

Relationship type affects the reliability of dispersal distance estimated using pedigree inferences in partially sampled populations: a case study involving invasive American mink in Scotland

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1 **Relationship type affects the reliability of dispersal distance estimated using pedigree**
2 **inferences in partially sampled populations: a case study involving invasive American**
3 **mink in Scotland**

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11 **Running title:** Testing pedigree-based estimates of dispersal

12

13 **Abstract**

14 Estimating dispersal - a key parameter for population ecology and management - is
15 notoriously difficult. The use of pedigree assignments, aided by likelihood-based softwares,
16 has become popular to estimate dispersal rate and distance. However, the partial sampling of
17 populations may produce false assignments. Further, it is unknown how the accuracy of
18 assignment is affected by the genealogical relationships of individuals and is reflected by
19 software-derived assignment probabilities. Inspired by a project managing invasive American
20 mink (*Neovison vison*), we estimated individual dispersal distances using inferred pairwise
21 relationships of culled individuals. Additionally, we simulated scenarios to investigate the
22 accuracy of pairwise inferences. Estimates of dispersal distance varied greatly when derived

23 from different inferred pairwise relationships, with mother-offspring relationship being the
24 shortest (average = 21 km) and the most accurate. Pairs assigned as maternal half-siblings
25 were inaccurate, with 64-97% falsely assigned, implying that estimates for these relationships
26 in the wild population were unreliable. The false assignment rate was unrelated to the
27 software-derived assignment probabilities at high dispersal rates. Assignments were more
28 accurate when the inferred parents were older and immigrants and when dispersal rates
29 between subpopulations were low (1 and 2%). Using 30 instead of 15 loci increased pairwise
30 reliability, but half-sibling assignments were still inaccurate (> 59% falsely assigned). The
31 most reliable approach when using inferred pairwise relationships in polygamous species
32 would be not to use half-sibling relationship types. Our simulation approach provides
33 guidance for the application of pedigree inferences under partial sampling and is applicable to
34 other systems where pedigree assignments are used for ecological inference.

35

36 **Keywords:** Dispersal distance, pedigree inference, genetic markers, simulations, polygamous
37 species

38 **Introduction**

39 Dispersal distance, defined as the distance travelled by an individual dispersing from the natal
40 or breeding patch to a new settlement location, is a key parameter in many ecological models
41 and critical for the successful management of populations (Sutherland *et al.* 2013). Whether
42 for native or introduced species, dispersal plays a central role in population expansion and
43 persistence by influencing connectivity between fragmented habitat patches or driving range
44 shifts. Dispersal distance therefore defines the relevant spatial scale for management actions
45 (Schaub *et al.* 2010). However, obtaining accurate estimates of dispersal distance is
46 notoriously challenging.

47

48 Classical direct methods for inferring dispersal distance include field-based observations,
49 radio-tracking, or physical tagging, which often have high associated costs, whilst producing
50 relatively little data (Dingle 1996). The accessibility of genetic markers, such as microsatellite
51 loci and single nucleotide polymorphisms, has made it possible to complement, or substitute,
52 these methods by inferring pedigree relationships among the individuals in a population
53 (Wilson & Rannala 2003; Guichoux *et al.* 2011; Norman & Spong 2015). When combining
54 inferred pedigree relationships with location data, natal dispersal distance can be inferred. The
55 relationships most frequently used to infer dispersal distances are pairwise relationships
56 because breeding site-faithful parents and/or non-dispersed siblings provide information on
57 the natal location of the individuals (e.g., García *et al.* 2007; Planes *et al.* 2009; Christie *et al.*
58 2010; Lambin *et al.* 2012; Almany *et al.* 2013; Norman & Spong 2015).

59

60 A major common challenge with pedigree analyses is the potential for false assignments that
61 occur in data sets collected for natural wild populations which unavoidably results from the
62 partial sampling of individuals and of their genome (Koch *et al.* 2008; Leonarduzzi *et al.*
63 2012). Where the identity of neither parent is known a-priori, a large number of pairwise
64 comparisons of genotypes must be made between putative relatives, inflating the potential for
65 assignment errors, especially when inbreeding and polygamy occur (Wang 2012, 2014a).

66 Another issue arises when age cannot be determined; hence parent-offspring relationships are
67 unclear. Given these problems, any potential false relationship assignments will necessarily
68 result in inaccurate, and at times biased, estimations of dispersal distance, with important
69 consequences for both the understanding of spatial dynamics as well as the efficacy of species
70 management actions.

71

72 There are several software packages available for assessing kinship including: COLONY
73 (Jones & Wang 2009), CERVUS (Kalinowski *et al.* 2007), FAMOZ (Gerber *et al.* 2003) and
74 MASTERBAYES (Hadfield *et al.* 2006). These programs simultaneously assign sibships and
75 parentage using maximum likelihood based on the allele frequencies within the pool of
76 candidate parents and offspring. Inferred clusters of related individuals and pairwise putative
77 relationships are produced, along with a measure of assignment certainty (as a critical log-
78 likelihood score), confidence intervals, or assignment probabilities. From a statistical point of
79 view, the values of these measurements could be used as criteria to eliminate false
80 assignments, as they are all based on likelihoods given the observed data (i.e., the population
81 sample). Both the confidence intervals and the assignment probabilities assume that the
82 sample and input parameters are a precise representation of the actual population. However,
83 the accuracy of the obtained likelihood of an assignment may not reflect uncertainty
84 associated with the ecological complexity of the population (e.g., population spatial structure,
85 level of inbreeding, mating system), as well as the partial, and potentially biased, sampling of
86 wild populations (e.g., spatially aggregated or unevenly sampled cohorts). Likelihood-based
87 measures of assignment accuracy may thus be statistically, but not ecologically, reliable. In
88 this study, we used simulations to investigate the influence of key ecological parameters on
89 the accuracy of pedigree assignments inferred by COLONY for a partially sampled wild
90 population of a mobile mammalian predator. We used the full-likelihood algorithm in
91 COLONY, as it is widely used and was shown to out-perform the pairwise-likelihood
92 approaches of both CERVUS and FAMOZ, and was similar to MASTERBAYES (Walling *et*
93 *al.* 2010; Karaket & Poompuang 2012; Harrison *et al.* 2013).

