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*

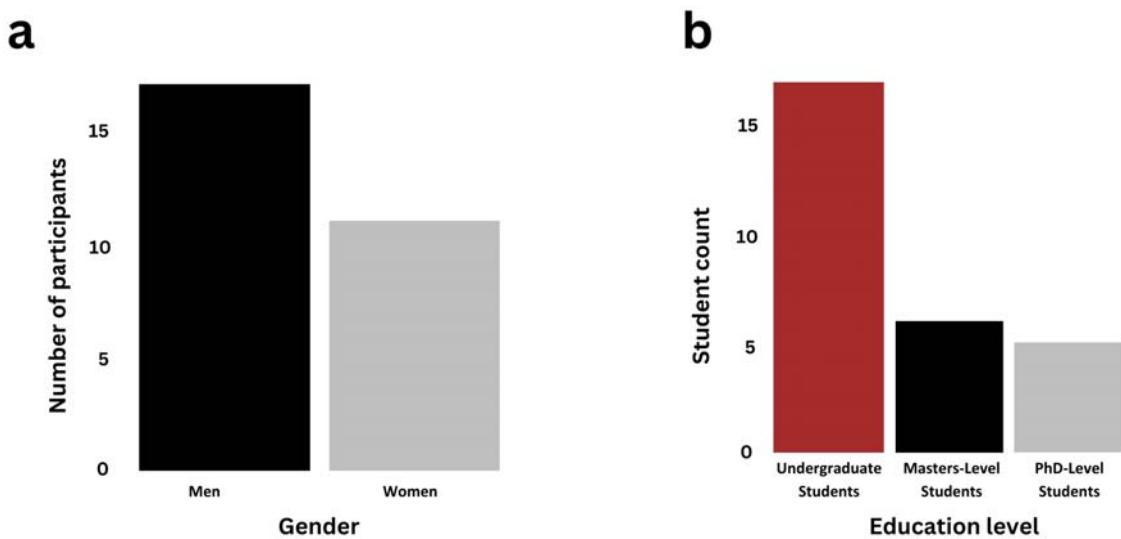
290 We tested *DadApp* on genotype data from 99 biallelic loci, for 30 individuals (10
291 trios). In all cases, the highest LOD score candidate matched the independently assigned
292 father in the Amboseli Baboon Research Project pedigree, where paternity assignment was
293 based on genotyping data 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



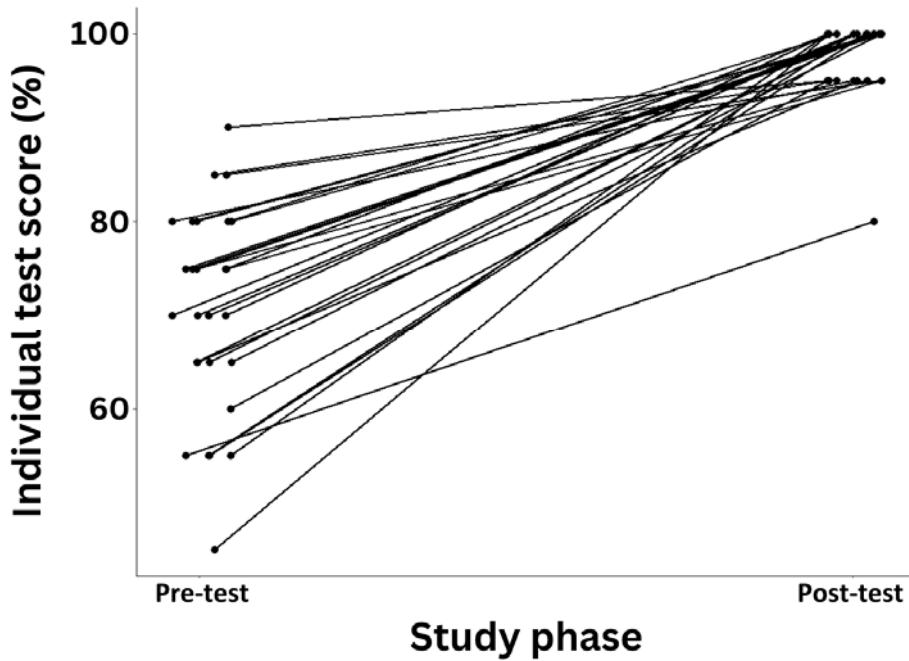
302 **Figure 2: Participant information.** Bar plot showing the distribution of participants by a)
303 Self-identified gender and b) Self-reported education level.

