Assessing the dynamics of hybridization through a matrix modelling approach

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1   **Title**

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Highlights

- We used projections to investigate genomic extinction in hybridizing populations
- Hybridization leads to genomic extinction in the absence of reproductive isolation
- Rare or depleted species are particularly vulnerable to genomic extinction
- Genomic extinction depends mainly on demographic parameters of parental species
- Maintaining healthy and abundant populations prevents genomic extinction

Abstract

Hybridization affects the evolution and conservation status of species and populations. Because the dynamics of hybridization is driven by reproduction and survival of parental and hybrid individuals, demographic modelling is a valuable tool to assess the effects of hybridization on population viability, e.g., under different management scenarios. While matrix models have been used to assess the long-term consequences of hybridization between crops and wild plants, to our knowledge they have not been developed for animal species. Here, we present a new matrix population model to project population dynamics in a system with two parental species or populations that interbreed. We consider the dynamics of males and females of the two parental groups as separate components, each described by species-specific vectors of initial abundance and projection matrices. Then we model hybridization as the production of hybrid fertile offspring due to the interaction of reproductive individuals of different parental species. Finally, we apply the model to two real-world case studies regarding a terrestrial and a marine mammal species in the presence of hybridization. Specifically, we investigate 1) the genomic extinction probability of two interbreeding dolphin species within a semi-enclosed gulf in Greece, under different hybrids' fitness scenarios, 2) the possible outcomes of wolf x dog hybridization events for an expanding wolf population in Italy, under different reproductive isolation scenarios, 3) the sensitivity of the probability of genomic extinction to the main demographic parameters in the two case studies.

1.   Introduction

Hybridization, defined as the interbreeding of individuals from genetically distinct populations, regardless of their taxonomic status (Allendorf et al., 2001) is recognized as a relatively common phenomenon both in plants and animals (Hewitt, 1988; Olden et al., 2004; Grabenstein and Taylor,

2018). Hybridization is most commonly observed between otherwise allopatric taxa that come into contact due to natural (natural hybridization) or anthoropogenic causes (anthropogenic hybridization, e.g., human encroachment or the release of non-native taxa). The widespread occurrence of natural hybridization is raising attention due to its implications in evolutionary biology (Abbott et al., 2016). Additionally, the increasing occurrence of anthropogenic hybridization is considered a significant threat to biodiversity (Rhymer and Simberloff, 1996; Seehausen et al., 2008; Crispo et al., 2011).

Hybridization can have different consequences for the evolution and conservation of species. If the fitness of hybrids is lower than that of parentals, hybridization can reinforce reproductive isolation between incompletely isolated species (Barton and Hewitt, 1985), but it can also cause extinction through demographic swamping (Allendorf et al., 2001; Wolf et al., 2001). If the fitness of the hybrids is greater than or equal to that of parental individuals, hybridization can cause fusion of species (Seehousen et al., 1997; Allendorf et al., 2001), genetic swamping (Allendorf et al., 2001), transfer of genetic material between species (potentially facilitating their adaptive evolution; Grant and Grant, 1992; Verhoeven et al., 2011), and the origin of new species (DeMarais et al., 1992). Understanding the potential consequences of hybrization is important to unveil evolutionary mechanisms such as how species integrity is maintained in the face of interspecific (and often intergeneric) gene flow (Crossman et al., 2016) and how new species can arise from the introduction of new allelic combinations generated by hybridization. Furthermore, understanding anthropogenic hybridization dynamics can help identify effective and timely management actions for threatened species. To this end there has been an effort to calibrate management actions to the severity of the threat by classifiying hybridization in different types (Allendorf et al., 2001; Bohling et al., 2016) based *inter alia* on hybrids fitness and relative abundance of admixed individuals (i.e., hybrids prevalence, Santostasi et al., 2019). Depending on the hybridization type, a variety of management actions can be more effective or feasible to avoid genomic extinction: from hybrids removal and/or sterilization to the management of the human disturbances that cause hybridization in the first place (Allendorf et al., 2001; Bohling et al., 2016).

It is often difficult to define hybridization types, *inter alia* because of lack of information about admixed individuals prevalence and fitness. Projection models can tackle this uncertainty by simulating hybridization dynamics under different biological/evolutionary scenarios (Wolf et al., 2001; Fredrickson and Hedrick, 2006). Sensitivity analysis and/or the simulation of different

92 possible management actions can also be used to provide management recommmendatios (Crouse

93 et al 1987; Cross and Beissinger 2001).

94 The first attempts to model hybridization-extinction dynamics had a genetic focus and were based

95 on changes in allelic frequencies at one or more loci (Huxel, 1999; Ferdy and Austerlitz, 2002).

96 Compared to genetic models, ecological models place a greater emphasis on life-history traits, by

97 explicitly examining the effects of fitness parameters (e.g., survival and reproductive rates) on the

98 hybridization outcome. Within the ecological approach, two types of model have been used to

99 model hybridization dynamics (Hall and Ayres, 2008): 1) individual-based models that simulate the

100 contribution of each individual to the hybridization dynamics of the entire population (e.g.,

101 Thompson et al., 2003; Hooftman et al., 2007), and 2) population-based models that can be used

102 when the mean fitness parameters of the main demographic stages are available (e.g., Wolf et al.,

103 2001; Campbell et al., 2002). Both modelling approaches were applied to hybridization in plant

104 species (Hall and Ayres, 2008; Todesco et al., 2016). However, to our knowledge, few studies used

105 individual-based models (Fredrickson and Hedrick, 2006; Nathan et al., 2019) and none used

106 population-based models to simulate hybridization dynamics in animal species.

107

108 Here, we develop a population-based approach to project the dynamics of animal hybridization. By

109 using a stage-based matrix model, and grouping individuals into genealogical categories, each

110 described by their mean fitness parameters (i.e., age-specific survival, per capita fertility rate), our

111 approach overcomes the need of realistic and accurate data at the individual level. To provide a

112 practical example of this modeling approach, we illustrate its application to two case studies. The

113 first refers to two delphinid species belonging to different genera, that interbreed in the Gulf of

114 Corinth, Greece (Bearzi et al., 2016; Antoniou et al., 2019): the striped dolphin *Stenella*

115 *coeruleoalba* and the common dolphin *Delphinus delphis*. The Mediterranean subpopulation of the

116 former species is classified as Vulnerable, and the latter as Endangered in the IUCN Red List

117 (Bearzi et al., 2003; Aguilar and Gaspari, 2012). Within the Gulf of Corinth, however, the

118 subpopulation of common dolphin would qualify as Critically Endangered due to its small size

119 (point estimate 22 individuals; Santostasi et al., 2016) and high (≥50%) probability of extinction in

120 three generations (Santostasi et al., 2018). Recently confirmed hybridization with the much more

121 abundant striped dolphin population (point estimate 1331 individuals; Santostasi et al., 2016)

122 threatens the persistence of common dolphins in the Gulf of Corinth (Antoniou et al., 2019;

123 Santostasi et al., 2018). We regard this as a case of anthropogenic hybridization, considering that

124 the steep decline of common dolphins due to anthropogenic impacts (Bearzi et al., 2003) locally

125 leads to a lack of available mates and to mating with more abundant species (Frantzis and Herzing,

126   2002; Antoniou et al., 2019). The possible hybridization outcomes for the two isolated dolphin

127   subpopulations in the Gulf of Corinth have not been previously explored (Antoniou et al., 2019).