94

95 The American mink (*Neovison vison*, hereafter mink) is a representative example of a highly
96 mobile species under management. The mink is widely distributed as an invasive non-native
97 species and the focus of a substantial control effort worldwide (see Bonesi & Palazón 2007;
98 Genovesi *et al.* 2012; Santulli *et al.* 2014). In northern Scotland, a large-scale participatory
99 project to control American mink has been underway since 2006 (Bryce *et al.* 2011). Central
100 to the mink control strategy are understanding the scale of dispersal, hence scope for
101 reinvasion, and identifying ‘hot spots’ in the landscape that may disproportionately contribute
102 immigrants. In a previous study, we used pedigree analyses to understand patterns of mink
103 dispersal and to infer levels of compensatory immigration in response to culling (Oliver *et al.*
104 2016). Whilst analyses provided useful insights about changes in immigration rate following
105 culling, we had the potential to provide more precise information about actual genetic
106 relationships and used them to infer specific dispersal movements. However, when using
107 COLONY, we observed notably different results in the estimate of dispersal distance
108 depending on the nature of the mating system assumed (i.e., monogamy or polygamy).
109 Estimates of dispersal distance also varied depending on the parental relationship of pairs of
110 inferred siblings, with estimates derived from full-siblings being substantially longer than
111 those from maternal half-siblings. This difference occurred despite inferences being well
112 supported by assignment probabilities. Rather than being specific to the present study, this
113 problem could arise in multiple systems, therefore broadly affecting inferences on ecological
114 processes based on dispersal estimates (e.g., Saenz-Agudelo *et al.* 2011; López-Sepulcre *et al.*
115 2013).

116

117 With this study, we aimed to improve the standard approach to ecological inferences based on
118 pedigree analyses that use field ecological data with incomplete sampling. We first

119 investigated whether dispersal distances estimated from inferred pedigrees varied in relation
120 to the relationship type (e.g., full- vs half-siblings) and also to the assignment probability
121 estimated by COLONY. Secondly, we analysed the accuracy of inferred pairwise assignments
122 (i.e., whether or not they were correct) in relation to the above-mentioned factors, as well as
123 the age and source of the true parents (i.e., immigrant versus local), the dispersal rate between
124 populations and the number of microsatellite loci used. We used the mink population from
125 NE Scotland as a study system for the analyses of the estimates of dispersal distance and also
126 as the basis for a set of simulation scenarios for testing the accuracy of inferred pairwise
127 assignments.

128

129 **Materials and methods**

130 Study species

131 Mink are diploid, have overlapping generations, female and male polygamy, and frequent
132 multiple paternities (Yamaguchi *et al.* 2004). Thus, a single litter can consist of full-siblings
133 (same mother and father) or maternal half-siblings (same mother but different father).

134 Besides, the offspring of different litters may also be paternal half-siblings (same father but
135 different mother). Mating takes place once per year in March-April, with a single litter of
136 typically 4-5 offspring (up to 12) born in May (Dunstone 1993; Melero *et al.* 2015). Adult
137 males and females have separate, though potentially overlapping territories (Melero *et al.*
138 2008). Siblings stay in the maternal territory under the mother's protection until dispersal
139 (circa September at five months old), at which point most juveniles leave the maternal
140 territory to seek a vacant territory, where they will typically settle in solitude by the end of the
141 year when they are sexually mature at eight months old (Dunstone 1993).

142

143 Age determination, DNA extraction and genotyping

144 The age of culled mink from the NE Scotland population was estimated by X-raying canine
145 teeth (Helldin, 1997) and subsequently, for those individuals deemed 10 months or older,
146 using tooth cementum analyses performed by Matson's Laboratory LLC (Manhattan,
147 Montana, USA). DNA was extracted using the DNeasy kit (Qiagen, US) following the
148 manufacturer's protocol. For all mink, genotyping was performed at 15 microsatellite loci
149 developed for mustelids: Mer009, Mer022, Mer041, Mvi054, Mvi057, Mvi232, Mvi111,
150 Mvi1321, Mvi1381, Mvi1843, Mvis022, Mvis072, Mvi4001, Mvi4031, Mvi4058 (O'Connell
151 *et al.* 1996; Anistoroaei *et al.* 2006; Vincent *et al.* 2011). Polymerase chain reaction (PCR)
152 amplifications were performed following Oliver *et al.* (2016).

153

154 Pedigree-based analysis

155 The reconstruction of litters was performed by pedigree analysis using COLONY 2.0.47
156 (Wang 2008). Individuals were categorised as putative mothers, fathers and offspring for each
157 generation (year) following age and sex determination. Input parameters were set to account
158 for mink biology: female and male polygamous mating systems without inbreeding
159 avoidance, as is suspected to be the case for mink. Polygamy creates a far more complex
160 problem of pedigree elucidation than monogamy. Thus, we selected the most stringent
161 likelihood settings for pedigree reconstruction. Genotyping error rate was set as 0% to
162 improve comparisons between the input genotypes and reduce the model computing time.
163 Allele scoring was performed by one or two independent observers and those individuals
164 whose genotype was ambiguous (< 1% of the total sampling) were removed and/or re-
165 genotyped. The probabilities for mothers and fathers being present in the sample are not

166 inferred by COLONY, but are rather set as an input parameter. We set them both at 50% in
167 the absence of other prior information.