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 -value = 2.037, p -value = 0.152) or
314 post-test stages ($df = 2$, F -value = 0.584, p -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 -value = 0.652
317 and p -value = 0.9152, respectively).

318



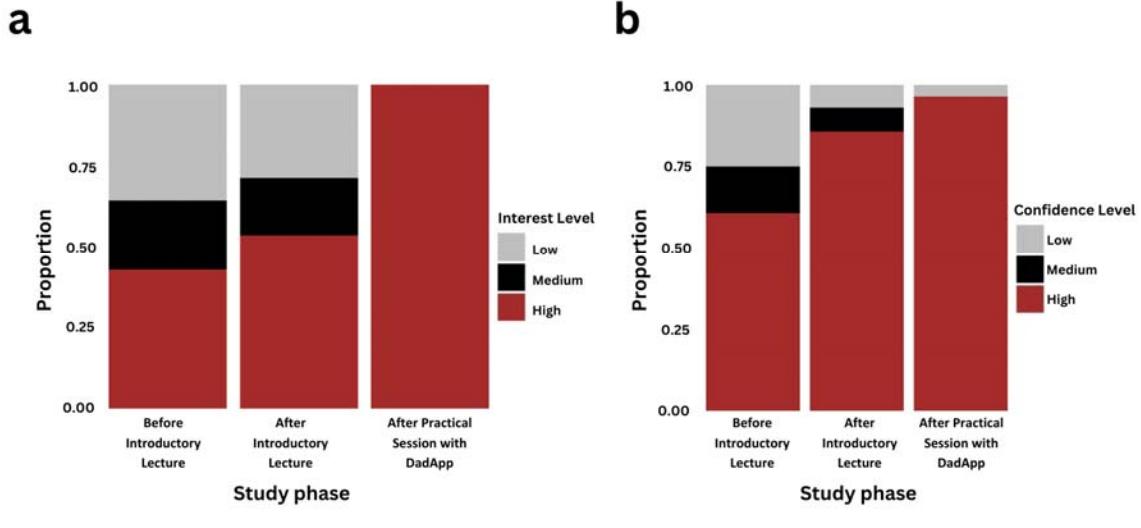
319

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 ± 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 = 9.485×10^{-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 ± 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 ± 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

409 **Acknowledgments**

410 We thank the Amboseli Baboon Research Project (ABRP) for financial support of the
411 project. We also thank Arielle Fogel for providing local ancestry/genotype data for the
412 Amboseli baboons to validate the Shiny App and all study subjects for their willingness to
413 participate. The research in this study was approved by the Kenyatta National Hospital-
414 University of Nairobi Ethics and Research Committee protocol no. P689/09/2023.

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

423 **References**

424 Alberts, S. C., & Altmann, J. (2012). The Amboseli Baboon Research Project: 40 Years of
425 Continuity and Change. In P. M. Kappeler & D. P. Watts (Eds.), *Long-Term Field*
426 *Studies of Primates* (pp. 261–287). Springer Berlin Heidelberg.

427 https://doi.org/10.1007/978-3-642-22514-7_12

428 Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From
429 mating opportunities to paternity success. *Animal Behaviour*, 72(5), 1177–1196.
430 <https://doi.org/10.1016/j.anbehav.2006.05.001>

431 Andrews, S. E., Runyon, C., & Aikens, M. L. (2017). The Math–Biology Values Instrument:
432 Development of a Tool to Measure Life Science Majors’ Task Values of Using Math in
433 the Context of Biology. *CBE—Life Sciences Education*, 16(3), ar45.
434 <https://doi.org/10.1187/cbe.17-03-0043>

435 Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters:
436 Both same-sex and opposite-sex relationships predict survival in wild female

437 baboons. *Proceedings of the Royal Society B: Biological Sciences*, 281(1793),

438 20141261. <https://doi.org/10.1098/rspb.2014.1261>

439 Bernardo, R. (2017). *BreedingGames* Software. *Crop Science*, 57(5), 2313–2313.
440 <https://doi.org/10.2135/cropsci2017.07.0419le>

441 Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-
442 male primate society. *Nature*, 425(6954), 179–181.
443 <https://doi.org/10.1038/nature01866>

444 Chang, W., Cheng, J., Allaire, J., Xie, Y., & McPherson, J. (2015, February 11). Package ‘shiny’.
445 CRAN. <http://shiny.rstudio.com>