128

129   In the second case study we evaluate the possible outcomes of hybridization between the wolf

130   (*Canis lupus*) and its domestic counterpart, the dog (*Canis lupus familiaris*). Hybridization between

131   wolves and dogs has been documented in several European countries and represents a well-known

132   threat to wolf conservation (Boitani, 2000; 2003). Still, little is known about the possible outcomes

133   of hybridization between wolves and dogs. Hybridization with dogs may represent a problem for

134   recovering wolf populations expanding into human-dominated landscapes, where few potential wolf

135   mates compete with free-ranging dogs that are abundant and widespread (Randi, 2008; Galaverni et

136   al., 2017). Although reproductive isolation due to behavioral or physiological barriers has been

137   often assumed to contrast introgressive hybridization (Vilà and Wayne, 1999; Randi and Lucchini,

138   2002; Galaverni et al., 2017), admixed wolf populations are increasingly being reported where

139   wolves live in close contact with free-ranging dogs population (e.g., Italy: Caniglia et al., 2013;

140   Galaverni et al., 2017; Salvatori et al., submitted).

141

142   The matrix model presented here allows quantitatively assessing the possibles outcomes of

143   hybridization (i.e., genomic extinction vs persistence) under different fitness scenarios. Providing

144   management recommendations is beyond the scope of this study, our model represents a valuable

145   tool to inform management once appropriately customized and parametrized. While our focus is on

146   mammalian species, the analytical approach described here is valid for other taxa, and it could be

147   adopted to project the dynamics of admixed populations for situations entailing both natural and

148   anthropogenic hybridization.

149

150   **2.   Methods**

151   **2.1 General model**

152   We consider a system in which there are two parental groups (T1 and T2) that interbreed and

153   produce an admixed progeny (H). We regard the admixed progeny as an absorbing state

154   encompassing all offspring produced by pairs of different parental groups, where at least one of the

155   parents is an admixed individual (Wolf et al., 2001). The possible crosses considered and the

156   produced progeny are listed in Table 1. Based on the assumed dynamics of interbreeding and

157   production of offspring, we project the future abundance of the three mixing groups over time. We

158   present the projections step by step with linear equations and we introduce the equivalent matrix

159 formulation to calculate the asymptotic growth rate and perform sensitivity analyses. Finally, we

160 discuss the behavior of the model by applying it to our case studies.

161

162 **Table 1.** Possible crosses in the system formed by two parental taxa (T1 and T2) and admixed

163 individuals (H).

Female parent	Male parent	Offspring
T1	T1	T1
T2	T2	T2
T1	T2	H
T2	T1	H
H	T1	H
H	T2	H
T1	H	H
T2	H	H
H	H	H

164

165 **2.1.1 Model equations**

166 We assume that parental and admixed groups have similar life cycles, with three age classes:

167 offspring (*C* individuals up to 1 year old), juveniles (*J* non-reproductive individuals up to 3 years

168 old) and adults (*A* reproductive individuals $\geq$ 3 years old). The transitions among age classes are

169 described by survival parameters (S) and the reproductive parameters are described by per capita

170 fertility rates (f). At time t, the total number of individuals of the different groups (the parentals and

171 the admixed) is:

172

173 $N_{\text{TOT}} = N_1 + N_2 + N_{\text{H}},$

174

175 where N_1 is the total number of individuals in group 1, N_2 is the total number of individuals in

176 group 2 and N_{H} is the total number of admixed individuals.

177

178 We model the dynamics of females and males separately. Below, we show the equations for

179 females. Each group at time t is composed by females (f) and males (m) belonging to the three

180 different age classes:

181

182 $N_{1\text{f}}(t) = C_{1\text{f}}(t) + J_{1\text{f}}(t) + A_{1\text{f}}(t),$

183 $N_{2\text{f}}(t) = C_{2\text{f}}(t) + J_{2\text{f}}(t) + A_{2\text{f}}(t),$

184 $N_{Hf}(t) = C_{Hf}(t) + J_{Hf}(t) + A_{Hf}(t).$

185

186 We assume that the probability of reproduction between adult females belonging to one group and

187 adult males belonging to one of the three other groups, is proportional to the relative abundances of

188 adult males $\alpha(t)$, $\beta(t)$ and $\gamma(t)$ which are given by the ratio between adult males (A_m) of one group

189 divided by the total number of adult males $TOT_m(t)$:

190

191 $\alpha(t) = A_{1m}(t) / TOT_m(t),$

192 $\beta(t) = A_{2m}(t) / TOT_m(t),$

193 $\gamma(t) = A_{Hm}(t) / TOT_m(t).$

194

195 Therefore, the number of offspring belonging to the parental group 1 produced at time t+1 is given

196 by the number of females surviving to time t+1, $A_{1f}(t)Sa_1$, multiplied by their per capita fertility rate

197 (f_1) multiplied by the relative abundance of adult males of group 1 $\alpha(t)$. The number of offspring

198 belonging to the parental group 2 produced at time t+1 is therefore:

199

200 $C_2(t+1) = A_{2f}(t)f_2Sa_2\beta(t).$

201

202 The number of admixed offspring produced by e.g., the crossing between females of the group 1

203 and males of the group 2 is calculated as $A_{1f}(t)f_1Sa_1\beta(t)$ and the total number of admixed offspring

204 at time t +1 is given by the sum of the contribution of all the possible crosses (Table 1):

205

206 $C_H(t+1) = A_1(t)f_1Sa_1\beta(t) + A_2(t)f_2Sa_2\alpha(t) + A_1(t)f_1Sa_1\gamma(t) + A_2(t)f_2Sa_2\gamma(t)$

207 $+ A_H(t)f_hSa_h\alpha(t) + A_H(t)f_hSa_h\beta(t) + A_H(t)f_hSa_h\gamma(t),$

208

209 where $A_{2f}(t)$ is the number of adult females of group 2 at time t, Sa_1 and Sa_2 are group-specific adult

210 survival values, f_1 and f_2 are the group-specific per capita fertility rates. Because we model

211 separately males and females, the number of offspring of each sex produced every year by each

212 group is obtained by multiplying the total number of offspring by 0.5, assuming a 50:50 sex ratio at

213 birth:

214

215 $C_{1f}(t+1) = C_{1m}(t+1) = C_1(t+1)0.5,$

216 $C_{2f}(t+1) = C_{2m}(t+1) = C_2(t+1)0.5,$

217 $C_{Hf}(t+1) = C_{Hm}(t+1) = C_H(t+1)0.5.$

218

219   Depending on the species mating system, hybridization can be modelled in different ways. For

220   example, for species in which only the dominant individuals reproduce, it can be convenient to

221   model hybridization at the level of the formation of the reproductive pairs. We consider this

222   situation when dealing with the wolf x dog case study (section 3.2).