168

169 Analysis of dispersal distance

170 Individual dispersal distances were estimated based upon the Euclidean distance between the
171 natal territory and the capture location of those genotyped mink from the empirical NE
172 Scotland population assumed to be post-dispersal at the time of the capture (i.e., > eight
173 months old). The approximate locations of natal territories were ascertained from the capture
174 location of the pedigree-inferred mother, as female mink tend not to disperse once they are
175 reproductively mature (Dunstone 1993). When the mother was not sampled, the natal location
176 was estimated from the capture location of inferred full-siblings or maternal half-siblings that
177 were younger than 5 months old and therefore likely pre-dispersal (i.e., siblings likely located
178 in the maternal territory). Inferred fathers were not used to inform natal locations, as the
179 settled location of males might change after roaming during the mating season (Dunstone
180 1993).

181

182 Simulated population scenarios

183 To test the accuracy of the inferred pairwise relationships, we used a set of simulations
184 depicting three scenarios. In Scenario 1 (S1), we simulated a population mimicking the
185 empirical NE Scotland mink population and its demographic and genetic dynamics over three
186 years. The NE Scotland mink population was previously identified combining analyses of
187 genetic clusters with analyses of the levels of relatedness and gene flow among populations
188 recognised by geographic location (Fraser *et al.* 2013). This scenario was used to estimate the
189 accuracy of inferred pairwise relationships for the specific case of the empirical NE Scotland

190 mink population. In Scenario 2, we simulated over three years three subpopulations that were
191 connected via a set of four different dispersal rates defined as the proportion of each
192 population moving into another population (1%, 2%, 10% or 20%), therefore yielding four
193 scenarios (S2.1-S2.4). The aim here was to understand the effect of the dispersal rate between
194 subpopulations on the accuracy of inferred pairwise relationships. The true dispersal rate
195 between subpopulations in the empirical NE Scotland mink population is unknown, although
196 Oliver *et al.* (2016) estimated that, on average, 30% of captured individuals were immigrants
197 (having no kin within 10 km of the capture location) based on kinship analysis. In Scenario 3,
198 we repeated those most contrasting simulations from Scenario 2 (S2.1 and S2.4) while
199 increasing the number of microsatellite loci from 15 to first 20 and then 30 for each
200 simulation. The aim was to test whether increasing the number of loci used increased the
201 accuracy of inferred pairwise relationships.

202

203 *Scenario 1: Mimicking the Scottish mink population*

204 We sought to mimic the empirical NE Scotland mink population using the spatial and genetic
205 structure described by Fraser *et al.* (2013). This comprised a central population surrounded by
206 two peripheral populations to the West and South, with little genetic divergence between the
207 three (Fig. 1a). Peripheral areas were previously shown to have been a source of immigrants
208 to the central population (Fraser *et al.* 2013). We therefore simulated a central population (P0
209 hereafter) and two peripheral populations (IP0_{*i*}), where *i* stands for each of the two peripheral
210 populations. Initial population sizes were set as the carrying capacities of the corresponding
211 empirical populations, calculated as the maximum number of occupied mink territories during
212 the duration of the project (approach and details in Melero *et al.* 2015). This resulted in 520
213 simulated individuals for P0 and 60 for IP0_{*i*}.

214

215 All simulated individuals were given a unique identifier and a 15-microsatellite loci genotype,
216 randomly generated from the allele frequencies of their corresponding empirical population,
217 using the software NOOKIE in MS2, a C program which simulates Mendelian inheritance of
218 markers from specified mating occasions and populations (Anderson & Dunham 2008;
219 <https://github.com/eriqande/nookie>).

220

221 Individuals simulated in P0 and IP0_i were crossed (bred) independently once in NOOKIE to
222 establish a gene pool that was in Hardy-Weinberg equilibrium. Once crossed, we discarded all
223 individuals in P0 and IP0_i and retained their offspring OF0 and OF-I0_i, maintaining the initial
224 population sizes. Population dynamics based on set breeding and survival parameters were
225 then simulated for three years using mink life-history data obtained from the literature, as well
226 as the empirical data collected from the NE Scotland population (Fig. 2, Table 1; see
227 simulation scheme in Fig. S1a).

228

229 We allowed some individuals from the simulated peripheral populations OF-I0_i and their
230 subsequent offspring OF-II_i and OF-I2_i to disperse into the simulated central population each
231 year (OF0-OF3). We assumed that 25% of juvenile survivors (i.e., offspring of each year that
232 survived until being reproductively active one year after birth) of the two peripheral
233 populations successfully settled in the simulated central population (Fig. S1a), based on
234 earlier estimates of the probability of an individual being an immigrant in the central
235 population (Oliver *et al.* 2016) and on the genetic differentiation of the populations (Fraser *et*
236 *al.* 2013). Throughout the simulation process, the resulting true genealogy (or pedigree), the
237 age, and the source and settlement locations (or populations) of individuals were recorded to

238 inform and to be compared with the subsequent inferences derived from pedigree analysis
239 with COLONY.

240

241 *Scenario 2: Simulating different dispersal rates between subpopulations*

242 The spatial and genetic structure of the three simulated subpopulations ($P0_i$) in this scenario
243 were based on three areas within the range of the empirical NE Scotland mink population
244 (areas Dee, Spey and Tay; Fig. 1a). These areas were chosen as being the most genetically
245 distinct based on global and pairwise measures of absolute genetic differentiation using Jost's
246 D (D_{ST}) per year and along all years calculated using DEMETics (Gerlach *et al.* 2010; mean
247 D_{ST} values Dee-Spey = 0.26 (0.08-0.37), Dee-Tay = 0.11 (0.04-0.15), Spey-Tay = 0.13 (0.06-
248 0.28)).