446 Chapais, B. (2001). Primate Nepotism: What is the Explanatory Value of Kin Selection?
447 *International Journal of Primatology*, 22(2), 203–229.
448 <https://doi.org/10.1023/A:1005619430744>

449 Chapais, B., & Berman, C. M. (Eds.). (2004). *Kinship and behavior in primates*. Oxford
450 University Press.

451 Clark, R. C., & Mayer, R. E. (Eds.). (2016). *e-Learning and the Science of Instruction: Proven
452 Guidelines for Consumers and Designers of Multimedia Learning* (1st ed.). Wiley.
453 <https://doi.org/10.1002/9781119239086>

454 Dal Pesco, F., Trede, F., Zinner, D., & Fischer, J. (2021). Kin bias and male pair-bond status
455 shape male-male relationships in a multilevel primate society. *Behavioral Ecology
456 and Sociobiology*, 75(1), 24. <https://doi.org/10.1007/s00265-020-02960-8>

457 De Moor, D., Roos, C., Ostner, J., & Schülke, O. (2020). Bonds of bros and brothers: Kinship
458 and social bonding in postdispersal male macaques. *Molecular Ecology*, 29(17),
459 3346–3360. <https://doi.org/10.1111/mec.15560>

460 Doi, J., Potter, G., Wong, J., Alcaraz, I., & Chi, P. (2016). Web Application Teaching Tools for
461 Statistics Using R and Shiny. *Technology Innovations in Statistics Education*, 9(1).
462 <https://doi.org/10.5070/T591027492>

463 Fawcett, L. (2018). Using Interactive Shiny Applications to Facilitate Research-Informed
464 Learning and Teaching. *Journal of Statistics Education*, 26(1), 2–16.
465 <https://doi.org/10.1080/10691898.2018.1436999>

466 Fawcett, T. W., & Higginson, A. D. (2012). Heavy use of equations impedes communication
467 among biologists. *Proceedings of the National Academy of Sciences*, 109(29), 11735–
468 11739. <https://doi.org/10.1073/pnas.1205259109>

469 Freeman, S., Eddy, S. L., McDonough, M., Smith, M. K., Okoroafor, N., Jordt, H., &
470 Wenderoth, M. P. (2014). Active learning increases student performance in science,
471 engineering, and mathematics. *Proceedings of the National Academy of Sciences*,
472 111(23), 8410–8415. <https://doi.org/10.1073/pnas.1319030111>

473 Galezo, A. A., Nolas, M. A., Fogel, A. S., Mututua, R. S., Warutere, J. K., Siodi, I. L., Altmann,
474 J., Archie, E. A., Tung, J., & Alberts, S. C. (2022). Mechanisms of inbreeding avoidance
475 in a wild primate. *Current Biology*, 32(7), 1607-1615.e4.
476 <https://doi.org/10.1016/j.cub.2022.01.082>

477 González, J. A., López, M., Cobo, E., & Cortés, J. (2018). Assessing Shiny apps through
478 student feedback: Recommendations from a qualitative study. *Computer*

479 *Applications in Engineering Education*, 26(5), 1813–1824.

480 <https://doi.org/10.1002/cae.21932>

481 Guo, S., Huang, K., Ji, W., Garber, P. A., & Li, B. (2015). The role of kinship in the formation of
482 a primate multilevel society. *American Journal of Physical Anthropology*, 156(4),
483 606–613. <https://doi.org/10.1002/ajpa.22677>

484 Haak, D. C., HilleRisLambers, J., Pitre, E., & Freeman, S. (2011). Increased Structure and
485 Active Learning Reduce the Achievement Gap in Introductory Biology. *Science*,
486 332(6034), 1213–1216. <https://doi.org/10.1126/science.1204820>

487 Hague, S. S. (2011). Fantasy Seed Company: A Role Playing Game for Plant Breeding Courses.
488 *Journal of Natural Resources and Life Sciences Education*, 40(1), 168–171.
489 <https://doi.org/10.4195/jnrlse.2010.0012u>

490 Hanč, J., Štrauch, P., Paňková, E., & Hančová, M. (2020). *Teachers' perception of Jupyter and*
491 *R Shiny as digital tools for open education and science* (Version 2). arXiv.
492 <https://doi.org/10.48550/ARXIV.2007.11262>