223

224   The number of female adults and juveniles at time t + 1 for the three groups are obtained as follows

225   (the equations are showed only for group 1):

226

227    $J_{1f}(t+1) = C_{1f}(t)Sc_1$

228    $A_{1f}(t+1) = J_{1f}(t)Sj_1 + A_{1f}(t)Sa_1$

229

230   where Sc, Sj and Sa are respectively survival probabilities for offspring, juveniles and adults. The

231   total number of females at time t + 1 is therefore:

232

233    $N_{1f}(t+1) = A_{1f}(t)f_1Sa_1\alpha(t)0.5 + C_{1f}(t)Sc_1 + J_{1f}(t)Sj_1 + A_{1f}(t)Sa_1$

234    $N_{2f}(t+1) = A_{2f}(t)f_2Sa_2\beta(t)0.5 + C_{2f}(t)Sc_2 + J_{2f}(t)Sj_2 + A_{2f}(t)Sa_2$

235    $N_{Hf}(t+1) = [A_{1f}(t)f_1Sa_1\beta(t) + A_{2f}(t)f_2Sa_2\alpha(t) + A_{1f}(t)f_1Sa_1\gamma(t) + A_{2f}(t)f_2Sa_2\gamma(t) + A_{Hf}(t)f_hSa_h\alpha(t) +$

236    $A_{Hf}(t)f_hSa_h\beta(t) + A_{Hf}(t)f_hSa_h\gamma(t)]0.5 + C_{Hf}Sc_h + J_{Hf}(t)Sj_h + A_{Hf}(t)Sa_h$

237

238   The number of male individuals in the three groups is obtained with the following equations:

239

240    $N_{1m}(t+1) = A_{1f}(t)f_1Sa_1\alpha(t)0.5 + C_{1m}Sc_1 + J_{1m}(t)Sj_1 + A_{1m}(t)Sa_1$

241    $N_{2m}(t+1) = A_{2f}(t)f_2Sa_2\beta(t)0.5 + C_{2m}Sc_2 + J_{2m}(t)Sj_2 + A_{2m}(t)Sa_2$

242    $N_{Hm}(t+1) = [A_{1f}(t)f_1Sa_1\beta(t) + A_{2f}(t)f_2Sa_2\alpha(t) + A_{1f}(t)f_1Sa_1\gamma(t) + A_{2f}(t)f_2Sa_2\gamma(t)$

243    $+ A_{Hf}(t)f_hSa_h\alpha(t) + A_{Hf}(t)f_hSa_h\beta(t) + A_{Hf}(t)f_hSa_h\gamma(t)]0.5 + C_{Hm}Sc_h + J_{Hm}(t)Sj_h + A_{Hm}(t)Sa_h$

244

245   **2.1.2 Matrix formulation**

246   The model above can be conveniently formulated as $N(t+1) = AN(t)$ where:

247

248    $$N(t) = [C_1(t)\, J_1(t)\, A_1(t)\, C_2(t)\, J_2(t)\, A_2(t)\, C_H(t)\, J_H(t)\, A_H(t)]^T$$

249

250   and

$$A = \begin{pmatrix}
0 & 0 & f_1 Sa_1 \alpha(t)0.5 & 0 & 0 & 0 & 0 & 0 & 0 \\
Sc_1 & Sj_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & Sa_1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & f_2 Sa_2 \beta(t)0.5 & 0 & 0 & 0 \\
0 & 0 & 0 & Sc_2 & Sj_2 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & Sa_2 & 0 & 0 & 0 \\
0 & 0 & f_1 Sa_1 (\beta(t) + \gamma(t))\,0.5 & 0 & 0 & f_2 Sa_2\,(\alpha(t) + \gamma(t))\,0.5 & 0 & 0 & f_h Sa_h(\alpha(t) + \beta(t) \\
0 & 0 & 0 & 0 & 0 & 0 & Sc_h & Sj_h & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Sa_h
\end{pmatrix}$$

251

252   In the following section, we consider two real-world scenarios illustrating the relevance of the

253   model described above. All the analyses are performed with the software R (R core team, 2018).

254

255   **2.2 Applications**

256   **2.2.1 Dolphin model**

257   We built stage-based matrices (Fig. 1; Taylor et al., 2007) for the two parental species and the

258   admixed individuals with the following stages: calf (individuals up to 1 year old), juveniles (non-

259   reproductive individuals up to species-specific age of first reproduction reported by Taylor et al.,

260   2007) and adults (individuals that reached the age of first reproduction). We used the available

261   stage-specific demographic parameters for the target populations in the Gulf of Corinth, Greece

262   (Santostasi et al., 2016) and we used parameters estimated for other populations of the same species

263   for the non available stage-specific demographic parameters (see Table 2 and Appendix A for

264   details about model parametrization). We built three fitness scenarios for admixed individuals

265   (Table 2): i) in the Null Model we assumed that admixed individuals had intermediate demographic

266   traits between the two species, ii) in the Hybrid Vigour scenario we assumed that hybrids have

267   higher survival (the upper 95% confidence limit estimated for the population by Santostasi et al.,

268   2016) and annual per capita fertility rate (the highest annual pregnancy rate reported for Atlantic

269   common dolphin subpopulations reported in Murphy et al., 2009) and that they become

270   reproductively mature earlier (having the youngest age of first reproduction between the two

271   parental species), iii) in the Outbreeding Depression scenario we assumed that admixed individuals

272   have lower survival (the lower 95% confidence limit estimated for this population by Santostasi et

273   al., 2016) and annual per capita fertility rate (the lowest annual pregnancy rate reported for Atlantic

274   common dolphin subpopulations reported in Murphy et al., 2009), and that they become

275   reproductivley mature later (having the oldest age of first reproduction between the two parental

276   species).

277
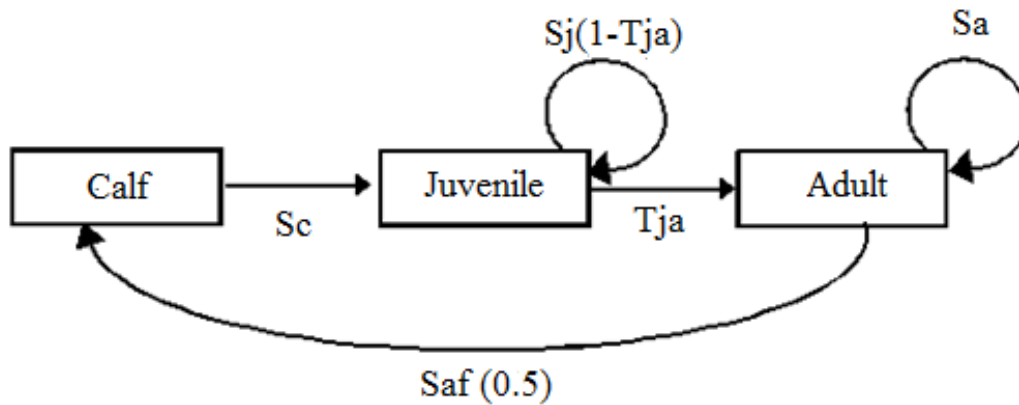
278

279 **Figure 1**. Life cycle used for the dolphin case study. Parameters are: Sc = survival of calves, Tja =

280 transition probability from the juvenile to the adult stage modelled as the survival of juveniles (Sj)

281 raised power of age of first reproduction - 1, Sa = survival of adults, f = per capita fertility rate,

282 approximated as the annual pregnancy rate.

283

284 **Table 2.** Demographic parameters used for projecting the abundance of striped and common

285 dolphins in the presence of hybridization using alternative parental and admixed individual fitness

286 scenarios.