249

250 The simulated subpopulation sizes and individual genotypes were obtained separately for the
251 three subpopulations following the same procedures as in Scenario 1, producing
252 approximately 60 individuals per population. As in Scenario 1, the three simulated
253 populations were crossed independently to allow allele and genotype ratios to equilibrate for
254 each OF_0 population, until measurements of pairwise $D_{ST} > 0.6$ (Table S1). Once crossed, we
255 also discarded all individuals in $P0_i$ but retained their offspring OF_0_i ($n_{total} = 800$).

256 Using the three OF_i populations, we simulated their demographic and population dynamics
257 using the same life-history parameters as Scenario 1 (Table 1, see simulation scheme in Fig.
258 S1b). Four scenarios, with varying dispersal rates between the three OF_i populations, were
259 defined as: S2.1 with the lowest dispersal rate of $r_d = 1\%$; S2.2 with $r_d = 2\%$; S2.3 with $r_d =$
260 10% ; and S2.4 with the highest rate of $r_d = 20\%$.

261

262 *Scenario 3: Increasing the number of loci used*

263 We repeated the procedure of Scenario S2.1 and S2.4 as those with most differing reliability
264 of their inferences (see results section), but using for each scenario first 20 and then 30 loci
265 instead of 15. The new loci were created based on randomly selecting allele frequencies of the
266 known 15 microsatellites. Thus, our simulation explored the change in power based on the
267 number of loci with similar allele variability to that observed in our empirical study without
268 the confounding effect of variability in allele frequencies (see levels of variability for S1, S2
269 and S3 in Table S2).

270

271 *Subsampling the simulated populations: mimicking the partial sampling of wild populations*

272 In each scenario, we mimicked the partial sampling of a wild population by subsampling a set
273 of individuals from the resulting simulated population at year three. For each scenario, the
274 resulting simulated population was composed of the pool of parents OF0_{S2}, OF1_{S1} and OF2,
275 and their juvenile offspring OF3, with all individuals identified and of known sex (Fig. 2 and
276 Fig. S1). The proportions subsampled were 67% of the juvenile offspring (OF3), 52% of adult
277 females (females in OF0_{S2}, OF1_{S1} and OF2) and 52% of adult males (males in OF0_{S2}, OF1_{S1}
278 and OF2). These proportions were chosen to reflect the proportion of captures in the empirical
279 wild NE Scotland mink population; calculated as the proportion of captures in the control year
280 with the highest number of captures in relation to corresponding initial population sizes
281 (maximum number of territories; approach and details in Melero *et al.* 2015).

282

283 The genotypes of the subsampled simulated individuals then were used as the candidate
284 parents and offspring for the COLONY input files, with inference procedures run using the
285 same conditions as described above for the analyses of the empirical NE Scotland population.

286

287 Statistical analyses

288 We used a Gaussian linear model to investigate whether the inferred relationship types or
289 likelihood-based assignment probability (P hereafter) explained variation in dispersal
290 distance. Inferred relationship types were categorised as mother-offspring, full-siblings, and
291 maternal half-siblings. We deemed father-offspring relationships uninformative about
292 dispersal.

293

294 To quantify the accuracy of the inferred relationships, we noted the rate of discrepancy
295 between the known simulated relationships and those inferred by COLONY per simulation,
296 which we refer to as assignment error rate hereafter. Assignment error rate included two types
297 of false pairwise assignments: false positives (Type I error, defined as inferred pairwise
298 relationships that were not true despite associated values of $P \geq 0.8$) and false negatives (Type
299 II error, defined as inferred pairwise relationships that were correct despite associated values
300 of $P < 0.5$). We included both error types because, whilst the first leads to false estimates of
301 ecological parameters such as, e.g., dispersal distance (given false relationships, and therefore
302 also natal locations, are inferred), the second adds error to the estimation of true values (by
303 overlooking true relationships), potentially biasing results at the population level (e.g.,
304 defining the risk of reinvasion). The assignment error rate was evaluated in relation to the
305 inferred relationship type (mother-offspring, father-offspring, full-siblings, maternal and
306 paternal half-siblings), P , and the age and origin (immigrant or local) of the true parents, since
307 we expected older and/or immigrant parents to be more genetically distinct than younger
308 and/or local parents and therefore easier to assign. The influence of dispersal rate between
309 subpopulations was also tested by comparing simulations of Scenario 2, because higher

310 assignment error rates are expected with low heterozygosity, and increased dispersal should
311 lead to higher heterozygosity within subpopulations (Saenz-Agudelo *et al.* 2009; Wang
312 2014b). Lastly, the effect of the number of loci was also tested comparing the simulations of
313 Scenario 3. Analyses were performed using generalised linear models (GLM), where
314 assignment error rate was set as the dependent variable fitted using a binomial distribution
315 (one for false assignments) and a complementary cloglog link to account for the amount of
316 zeros (Zuur *et al.* 2009).