493 Herrera-Pavo, M. Á. (2021). Collaborative learning for virtual higher education. *Learning,*
494 *Culture and Social Interaction*, 28, 100437.
495 <https://doi.org/10.1016/j.lcsi.2020.100437>

496 Hoban, S., Bertorelle, G., & Gaggiotti, O. E. (2012). Computer simulations: Tools for
497 population and evolutionary genetics. *Nature Reviews Genetics*, 13(2), 110–122.
498 <https://doi.org/10.1038/nrg3130>

499 Jia, L., Yao, W., Jiang, Y., Li, Y., Wang, Z., Li, H., Huang, F., Li, J., Chen, T., & Zhang, H. (2022).

500 Development of interactive biological web applications with R/Shiny. *Briefings in*

501 *Bioinformatics*, 23(1), bbab415. <https://doi.org/10.1093/bib/bbab415>

502 Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program

503 cervus accommodates genotyping error increases success in paternity assignment:

504 CERVUS LIKELIHOOD MODEL. *Molecular Ecology*, 16(5), 1099–1106.

505 <https://doi.org/10.1111/j.1365-294X.2007.03089.x>

506 Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2010). Corrigendum. *Molecular Ecology*,

507 19(7), 1512–1512. <https://doi.org/10.1111/j.1365-294X.2010.04544.x>

508 Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of Primate Social Systems.

509 *International Journal of Primatology*, 23(4), 707–740.

510 <https://doi.org/10.1023/A:1015520830318>

511 Kasprzak, P., Mitchell, L., Kravchuk, O., & Timmins, A. (2021). *Six Years of Shiny in*

512 *Research—Collaborative Development of Web Tools in R*.

513 <https://doi.org/10.48550/ARXIV.2101.10948>

514 Kober, N. (2015). *Reaching Students: What Research Says About Effective Instruction in*

515 *Undergraduate Science and Engineering* (p. 18687). National Academies Press.

516 <https://doi.org/10.17226/18687>

517 Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., Gowaty, P.

518 A., Green, J. L., Harte, J., Hubbell, S. P., O'Dwyer, J., Okie, J. G., Ostling, A., Ritchie,

519 M., Storch, D., & West, G. B. (2014). On Theory in Ecology. *BioScience*, 64(8), 701–

520 710. <https://doi.org/10.1093/biosci/biu098>

521 Marshall, T. C., Slate, J., Kruuk, L. E. B., & Pemberton, J. M. (1998). Statistical confidence for
522 likelihood-based paternity inference in natural populations. *Molecular Ecology*, 7(5),
523 639–655. <https://doi.org/10.1046/j.1365-294x.1998.00374.x>

524 Masi, S., Austerlitz, F., Chabaud, C., Lafosse, S., Marchi, N., Georges, M., Dessarps-Freichey,
525 F., Miglietta, S., Sotto-Mayor, A., Galli, A. S., Meulman, E., Pouydebat, E., Krief, S.,
526 Todd, A., Fuh, T., Breuer, T., & Ségurel, L. (2021). No evidence for female kin
527 association, indications for extragroup paternity, and sex-biased dispersal patterns in
528 wild western gorillas. *Ecology and Evolution*, 11(12), 7634–7646.
529 <https://doi.org/10.1002/ece3.7596>

530 Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and
531 kinship in wild chimpanzees. *Animal Behaviour*, 59(4), 885–893.
532 <https://doi.org/10.1006/anbe.1999.1389>

533 Morrison, R. E., Ndayishimiye, E., Stoinski, T. S., & Eckardt, W. (2023). Multiple mechanisms
534 for inbreeding avoidance used simultaneously in a wild ape. *Proceedings of the Royal
535 Society B: Biological Sciences*, 290(2009), 20231808.
536 <https://doi.org/10.1098/rspb.2023.1808>

537 Mwaura, D. K., Tung, J., & Anderson, J. (2023). *DadApp. A Shiny Web Server for calculating
538 parentage likelihood from genotype data* (Version 1) [Computer software]. [object
539 Object]. <https://doi.org/10.5281/ZENODO.8171382>

540 Nelson, C. E. (2008). Teaching evolution (and all of biology) more effectively: Strategies for
541 engagement, critical reasoning, and confronting misconceptions. *Integrative and
542 Comparative Biology*, 48(2), 213–225. <https://doi.org/10.1093/icb/icn027>

543 Neyhart, J. L., & Watkins, E. (2020). An active learning tool for quantitative genetics
544 instruction using *R* and *shiny*. *Natural Sciences Education*, 49(1).
545 <https://doi.org/10.1002/nse.2.20026>