Scenario	All scenarios		Null	Outbreeding	Hybrid Vigour
Individuals	Striped dolphin	Common dolphin	Admixed dolphin	Admixed dolphin	Admixed dolphin
Initial abundance	1331[1]	22[1]	55[1]	55[1]	55[1]
Per capita fertility rate (f)	0.25[2]	0.26[3]	0.26	0.19[4]	0.33[5]
Age of first reproduction	11[2]	9[3,6]	10	11	9
Calf survival (Sc)	0.80[7]	0.80[7]	0.80	0.80[7]	0.80[7]
Juvenile survival (Sj)	0.94[1]	0.94[1]	0.94	0.92[1]	0.96[1]
Transition probability from the juvenile to the adult stage (Tja)	0.94[(10)]	0.94[(8)]	0.94[(9)]	0.92[(10)]	0.96[(8)]
Adult survival (Sa)	0.94[1]	0.94[1]	0.94	0.92[1]	0.96[1]

287 [1]Gulf of Corinth, Greece (Santostasi et al., 2016); [2]Western Mediterranean (Calzada et al., 1995);

288 [3]Atlantic (Murphy et al., 2009); [4]Iberian (Murphy et al., 2009); [5]control group (Murphy et al.,

289 2009); [6]Eastern North Atlantic (Mannocci et al., 2012); [7]theoretical calculation by Taylor et al.,

290 (2007).

291

292   The mating systems of odontocete cetaceans (toothed whales) have been reported as either

293   polygynous (some males with multiple partners) or polygynandrous (both males and females with

294   multiple partners; Murphy et al., 2007). We assumed that mature females belonging to one species

295   would reproduce with mature males belonging to the same species, the other species or the admixed

296   individuals, proportionally to their relative abundance. We used deterministic projections (i.e., with

297   constant parameters) to compare the predicted time of extinction for the two species with and

298   without the hybridization effect. The matrix formulation corresponding to the dolphin model is

299   presented below. The subscript Sc refers to striped dolphin, the subscript Dd refers to common

300   dolphins the subscript h refers to admixed individuals. In the Appendix A we show the

301   corresponding R code, the linear equations, and we describe how to incorporate demographic

302   stochasticity.

303

304

$$
\begin{pmatrix}
0 & 0 & f_{Sc}Sa_{Sc}\,\alpha\,(t)0.5 & 0 & 0 & 0 & 0 & 0 & 0 \\
Sc_{Sc} & (1-Tja_{Sc})Sj_{Sc} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & Tja_{Sc} & Sa_{Sc} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & f_{Dd}Sa_{Dd}\,\beta\,(t)0.5 & 0 & 0 & 0 \\
0 & 0 & 0 & Sc_{Dd} & (1-Tja_{Dd})Sj_{Dd} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & Tja_{Dd} & Sa_{Dd} & 0 & 0 & 0 \\
0 & 0 & f_{Sc}Sa_{Sc}(\,\beta\,(t)+\,\gamma\,(t))\,0.5 & 0 & 0 & f_{Dd}Sa_{Dd}\,(\,\alpha\,(t)+\,\gamma\,(t))0.5 & 0 & 0 & f_{h}Sa_{h}(\,\alpha\,(t)+\,\beta\,(t) \\
0 & 0 & 0 & 0 & 0 & 0 & Sc_{h} & (1-Tja_{h})Sj_{h} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & Tja_{h} & Sa_{h}
\end{pmatrix}
$$

305

2.2.2. Wolf x dog model

306

307 To model wolf life cycle we used the pre-breeding stage-structured model described in Marescot et
308 al,. (2012), that simplifies the complex wolf social structure in four age- and social-stages:
309 yearlings, individuals in dispersal, subordinates, and breeders (Fig. 2). Only the dominant couple
310 breeds, producing a single litter of pups every year. The pups that survived their first year
311 (yearlings), may survive to their second year (probability Sj) and disperse (probability Pdi), or they
312 may remain in the natal pack (probability 1 - Pdi) as subordinates (sexually mature individuals 1 to
313 2 years old, inhibited from breeding by the presence of breeders; Zimen, 1975). The model makes
314 the following assumptions (Marescot et al., 2012): 1) if subordinates survive (with probability Ss)
315 one year in the natal pack they will then leave and become individuals in dispersal by their 3rd year
316 of age; 2) the subordinates never directly transition to being breeders; 3) individuals in dispersal can
317 either die or survive (with probability Sd), and gain access to reproduction (with probability Pes) or
318 remain dispersers (with probability 1-Pes); 4) breeders never lose their status remaining in the
319 breeder stage and surviving with probability Sa. To run the projections we used the demographic
320 parameters that were estimated for the expanding wolf population in the Italian Alps (Marucco et
321 al., 2009; 2010) in which hybridization has not been detected yet (Fabbri et al., 2007). The details
322 about model parametrization are shown in Appendix B.

323

324
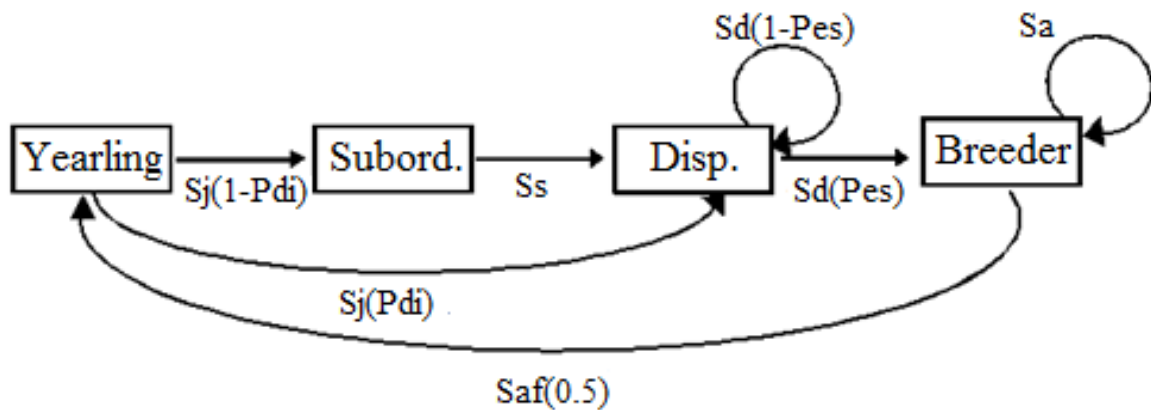
Figure 2. Life cycle for the wolf case study. Parameters are: Sj = survival of yearlings, Ss = survival of subordinates (yearlings and adults), Sd = survival of dispersers (yearlings and adults), Sa = survival of breeders, f = annual per capita fertility rate approximated as the litter size, Pdi = probability of going in dispersal, Pes = probability of establishing a pack.

329

330 We modeled hybridization at the level of the formation of the reproductive pairs. Hybridization was
331 documented in the almost totality of cases to occur between female wolves and male dogs (Randi et
332 al., 2008; Godinho et al., 2011, Pacheco et al., 2017), while the opposite case of hybridization

333   between male wolves and female dogs appears to be rare (Hindrickson et al., 2012). Therefore, in

334   the model we did not consider reproductive pairs formed by male wolves and female dogs. For

335   simplicity, we did not model the occurrence of backcrossing to dogs (the reproduction of admixed

336   individuals and dogs; Table 3). We assumed that a constant number of reproductive events happen

337   every year between female wolves and male dogs (parameter *frd*). The probability of the formation

338   of a reproductive pair between a female wolf and male wolf at time t +1 is therefore expressed as

339   the product between the abundance of wolf females in dispersal (Df_w) by their survival (Sd_w) by the

340   probability that a female wolf establishes a pack (Pes_w) by the relative abundance of wolf males in

341   dispersal $\alpha(t)$. The probability of formation of wolf-dog reproductive pairs, and of reproductive

342   pairs in which at least one individual is admixed, is formulated in Table 3.