317

318 **Results**

319 *How far do real mink disperse?*

320 The estimated dispersal distances for the empirical NE Scotland mink population for all
321 individuals genotyped had a median = 27.7 km, mean = 37.1 km, min = 0 km, 1st quartile =
322 10.6 km, 3rd quartile = 54.9 km and max = 162.4 km. The mean dispersal distance was nearly
323 twice as large when estimated using inferred maternal half-siblings (39 km, $n = 756$) for
324 inferring the natal location than when estimated using mother-offspring relationships (21 km,
325 $n = 312$), and the value of the third quartile increased 1.5-fold (40 to 58 km; Fig. 1b-d). The
326 distance estimates using mother-offspring and full-sibling relationship types (mean = 28 km,
327 $n = 38$) were equivalent and statistically significantly shorter than the estimates for half-
328 siblings (half-siblings *vs* mother-offspring, HS *vs* MO, $F_{2, 478} = 4.11$; p -value < 0.001). The
329 estimated dispersal distance decreased significantly as the assignment probability increased,
330 with a 2-fold decrease for inferred relationships with $P \geq 0.8$ relative to those with $P \leq 0.1$
331 (Estimate _{p} = -31.83 km; $F_{1, 479} = -4.53$; p -value < 0.001; Fig. 3); demonstrating that choice of
332 P would affect biological inference.

333

334 *Scenario 1: What influences assignment error rate in the mimicked Scottish mink population?*

335 Fifty-five per cent of all of inferred pairwise relationships under Scenario 1 were false

336 positive assignments, which can be clearly seen in Fig. 4. Of these, 90% were given an

337 assignment probability value of $P > 0.9$ by COLONY. A small percentage (0.7%) were false

338 negatives with $P < 0.5$ (details in Table S3).

339

340 The inferred relationship type had a clear and significant impact on assignment error rate,

341 being lowest for full-siblings (5.2%) and highest for maternal and paternal half-siblings (64.5

342 and 71.9%, respectively; Table S3). Inferred mother- and father-offspring relationships had

343 equal reliability with an average assignment error rate of 13.2%, but were less reliable than

344 full-siblings (FS *vs* MO, Estimate_{fs} = -2.04, SD_{fs} = 1.01, $F_{3, 833} = 4.11$; p -value = 0.04;

345 Binomial GLM). However, the assignment error rate for half-siblings was significantly higher

346 than for both mother- and father-offspring relationships (MHS *vs* MO, Estimate_{hs} = 0.86, SD_{hs}

347 = 0.18, $F_{3, 833} = 4.65$; p -value < 0.001; Figs. 4 and 5). The assignment error rate decreased as

348 P increased (Estimate = -2.20, SD = 0.68, $F_{1, 835} = -3.24$; p -value > 0.019, $r^2 = 0.17$) for all of

349 the inferred relationship types (p -values $P_{\text{relationship type}} > 0.53$, interaction dismissed during

350 model selection), although model predictions differed between them (Fig. 4). Whilst the

351 origin of each parent (local or immigrant) did not affect the assignment error rate (averages of

352 10.3% and 20.3%, respectively; $F_{1, 835} = 0.03$; p -values > 0.98), parental age did, with

353 assignment error rate being approximately 1.6 times lower when at least one parent was older

354 than one year (from an average error rate of 38.7% to 24.2% and 16.7% when at least one

355 parent was three, two and one year old, respectively; $F_{2, 833} = -2.17$ and -4.34 , p -values =

356 0.007 and < 0.001, respectively).

357

358 *Scenario 2: What influences assignment error rate?*

359 The assignment error rate increased with increasing dispersal rate, being similar for
360 simulations S2.1 and S2.2 at 40% ($r_{S2.1} = 0.01$ vs $r_{S2.2} = 0.02$; $F_{3, 11061} = -0.59$; p -value = 0.55),
361 but being 1.15- and 2-fold higher in simulations S2.3 and S3.4, respectively, at 46 and 85%
362 approximately ($r_{S2.3}=0.1$ and $r_{S2.4}=0.2$; $F_{3, 11061} = 4.05$ and 33.24 , p -values < 0.001; Fig. 5 and
363 Table S3).

364

365 Mother- and father-offspring relationships consistently had the highest assignment accuracies,
366 with an error range of 17-56.6% for S2.1 and S2.4, whereas half-sibling assignments were
367 always the least reliable, with a range of 61.8-97% for S2.2 and S2.4 (Table 2; Fig. S2 and
368 Table S3). The usefulness of P as a predictor of assignment error rate decreased with the
369 dispersal rate. When dispersal rate was low in S2.1 and S2.2, the assignment error rates were
370 estimated to decrease 1.2- and 1.5-fold, respectively, while P increased from ≤ 0.2 to ≥ 0.8 .
371 This was not the case in S2.3 and S2.4, the scenarios with highest dispersal rates, where no
372 relationship between P and assignment error was detected, although P in S2.3 had similar
373 patterns to those seen in S2.1 and S2.2 (Table 2 and Fig. S2). Both the age and origins of
374 parents were also influential. Having at least one older parent (two and three years old)
375 reduced the assignment error rate by 1.7-2.3 times compared to having one-year-old parents
376 in S2.1 and S2.2 (from 40 to 23 and 17% on average), a pattern to which we return in the
377 discussion. However, this effect was not found in S2.3 or S2.4. Having immigrant parents
378 reduced the assignment error rate by 1.6 times (from 44 to 28% on average), but only in S2.1
379 and S2.2 (Table 2).

380

381 *Scenario 3: What is the impact of increasing the number of loci on assignment error rate?*

382 The overall assignment error rate of simulations with low dispersal rate ($r_{S2.1} = 0.01$) did not
383 differ when using 15 or 20 loci with an average error rate of 46 and 43%, respectively;
384 however, it decreased 1.5-fold to 30% when using 30 loci ($F_{3, 9305} = 0.10$, p -values = 0.03;
385 Table S4). However, when dispersal rate was high ($r_{S2.4} = 0.2$), the error rate decreased to *ca.*
386 half from *ca.* 85% when using 15 loci to 40% and 39% when using 20 and 30 loci,
387 respectively ($F_{3, 7843} = -2.00$ and -20.2 , p -values < 0.001 ; Table S4).