546 Nguyen, N., Van Horn, R. C., Alberts, S. C., & Altmann, J. (2009). "Friendships" between new
547 mothers and adult males: Adaptive benefits and determinants in wild baboons
548 (*Papio cynocephalus*). *Behavioral Ecology and Sociobiology*, 63(9), 1331–1344.
549 <https://doi.org/10.1007/s00265-009-0786-6>

550 Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J., & Vigilant, L. (2008). Kin-biased social
551 behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal*
552 *Behaviour*, 76(1), 187–199. <https://doi.org/10.1016/j.anbehav.2008.01.020>

553 Petty, L. E., Phillipi-Falkenstein, K., Kubisch, H. M., Raveendran, M., Harris, R. A., Vallender,
554 E. J., Huff, C. D., Bohm, R. P., Rogers, J., & Below, J. E. (2021). Pedigree reconstruction
555 and distant pairwise relatedness estimation from genome sequence data: A
556 demonstration in a population of rhesus macaques (*Macaca mulatta*). *Molecular*
557 *Ecology Resources*, 21(4), 1333–1346. <https://doi.org/10.1111/1755-0998.13317>

558 Platek, S. M., & Shackelford, T. K. (Eds.). (2006). *Female infidelity and paternal uncertainty:*
559 *Evolutionary perspectives on male anti-cuckoldry tactics*. Cambridge University Press.

560 Pusey, A. (1990). Mechanisms of Inbreeding Avoidance in Nonhuman Primates. In J. R.
561 Feierman (Ed.), *Pedophilia* (pp. 201–220). Springer New York.
562 https://doi.org/10.1007/978-1-4613-9682-6_8

563 Qureshi, M. A., Khaskheli, A., Qureshi, J. A., Raza, S. A., & Yousufi, S. Q. (2023). Factors
564 affecting students' learning performance through collaborative learning and

565 engagement. *Interactive Learning Environments*, 31(4), 2371–2391.

566 <https://doi.org/10.1080/10494820.2021.1884886>

567 Rentof, J.-K., Chamberlain, C., & Sard, N. M. (2024). Evaluating factors that affect full- and

568 half-sibling inferences via genetic pedigree reconstruction without parental

569 genotypes. *Journal of Great Lakes Research*, 50(2), 102282.

570 <https://doi.org/10.1016/j.jglr.2023.102282>

571 Rosenbaum, S., & Silk, J. B. (2022). Pathways to paternal care in primates. *Evolutionary*

572 *Anthropology: Issues, News, and Reviews*, 31(5), 245–262.

573 <https://doi.org/10.1002/evan.21942>

574 Sard, N. M., Hunter, R. D., Roseman, E. F., Hayes, D. B., DeBruyne, R. L., & Scribner, K. T.

575 (2021). Pedigree accumulation analysis: Combining methods from community

576 ecology and population genetics for breeding adult estimation. *Methods in Ecology*

577 *and Evolution*, 12(12), 2388–2396. <https://doi.org/10.1111/2041-210X.13704>

578 Shou, W., Bergstrom, C. T., Chakraborty, A. K., & Skinner, F. K. (2015). Theory, models and

579 biology. *eLife*, 4, e07158. <https://doi.org/10.7554/eLife.07158>

580 Slate, J., Marshall, T., & Pemberton, J. (2000). A retrospective assessment of the accuracy of

581 the paternity inference program cervus. *Molecular Ecology*, 9(6), 801–808.

582 <https://doi.org/10.1046/j.1365-294x.2000.00930.x>

583 Smith, M. K., & Wood, W. B. (2016). Teaching Genetics: Past, Present, and Future. *Genetics*,

584 204(1), 5–10. <https://doi.org/10.1534/genetics.116.187138>

585 Soderberg, P., & Price, F. (2003). An examination of problem-based teaching and learning in

586 population genetics and evolution using EVOLVE, a computer simulation.

587 *International Journal of Science Education*, 25(1), 35–55.