343

344   **Table 3.** Probability of formation of the reproductive pairs considered in the model. $Df_w =$

345   abundance of wolf females in dispersal, $Pes_w =$ probability that a female wolf establishes a pack,

346    $Pes_h =$ probability that an admixed female establishes a pack, frd = constant annual frequency of

347   reproductive events between female wolves and male dogs, $\alpha(t) =$ relative abundance of male

348   wolves in dispersal, $\gamma(t) =$ relative abundance of admixed males in dispersal.

Female parent	Male parent	Probability
W	W	$Df_w sd_w pes_w \alpha(t)$
W	D	$Df_w sd_w pes_h frd(t)$
W	H	$Df_w sd_w pes_h \gamma(t)$
H	W	$Df_w Sd_h pes_h \gamma(t)$
H	H	$Df_w Sd_h pes_h \gamma(t)$

349

350   For wolves, we used the probability of establishing a pack calculated by Marescot et al., (2012).

351   Such annual probability varies uniformly between 0.3 to 0.7. For the Null Model, we assigned the

352   the same average value (Pes=0.5) to wolves and admixed individuals. We produced two alternative

353   scenarios of reproductive isolation by simulating a reduced probability of establishing a pack for

354   admixed females. In one scenario (Reproductive Isolation 1), we attributed the average value (0.5)

355   to wolves and the minimum value (0.3) to the admixed individuals. In the second scenario

356   (Reproductive Isolation 2) we assigned the maximum probability of establishing a pack to wolves

357   (0.7) and the minimum probability (0.3) to the admixed individuals (Table 4). We used the

358   prevalence of hybrids as a measure to define the type of hybridization reached at the end of the

359   projection time-frame. The matrix formulation corresponding to the wolf x dog model is presented

360   below.

361

$$\begin{pmatrix}
0 & 0 & 0 & f_w Sa_w 0.5 & 0 & 0 & 0 & 0 \\
Sj_w pd_w & 0 & Ss_w & 0 & 0 & 0 & 0 & 0 \\
Sj_w(1-pd_w) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & Sd_w pes_w \alpha(t) & 0 & Sa_w & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & f_h Sa_h 0.5 \\
0 & 0 & 0 & 0 & Sj_h pd_h & 0 & Ss_h & 0 \\
0 & 0 & 0 & 0 & Sj_h(1-pd_h) & 0 & 0 & 0 \\
0 & Sd_w pes_h(frd+\gamma(t)) & 0 & 0 & 0 & Sd_h pes_h(\alpha(t)+\gamma(t)) & 0 & Sa_h
\end{pmatrix}$$

362

363 In the Appendix B we show the corresponding R code and the linear equations.

364

365 **Table 4.** Demographic parameters used for projecting the abundance of wolves and admixed

366 individuals in the presence of hybridization.

Scenario	Null Model		Repro. Isolation 1		Repro. Isolation 2	
Individual	Wolf	Admixed	Wolf	Admixed	Wolf	Admixed
Initial abundance (reproductive pairs)	6^1	0	6^1	0	6^1	0
Average litter size (f)	3.387^1	3.387^1	3.387^1	3.387^1	3.387^1	3.387^1
Juvenile survival (Sj)	0.551^1	0.551^1	0.551^1	0.551	0.551^1	0.551
Subordinate survival (Ss)	0.82^1	0.82^1	0.82^1	0.82^1	0.82^1	0.82^1
Disperser Survival (Sd)	0.69^2	0.69^2	0.69^2	0.69^2	0.69^2	0.69^2
Breeder survival (Sa)	0.82^3	0.82^3	0.82^3	0.82^3	0.82^3	0.82^3
Probability of dispersing (Pdi)	0.25^4	0.25^4	0.25^4	0.25^4	0.25^4	0.25^4
Probability of establishing a pack (Pes)	$0.5^{4,5}$	$0.5^{4,5}$	$0.5^{4,5}$	$0.3^{4,5}$	$0.7^{4,5}$	$0.3^{4,5}$

367 [1]Marucco et al., 2010; [2]Blanco and Cortés 2007; [3]Marucco et al., 2009; [4]Mech and Boitani, 2003;

368 [5]Marescot et al., 2012.

369

370 **3. Sensitivity analysis**

371 We performed a sensitiviy analysis to explore the relationship between the hybridization outcome

372 (genomic extinction vs persistence of parental and admixed populations after 50 years) and the

373 demographic parameters of parental species and admixed individuals (Mc Carthy et al., 1995; Cross

374 and Beissinger, 2001). Here, we use "genomic extinction" to refer to the disappearence of parental

375 individuals from the population (Allendorf et al 2001). We generated 15,000 parameter sets by

376 drawing them from uniform distributions (Table 5) to emphasize the effects of variability in vital

377 rates on model sensitivity (Cross and Beissinger, 2001). We projected population abundance with

378 each parameter set and cheked if the population went extinct or not using a quasi-extinction

379 threshold of 5 parental mature females. We conducted logistic regressions to explore the

380 relationship between the probability of genomic extinction of the two parental species as response

381 variables and demographic parameters used in the projections as independent explanatory variables.

382 For each regression we built full models including all the parameters and used a backward stepwise

383 selection procedures to identify the sets of parameters of potential importance (Fredrickson and

384 Hedrick, 2006). From those sets of parameters we ranked their relative importance in affecting the

385 probability of genomic extinction of the parental species based on their standardized regression

386 coefficients which are the regression coefficient divided by their standard error (Cross and

387 Beissinger, 2001). In the Appendix A and B we show the code to peform the logistic regression

388 sensitivity analysis and how to perform a sensitivity analysis of the asymptotic growth rate using

389 the matrix formulation for the two case studies (R codes are also reported there).

390

391 **Table 5**. Demographic parameters range used for drawing the demographic parameters from

392 uniform distributions to project the abundance of parental and admixed individuals. These

393 parameters are also used as explanatory variables in the logistic regression sensitivity analysis.

Striped x common dolphins		
Individual	Parameter	Range
Common dolphin	Initial abundance	16-32[1]
	Age of first reproduction	9-11[2,3,4]
	Calf survival	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility	0-0.33[2,3]

Individual	Parameter	Range
	rate	
Admixed dolphins	Initial abundance	36-84[1]
	Age of first reproduction	9-11[2,3,4]
	Calf survival	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility rate	0-0.33[2,3]
Striped dolphin	Initial abundance	1331-1578[1]
	Age of first reproduction	9-11[2,3,4]
	Calf	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility rate	0-0.33[2,3]

Wolf x dog		
Individual	Parameter	Range
Wolf	Annual per capita fertility rate	0-4.5[5]
	Juvenile survival	0.2-1
	Subordinate survival	0.2-1
	Disperser Survival	0.2-1
	Breeder survival	0.2-1
	Probability of dispersing	0-0.4[5]
	Probability of esablishing a pack	0-0.7[6]
Admixed	Annual per capita fertility rate	0-4.5[5]
	Juvenile survival	0.2-1
	Subordinate survival	0.2-1
	Disperser Survival	0.2-1
	Breeder survival	0.2-1
	Probability of dispersing	0-0.4[5]
	Probability of esablishing a pack	0-0-7[6]
Dog	Frequency of mating with dogs	0-1

394 [1]Gulf of Corinth, Greece (Santostasi et al., 2016); [2]Western Mediterranean (Calzada et al., 1995);

395 [3]control group (Murphy et al., 2009); [4]Eastern North Atlantic (Mannocci et al., 2012); [5]Mech and

396 Boitani, 2003; [6]Marescot et al., 2012

397

398 **Results**

399 **3.1 Striped x common dolphin model**

400   Comparing the projections with and without hybridization, we see that when hybridization is
401   ignored, the model predicts an exponential population growth (Fig. 3). When the impact of
402   hybridization is taken into account, the least abundant species (the common dolphin) reaches the
403   quasi-extinction threshold after 16 years, no matter the hybrid fitness scenario. In the Null Model
404   and in the Hybrid Vigour scenario, the growth rate of the most abundant species (the striped
405   dolphin) is also affected, becoming negative after about 40 years in the first scenario and after about
406   30 years in the second. In the absence of mechanisms that counter hybridization (e.g., assortative
407   mating), the population will eventually be composed of a continuum of hybrid classes (the
408   "complete admixture" hybridization type described by Allendorf et al., 2001; Fig. 4). Conversely,
409   under the Outbreeding Depression scenario, striped dolphin population abundance is expected to
410   increase in the next 100 years, predicting a "widespread introgression" hybridization type (i.e., the
411   coexistence of admixed and parental individuals; Fig. 4).