388
389 Increasing the number of loci from 15 to 20 and 30 decreased the error rate for mother- and
390 father-offspring relationships, as well as of that of full-siblings for all simulations (range 0.7-
391 11.3%; Table S4) with these relationship types being equally reliable. Half-siblings
392 assignments were still not reliable, with error rates ranging from 59.4-97.3% and 59.9-84%
393 when using 20 and 30 loci, respectively (Table 3 and Table S4). The error rate decreased 1.2-
394 and 1.7-fold when P increased from ≤ 0.2 to ≥ 0.8 for both dispersal rates when using 30 loci
395 (Table 3), but it was unreliable for half-siblings in all simulations (Fig. S3). Having parents
396 older than one year old reduced the error rate by 3.7 and 6.4 times (from 58% to 15% and 9%
397 on average, respectively, for one-to-three years old) when dispersal rate was low ($r_{S2.1} = 0.01$),
398 but not when it was high ($r_{S2.4} = 0.2$) using either 20 or 30 loci. The same pattern occurred in
399 relation to the origins of the parents; individuals with at least one immigrant parent were 1.22
400 times more likely to be properly linked to a relative than when their parents were local (from
401 42 to 34% on average) if dispersal rate was low using 20 or 30 loci (Table 3).

402

403 **Discussion**

404 Using simulations, we assessed the accuracy of inferences of different pairwise relationships
405 derived from pedigree analysis using COLONY with data consisting of multiple

406 microsatellite genotypes for individuals from partially sampled wild populations, a system
407 that is typical of field-based ecological studies. We used a data set on invasive American
408 mink populations in NE Scotland to parameterize our models. We found that different types
409 of pairwise relationships were reconstructed with variable assignment error rates, and hence
410 that inference of dispersal distances based on pedigree reconstruction would be strongly
411 affected by the type of relationship being examined. Mother-offspring relationships and
412 relationships involving full-siblings yielded the most reliable relationship reconstructions. In
413 contrast, inferred maternal half-sibling pairs were nearly always unreliable, illustrating the
414 perceived difficulty of making pedigree inferences in species with polygamy and multiple
415 paternity (e.g., rainforest birds, Woltmann *et al.* 2012). However, the ecological reality is that
416 multiple paternities are commonplace in many species, but the accuracy of pedigree
417 inferences in their presence are frequently overlooked (e.g., water voles, Telfer *et al.* 2003;
418 capercaillie, Kormann *et al.* 2012; Roanoke logperch, Roberts *et al.* 2016). The assumed rate
419 of dispersal in the simulated populations, the age of the parent and whether they were
420 themselves dispersers - parameters themselves rarely known with certainty in field studies -
421 also impacted the accuracy of pedigree reconstruction. However, the impact of each of these
422 varied depending on the context of population structure and dispersal rate. Additionally, the
423 likelihood-based assignment probability (P) provided by the software was a good predictor of
424 accuracy when dispersal rates between subpopulations were low ($< 20\%$) or when number of
425 loci used was higher than in most field studies (e.g. 30), but not otherwise.

426

427 *Estimates of dispersal distance*

428 The impact of the low reliability of inferred maternal half-sibling pairs was evident in the
429 analyses of estimated individual dispersal distances for the empirical NE Scotland population,

430 which was the focal ecological question underpinning our application of the pedigree-based
431 approach. Estimates of dispersal distance averaged 21-28 km when using mother-offspring
432 and full-siblings, shown by simulation to be the most reliable relationships. The estimate
433 increased to 37.1 km when including maternal half-siblings (39 km when using maternal half-
434 siblings only), the least reliable relationship type. The difference was larger still when
435 considering upper quartiles of the dispersal distance distributions. We interpret this difference
436 as reflecting the fact that inferred maternal half-sibling relationships include numerous falsely
437 assigned relationships. *In extremis*, false assignments imply falsely pairing individuals that
438 are randomly distributed in space. Thus, in a hypothetical situation in which all pairwise
439 relationships were false, estimated dispersal distance would approach the mean pairwise
440 distance between all individuals, which is bound to upwardly bias estimates relative to real
441 dispersal wherever the study area is larger than dispersal distance. Applications of the
442 pedigree reconstruction approach should therefore ensure that inferences are robust to the use
443 of different relationship types; otherwise, as observed here, the consequences for our
444 ecological understanding could be substantial.

445

446 Estimated dispersal distance gradually shrank with the increase of the assignment probability
447 provided by COLONY. This is an indication of the potential usefulness of P to predict the
448 accuracy of inferred estimates for the specific case of the empirical NE Scotland population.
449 We note however that in the case of maternal half-siblings, the predicted assignment error rate
450 at $P = 1$ was still 50% and therefore useless or, worse, misleading.

451

452 *Factors affecting assignment error rate*

453 The assignment error rate of the inferred pairwise relationship types increased with increasing
454 simulated dispersal rate between neighbouring subpopulations, with an increase from 40% in
455 simulations with 1 and 2% dispersal rate (Scenarios S2.1 and S2.3) to approximately 85% in
456 Scenario S2.4 with 20% dispersal. Excluding half-siblings reduced the assignment error rate
457 in the scenarios with lower dispersal rate, resulting in 21% error rate in S2.1 and S2.2 and in
458 31% in S2.3 when excluding half-siblings, but not in the scenario with the highest dispersal
459 rate (76% error rate in S2.4). The increased dispersal rate in the simulated scenarios led to
460 reduced population genetic differentiation between and increased heterozygosity within the
461 three subpopulations (Table S1), which negatively affected the accuracy of parentage
462 assignments (Cornuet *et al.* 1999; Wang 2002; Saenz-Agudelo *et al.* 2009). Likewise,
463 assignment error rate was lower when specifically involving immigrant parents, but only
464 when dispersal rates were low (1 and 2%) such that immigrants originated from more
465 genetically differentiated populations.