588 <https://doi.org/10.1080/09500690110095285>

589 Speth, E. B., Momsen, J. L., Moyerbrailean, G. A., Ebert-May, D., Long, T. M., Wyse, S., &

590 Linton, D. (2010). 1, 2, 3, 4: Infusing Quantitative Literacy into Introductory Biology.

591 *CBE—Life Sciences Education*, 9(3), 323–332. <https://doi.org/10.1187/cbe.10-03-0033>

592 0033

593 Städele, V., Pines, M., Swedell, L., & Vigilant, L. (2016). The ties that bind: Maternal kin bias

594 in a multilevel primate society despite natal dispersal by both sexes. *American*

595 *Journal of Primatology*, 78(7), 731–744. <https://doi.org/10.1002/ajp.22537>

596 Städele, V., & Vigilant, L. (2016). Strategies for determining kinship in wild populations using

597 genetic data. *Ecology and Evolution*, 6(17), 6107–6120.

598 <https://doi.org/10.1002/ece3.2346>

599 Städele, V., Vigilant, L., Strum, S. C., & Silk, J. B. (2021). Extended male–female bonds and

600 potential for prolonged paternal investment in a polygynandrous primate (*Papio*

601 *anubis*). *Animal Behaviour*, 174, 31–40.

602 <https://doi.org/10.1016/j.anbehav.2021.01.017>

603 Strier, K. B. (2008). The Effects of Kin on Primate Life Histories. *Annual Review of*

604 *Anthropology*, 37(1), 21–36.

605 <https://doi.org/10.1146/annurev.anthro.37.081407.085218>

606 Subhash, S., & Cudney, E. A. (2018). Gamified learning in higher education: A systematic

607 review of the literature. *Computers in Human Behavior*, 87, 192–206.

608 <https://doi.org/10.1016/j.chb.2018.05.028>

609 Van Horn, R. C., Altmann, J., & Alberts, S. C. (2008). Can't get there from here: Inferring
610 kinship from pairwise genetic relatedness. *Animal Behaviour*, 75(3), 1173–1180.
611 <https://doi.org/10.1016/j.anbehav.2007.08.027>

612 Vickrey, T., Rosploch, K., Rahamanian, R., Pilarz, M., & Stains, M. (2015). Research-Based
613 Implementation of Peer Instruction: A Literature Review. *CBE—Life Sciences
614 Education*, 14(1), es3. <https://doi.org/10.1187/cbe.14-11-0198>

615 Vilgalys, T. P., Fogel, A. S., Anderson, J. A., Mututua, R. S., Warutere, J. K., Siodi, I. L., Kim, S.
616 Y., Voyles, T. N., Robinson, J. A., Wall, J. D., Archie, E. A., Alberts, S. C., & Tung, J.
617 (2022). Selection against admixture and gene regulatory divergence in a long-term
618 primate field study. *Science*, 377(6606), 635–641.
619 <https://doi.org/10.1126/science.abm4917>

620 Wang, S. L., Zhang, A. Y., Messer, S., Wiesner, A., & Pearl, D. K. (2021). Student-Developed
621 Shiny Applications for Teaching Statistics. *Journal of Statistics and Data Science
622 Education*, 29(3), 218–227. <https://doi.org/10.1080/26939169.2021.1995545>

623 Wellens, K. R., Lee, S. M., Winans, J. C., Pusey, A. E., & Murray, C. M. (2022). Female
624 chimpanzee associations with male kin: Trade-offs between inbreeding avoidance
625 and infanticide protection. *Animal Behaviour*, 190, 115–123.
626 <https://doi.org/10.1016/j.anbehav.2022.06.001>

627 Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal
628 relatedness and age proximity regulate social relationships among adult female
629 rhesus macaques. *Proceedings of the National Academy of Sciences*, 98(24), 13769–
630 13773. <https://doi.org/10.1073/pnas.241210198>

631 Williams, K. R., Wasson, S. R., Barrett, A., Greenall, R. F., Jones, S. R., & Bailey, E. G. (2021).

632 Teaching Hardy-Weinberg Equilibrium using Population-Level Punnett Squares:

633 Facilitating Calculation for Students with Math Anxiety. *CBE—Life Sciences Education*,
634 20(2), ar22. <https://doi.org/10.1187/cbe.20-09-0219>

635 Winterer, J. (2001). A Lab Exercise Explaining Hardy-Weinberg Equilibrium and Evolution
Effectively. *The American Biology Teacher*, 63(9), 678–687.

636 <https://doi.org/10.2307/4451215>

638 Zhang, D. (2005). Interactive Multimedia-Based E-Learning: A Study of Effectiveness.
639 *American Journal of Distance Education*, 19(3), 149–162.

640 https://doi.org/10.1207/s15389286ajde1903_3

641

642

643

644

645

646

647

648