412
413
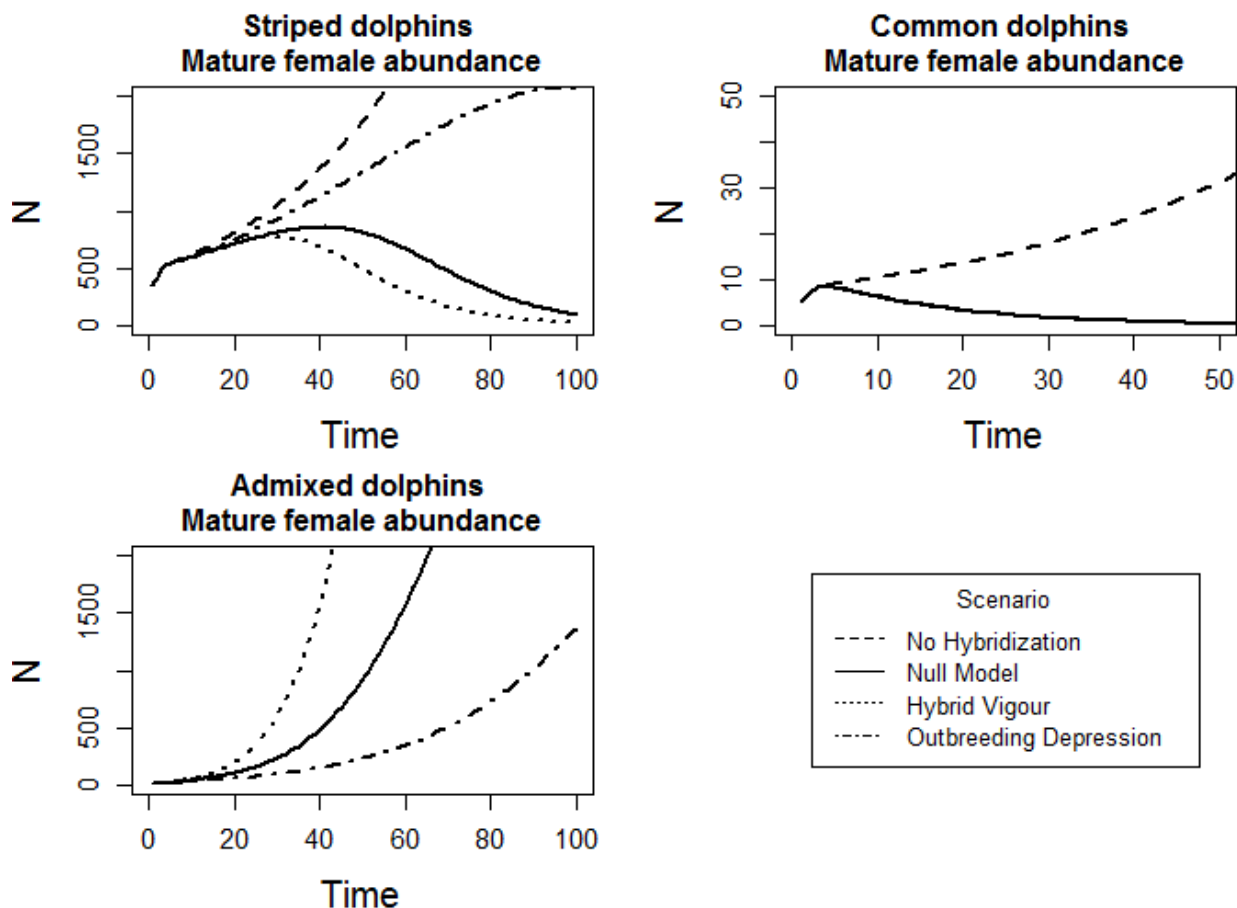
414
415   **Figure 3.** Population trajectories of striped, common and admixed dolphins under different parental
416   and admixed individuals fitness scenarios (the continuos line represent the Null Model while
417   different type of dashed lines represent the model in absence of hybridization, the Outbreeding
418   Depression Scenario and the Hybrid Vigour Scenario).