466

467 At lower dispersal rates, the accuracy of inferences was not improved by increasing from 15
468 to 20 loci, but did when 30 loci were used (from 40% using 15 and 20 loci, to 29% using 30
469 loci). While at high dispersal rates, error decreased from 85% using 15 loci, to 40% using 20
470 and 30 loci. In all cases, excluding half-siblings reduced the error to < 10% using 20 loci and
471 < 6% when using 30. This indicates the improvement provided by increasing the number of
472 loci at both low and high dispersal rates for all relationship types except for half-siblings.

473

474 Overall, mother-offspring and full-sibling relationships were consistently the most reliably
475 assigned relationship type in most simulations, although assignment reliability at the highest
476 dispersal rate (20%, S2.4) was poor (assignment error rate = 57 and 72% for MO and FS

477 respectively) when using only 15 loci, in contrast to the very poor assignment error rate of
478 maternal half-siblings, which was consistently higher than 56% in all simulations. Given that
479 our findings are extendable to the numerous examples of partially sampled and polygamous
480 natural systems, we advocate that polyandry should be allowed when COLONY, or
481 equivalent software, is used, but that the pairwise assignment involving half-siblings should
482 be considered separately from the other, more reliable, assignments, if at all.

483

484 The reliability of assignment probability provided by COLONY to reflect the confidence in
485 assignment depended on the ecological circumstances mimicked by the simulations (i.e.,
486 increased dispersal rate reduced its reliability). Because the probability is constrained by the
487 data provided, as the data become more complex – as happens with the increase of dispersal
488 rate - then the likelihood that these P -values reflect reality diminishes. This ecological context
489 dependence is an undesirable property that undermines the value of the metric for practical
490 applications where the true ecological context is not known. Although the uncertainty in
491 assignment is not easily resolvable, our simulations support the suggestion that increasing the
492 number of loci improves the confidence of the assignment probability (Harrison *et al.* 2013).
493 This improvement occurred for all parent-offspring and full sibling relationships with error
494 rates $< 10\%$ for all simulations with 20 or 30 loci independently of P . The increase of the
495 number of loci also increased the reliability of P for half-siblings but only when dispersal rate
496 was high, with average increases of ca. 1.12 and 1.1 times, respectively, for 20 and 30 loci.
497 However, the fact that all error rates of half-siblings were $> ca. 60\%$ independently of the
498 values of P (Fig. S3) indicates a lack of accuracy of these relationship types despite the
499 increase of the number of loci.

500

501 As the age of parents increased, the assignment error rate decreased for all relationship types.
502 Erroneous assignments are more likely to occur between related individuals (e.g., aunt-
503 offspring relationships) than between random individuals, since the former are genetically
504 more distinct. Therefore, we interpret this outcome as reflecting the fact that, probabilistically,
505 older individuals should have fewer close relatives alive amongst the potential parent sample.
506 Assignments involving older parents had lower error rates for all but the two scenarios with
507 the highest dispersal rates (S2.3 and S2.4) independently of the number of loci used, which is
508 likely due to the confounding influence of lower genetic differentiation between the three
509 subpopulations. Although the age of the parents is a difficult variable to measure in field
510 situations, it is of particular interest for harvested or culled species, such as mink, that are
511 under long-term control. Indeed, that population age structure is driven downwards to consist
512 primarily of juveniles and subadults with increasing years of control (Melero *et al.* 2015).
513 This process ultimately could lead to a decrease in the accuracy of pedigree inferences
514 through the duration of a control programme.

515

516 Nevertheless, despite clear limitations and the salient grounds for greater caution than has
517 hitherto been applied (e.g., by Lambin *et al.* 2012; Kormann *et al.* 2012), the parentage
518 reconstruction approach scrutinised in this paper nevertheless provides information on
519 dispersal distance that would otherwise be unobtainable. The importance of the error rate, and
520 resulting potential bias in estimating dispersal parameters, obviously depends on the specific
521 application, since error rates that may be intolerable in a heritability or animal model analysis
522 may make little difference in inferences about some populations-level variables such as
523 dispersal rate along gradients of density. Artificially inflating the tail of a dispersal
524 distribution, a consequence of assignment error rate, may lead to overestimations of range

525 spread (Kot *et al.* 1996) and predicted recolonisation rate, but our analyses imply that sub-
526 setting dispersal distance data by relationship type would provide a way to detect any such
527 bias, if present.

528

529 *Conclusions*

530 Overall, although the simulations that we implemented could easily be repeated or extended
531 to mimic specific study systems, many of our findings on the accuracy of parentage
532 relationships assignments are applicable to other systems and could be used as rules-of-thumb
533 for situations where ecological information is limited. Additionally, the inherent weakness
534 identified here apply not only to the use of inferred pedigree assignments, but also to other
535 current methodologies aiming to address similar questions in partially sampled populations,
536 even though the specific sources of error and bias may vary. The use of large numbers of
537 SNPs for example, provides for greater subsampling of the genome than microsatellites, but
538 in most realistic field scenarios, the limitations of partial sampling of the pool of potential
539 parents and of the number of available loci will remain (e.g., Norman & Spong 2015). Our
540 findings provide an alternative solution to identify and reduce the limitations of ecological
541 inferences from pairwise analyses of wild populations.

542

543 Alternatively, when using inferred pairwise relationships from partially sampled populations
544 to estimate ecological parameters, such as dispersal distance, a conservative approach is to use
545 only mother-offspring and full-sibling relationships, and not use inferred half-sibling
546 relationships. Whilst this approach could potentially be wasteful of data, under no scenario
547 were these relationships sufficiently reliable to inform, rather than bias, data sets. Since the
548 utility of P and age and origin of the parents depends on the dispersal rate, an exercise such as

549 that demonstrated in Scenario 1 (i.e., simulating the population of interest) should help to
550 identify the most reliable relationship types and their levels of influence.