419

Prevalence
**Total population**
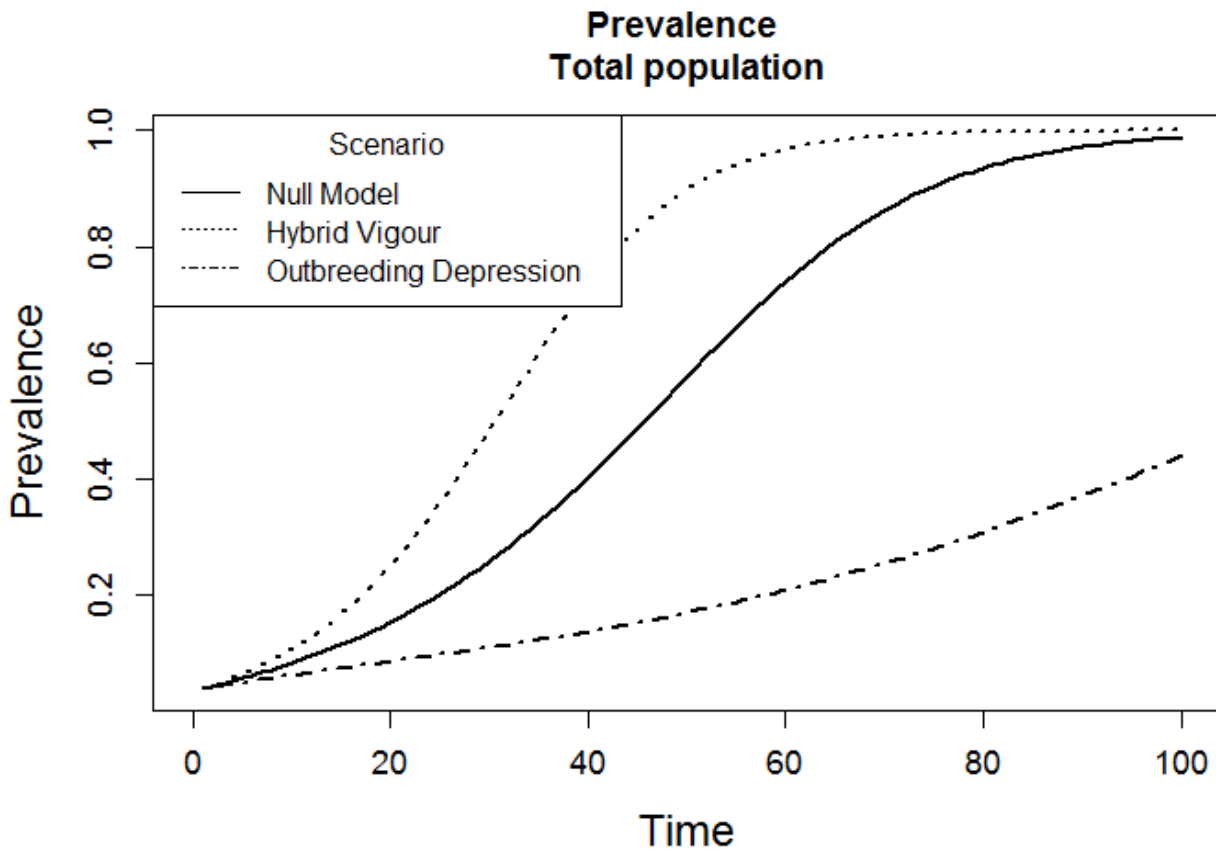
420

421   **Figure 4.** Projected prevalence of striped x common dolphin hybrids in the mixed dolphin

422   population of the Gulf of Corinth, Greece under different parental and admixed individuals fitness

423   scenarios (the continuos line represent the Null Model while different type of dashed lines represent

424   the Outbreeding Depression Scenario and the Hybrid Vigour Scenario).

425

426   **3.2 Wolf x dog model**

427   Depending on the scenario, hybridization had different final outcomes. In the Null Model all the

428   scenarios reached complete admixture (prevalence of hybrids = 1) after 50 years and prevalence

429   increased more rapidly at the increasing of the recurrent gene flow from dogs (Fig. 5, upper-left

430   panel). The reproductive isolation scenarios showed different outcomes. In the scenario with the

431   weakest reproductive isolation (Reproductive Isolation 1) the prevalence increased less rapidly

432   compared to the Null Model (Fig. 5, upper-right panel) but did not reach an asymptote, heading

433   towards a final outcome of complete admixture (Allendorf et al., 2001). In the scenario of strongest

434   reproductive isolation (Reproductive Isolation 2), prevalence reached an asymptote whose final

435   value increased at the increasing of the intensity of the recurrent gene flow from dogs (Fig. 5,

436   lower-left panel). In this last case the final outcome is the co-existence of admixed and parental

individuals with a constant prevalence of hybrids (assuming that all the demographic parameters

remain constant over time). This last scenario falls into the definition of "widespread introgression"

(Allendorf et al., 2001).
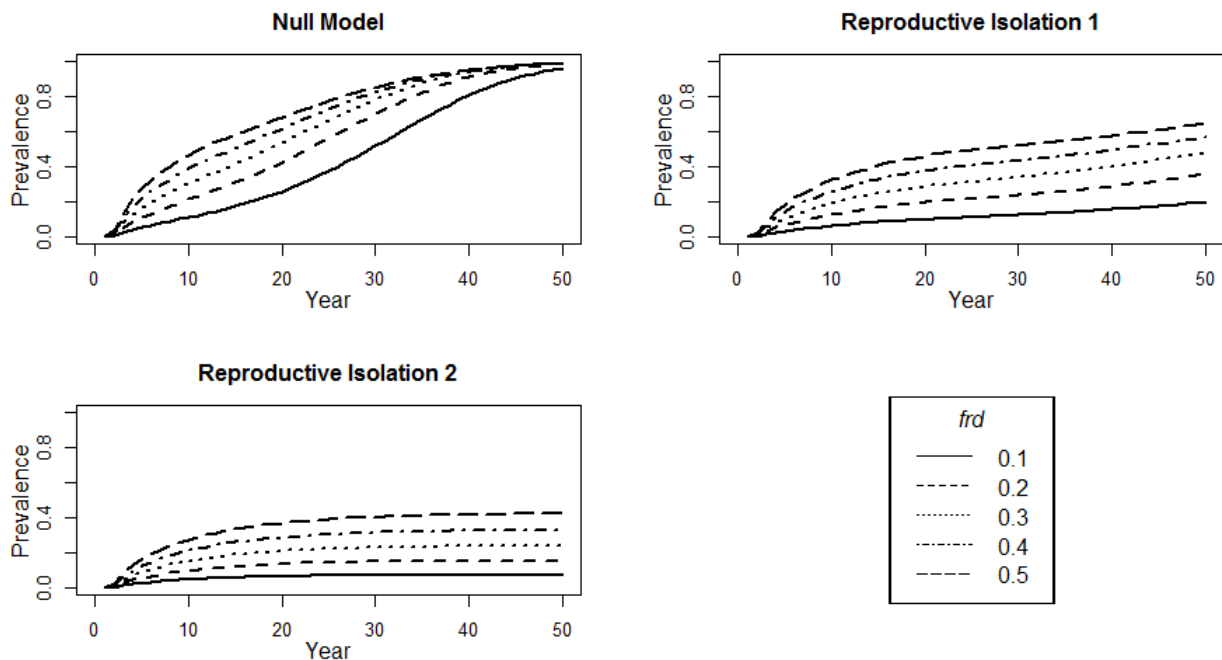
Figure 5. Projected prevalence of wolf x dog hybrids under increasing levels of recurrent gene flow

from dogs (parameter *frd*) and under different reproductive isolation scenarios: the Null Model

(upper-left panel), the Reproductive Isolation 1 scenario (upper-right panel). and the Reproductive

Isolation 2 scenario (lower-left panel).

Sensitivity analysis

For the dolphin case study the probability of genomic extinction of both striped and common

dolphins was most affected by the survival of mature individuals followed by juvenile survival with

almost the same relative importance (Table 6). However, for common dolphins, the initial

abundance was also important (Table 6).

Table 6. Logistic regression sensitivity analysis results for striped and common dolphin population

projections in the presence of hybridization. The parameters are sorted in descending order of

relative importance, evaluated by looking at the standardized regression coefficients. Sa = adult

survival, Sj = juvenile survival, Sc = calf survival, f = annual per captita fertility rate, ia = initial

abundance. The subscript Sc refers to striped dolphin parameters, the subscript Dd refers to

common dolphin parameters, the subscript h refers to admixed individuals parameters.

Striped dolphin genomic extinction probability				
Parameter	Coefficient	Standard Error	Standardized Coefficient	p value
Sa_{Sc}	-92.90	3.65	-25.44	0.00
Sj_{Sc}	-10.28	0.49	-20.87	0.00
Sc_{Sc}	-2.99	0.33	-9.21	0.00
f_{Sc}	-7.52	1.76	-4.26	0.00
afr_{Sc}	0.24	0.10	2.40	0.02
f_{Dd}	-3.49	1.75	-1.99	0.05
Sj_{Dd}	-0.59	0.31	-1.92	0.05
ia_h	-0.01	0.01	-1.91	0.06
Sa_{Dd}	0.51	0.31	1.64	0.10
Common dolphin genomic extinction probability				
Parameter	Coefficient	Standard Error	Standardized Coefficient	p value
Sa_{Dd}	-91.40	6.30	-14.50	0.00
Sj_{Dd}	-9.13	0.69	-13.24	0.00
ia_{Dd}	-0.30	0.03	-10.78	0.00
Sc_{Dd}	-1.61	0.47	-3.43	0.00
Sa_{Sc}	1.46	0.43	3.38	0.00
Sa_h	1.17	0.44	2.63	0.01
afr_{Sc}	-0.23	0.15	-1.58	0.11

459

460 For the wolf x dog case study, our sensitivity analysis showed that wolf genomic extinction

461 probability was mostly affected by wolf breeder survival (Sa_w), followed by annual frequency of

462 mating with dogs (*frd*), wolf access to reproduction (i.e., probability of establishing a pack, pes_w)

463 and annual wolf per capita fertility rate f_w, with the same relative importance (Table 7).