551

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560

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690

691 **Data Accessibility**

692 Empirical field data of the culled American mink in NE Scotland (ID, sex, age, year) and their
693 genotypes at 15 microsatellites loci; initial simulation data for S1 (P0 and IP0_i), and S2 and
694 S3 (P0_{Dec}, P0_{Spey} and P0_{Tay}); and R codes for the mink life-history parameters used for the
695 simulations can be found archived in Dryad. DOI: <http://dx.doi.org/10.5061/dryad.cj0k2>
696 The Nookie software (Anderson & Dunham 2008) and its source code is freely available at
697 <https://github.com/eriqande/nookie>.

698

699 **Author Contributions**

700 Y.M., M.K.O. and X.L. conceived the study questions and design. Y.M. and M.K.O.
701 genotyped the culled mink, performed the pedigree analyses and estimated dispersal distance.
702 Y.M. performed the simulations and the statistical analyses. X.L. supervised the research.
703 Y.M., M.K.O. and X.L. interpreted the results and wrote the manuscript.

704

705 **Fig. 1** Empirical data from the NE Scotland mink population. (a) The spatial structure: a
706 central population (dots, $n = 728$ sampled individuals) and two peripheral populations (white
707 squares, $n = 117$ and yellow squares, $n = 134$), as used for Scenario 1. For Scenario 2 we used
708 mink data from three main river catchments: the Spey (white squares), Tay (yellow squares)
709 and Dee (red dots, $n = 189$). Estimated natal capture locations (orange triangles), offspring
710 post-dispersal capture locations (blue dots), estimated dispersal distance with $P < 0.8$ (blue
711 dashed lines) and ≥ 0.8 (green solid lines) and corresponding histograms derived from
712 inferred: (b) mother-offspring, (c) full-sibling and (d) maternal half-sibling relationships.

713 **Fig. 2** Simplified scheme of simulated mink reproduction, not including immigration from
714 peripheral areas (full details in Fig. S1a). P0 stands for the central population. OF $_j$ stands for
715 the offspring of each j^{th} generation 0-3, where OF0 is in Hardy-Weinberg equilibrium. Light
716 grey shows offspring, medium grey for one-year survivors, and dark grey for two-year
717 survivors. Individuals inside a box show the pool of parents reproducing that year, solid
718 arrows link surviving individuals, dashed arrows link parents and offspring. Subsampling was
719 done in year three, when three cohorts and their offspring are present.
720

721 **Fig. 3** Estimated individual dispersal distance (in m, denoted with circles) derived from
722 inferred pairwise assignments, in relation to the assignment probability (P) of these
723 assignments. Lines relate to the best fit linear model predictions of the relation between
724 distance and P for mother-offspring (black outlines unfilled, $n = 312$), full-siblings (full grey
725 circles and dark grey lines, $n = 38$) and maternal half-siblings (unfilled light grey outlines and
726 light grey lines, $n = 756$) relationship types. Shaded areas bounded by dotted lines show the
727 95 % CIs. Observations with $P \sim 1$ on the x -axis have had a slight lateral offset applied to aid
728 visualisation.
729

730 **Fig. 4** Assignment error rate (false positives are circles scoring 0% error and $P \geq 0.8$; false
731 negatives are dots scoring 100% and $P < 0.5$), and its model-derived predictions (lines) in
732 relation to the assignment probability P under Scenario 1, for: (a) mother-offspring (black
733 circles and lines, $n = 312$) and father-offspring (grey circles and grey shadowed lines, $n =$
734 239), and (b) full-siblings (black circles and lines, $n = 38$) and maternal half-sibling
735 relationship type (light grey circles and grey shaded area, $n = 756$). Continuous lines relate to
736 the estimated fit setting values for other parameters as origin = local and age = two years old
737 (median); dashed lines denote the 95 % CIs.
738

739 **Fig. 5** Assignment error rate for each inferred pairwise relationship type in the simulations for
740 Scenario 1 and Scenario 2 (S2.1-S2.4) with r_d standing for the dispersal rate.

741

742

743 **Supporting Information**

744 Additional supporting information may be found in the online version of this article.

745

746 **Fig. S1** Full simulation scheme of: (a) Scenario 1 and (b) Scenario 2.

747

748 **Fig. S2** Assignment error rate and its model-derived predictions in relation to the assignment
749 probability P for mother-offspring, father-offspring, full-siblings and half-sibling relationship
750 type for simulations S2.1-S2.4 all with 15 loci.

751

752 **Fig. S3** Assignment error rate and its model-derived predictions in relation to the assignment
753 probability P for mother-offspring, father-offspring, full-siblings and half-sibling relationship
754 type for simulations S2.1 and S2.4 all with 20 and 30 loci.

755

756 **Table S1** Pairwise genetic differentiation and heterozygosity of the simulated populations at
757 Year 1 for Scenario 2.

758

759 **Table S2** Number of alleles, allelic richness and heterozygosity per locus and population of
760 the simulated populations at Year 1 for (a) Scenario 1, (b) Scenario 2 and (c) Scenario 3.

761

762 **Table S3** Percentage of assignment error rate of inferred assignments per relationship type
763 categorised as false positives and true assignments in relation to the assignment probability
764 (P) for Scenario 1 and Scenario 2.

765

766 **Table S4** Percentage of assignment error rate of inferred assignments per relationship type
767 categorised as false positives and true assignments in relation to the assignment probability
768 (P) for Scenario 3.

769