464

465 **Table 7.** Logistic regression sensitivity analysis results for the wolf population projections in the

466 presence of hybridization with dogs. The parameters are sorted in descending order of relative

467 importance, evaluated by looking at the standardized regression coefficients. Sa = annual breeder

468 survival, f = fertility (approximated as litter size), Pes (probability of establishing a pack), *frd* =

469 annual frequency of mating with dogs, Sj = annual juvenile survival, Sd = annual disperser survival,

470 Ss = annual subordinate survival, pdi = annual probability of dispersal. The subscript w indicates

471 wolf demographic parameters and the subscript h indicates admixed demographic parameters.

	Coefficient	Standard Error	**Standardized Coefficient**	p value

Sa$_w$	-47.40	2.03	**-23.32**	0.00
f$_w$	-1.17	0.07	**-16.89**	0.00
pes$_w$	-7.14	0.44	**-16.05**	0.00
frd	5.09	0.32	**16.03**	0.00
Sj$_w$	-4.54	0.35	**-13.05**	0.00
Sd$_w$	-3.83	0.34	**-11.29**	0.00
Ss$_w$	-2.62	0.32	**-8.24**	0.00
Sj$_h$	0.97	0.30	**3.21**	0.00
pdi$_w$	-1.38	0.59	**-2.34**	0.02
Sa$_h$	0.52	0.31	**1.70**	0.09

472

473

3. Discussion

Identifying the demographic factors affecting the outcome of hybridization helps both understanding evolutionary mechanisms and developing meaningful management and conservation measures when hybridization is a threat (Bohling et al., 2016). Compared to the genetic approach (Huxel, 1999; Ferdy and Austerlitz, 2002), our model has the advantage of making the link between hybridization and both demographic (e.g., demographic stochasticity) and ecological factors (e.g., environmental stochasticity). Moreover, our approach allows to relate the viability of the population to the contribution of different fitness components (such as survival and reproductive rates), ultimately providing the basis for sensitivity analyses.

On the other hand, ignoring genetic processes can be an important limitation (Hall and Ayres, 2008). In its present formulation, our model does not make a distinction between ancient (later generations backcrosses) and recent hybrids (first and second generation hybrids), which raises two issues. First, because later generations backcrosses have a limited mixed genomic content, in several cases they are indistiguishable from parentals with the current diagnostic techniques (Vähä and Primmer, 2006). Second, later generations backcrosses are often considered as parentals from a management perspective. For example, in the management of the anthropogenic hybridization between bontebok *Damaliscus pygargus pygargus* and blesbok *D. p. phillipsi* in South Africa, van Wick et al., (2016) considered that backrosses to parental bonteboks with ≥ 90% of bontebok genes are not to be removed from the population. In the management of the red wolf and coyote, canids with > 87.5 % of red wolf genes are classified as red wolves and not sterilized or culled (Gese et al., 2015). To overcome this limitation, it may be desirable to split the "admixed" group into recent and ancient hybrids, and pool the ancient hybrids together with the parental populations. The threshold between the two groups could be set according to the defined acceptable threshold of admixture in the parentals, while also considering the power of the diagnostic system (Vähä and Primmer, 2006; van Wick et al., 2016). Despite these limitations, our modelling framework provides a clear way to make explicit the assumptions underlying the definition of hybrids (Thompson et al., 2003).

Even though population-based approaches like the one described here require less-detailed information compared to individual-based approaches (Hall and Ayres, 2008), one still needs to know the survival and reproductive rates for all the population stages, and these may be unavailable for the target population. In this study, we overcome such limitation by resorting to parameters estimated for other populations, which may introduce an unknown level of uncertainty. Moreover, estimates of demographic rates of admixed individuals were not available and are likely to be

508   unavailable in many studies. In such cases, one would need to make assumptions regarding admixed

509   individuals survival and fertility rates. However, sensitivity analysis showed that genomic

510   extinction probability was largely affected by the demographic parameters of parentals, whereas the

511   parameters of admixed individuals had a lower relative importance. Nonetheless, the sensitivity of

512   model predictions to unknown parameters should be tested through sensitivity analyses, and should

513   be taken into account by considering different scenarios. Moreover, the comparison alternative

514   simulated scenarios with empirical data (i.e the observed prevalence trends) can provide insight on

515   the evolutionary mechanism shaping the observed patterns.

516

517   Another important limitation is that, for simplicity and for the absence of species-specific

518   information, we assumed random mating and did not model more complex mating choice scenarios

519   that could lead to assortative mating. If information about assortative mate choice is available, it can

520   be modelled by changing the reproduction coefficients (α, β and γ in paragraph 2.1.1) from being

521   proportional to the relative abundance of mature males to reflecting the observed percentage of

522   conspecific and heterospecific matings.

523

524   At the moment, our projections cannot be validated due to the absence of long-term data on the

525   quantitative evaluation of hybridization for the two case-studies. However, the predicted outcomes

526   are consistent with previous studies showing that hybridization can lead to rapid genomic extinction

527   in the absence of reproductive isolation (Huxel, 1999) or other forms of segregation (Wolf et al.,

528   2001; Fredrickson and Hedrick 2006). Two studies on wolf x dog hybridization (Santostasi et al.,

529   2019; Salvatori et al., 2019) showed that the prevalence of hybrids can locally reach high levels

530   (around 50%) where reproductive isolation between wolves and dogs is disrupted by anthropogenic

531   disturbance (e.g., presence of free ranging dogs, food provisioning, high wolf anthropogenic

532   mortality), supporting the results of our projections. We suggest that, given the importance of

533   reproductive isolation mechanisms in determining the wolf x dog hybridization outcome, more

534   research should be addressed to understand to what extent and in which circumstances those

535   mehcanisms are effective in contrasting wolf x dog hybridization. In absence of such information,

536   the absence of strong reproductve isolation should be assumed as a precautionary measure.

537

538   Studies on hybridization dynamics in cetaceans that could be used to validate our results are absent.

539   However, our finding that the genomic extinction risk for the parental population increases as their

540   initial frequency decreases, making the least abundant species particularly vulnerable, is consistent

541   with previous studies (Allendorf et al., 2001; Epifanio and Philipp, 2001).

542

543 We stress that the interest of our model is not the production of absolute predictions of population

544 fate. Being long term hybridization dynamics otherwise difficult to test empirically, the practical

545 value of our model is to illustrate the expected relative outcomes of alternative biological and

546 managament scenarios. The comparison of those outcomes can be useful to hihglight future

547 research priorities and to inform decision-making in a context of uncertainty (Gervasi and Ciucci

548 2018).

549

550 In alternative, not acknowledging hybridization in the projections may lead to underestimating the

551 risk of genomic extinction. The common dolphin (the least abundant species) had a 100%

552 probability of going extinct after a relatively short time (16 years) regardless the fitness scenario. A

553 previous count-based projection (Santostasi et al., 2018) did not include the effect of hybridization

554 (although it included the effect of demographic stochasticity) and estimated a considerably lower

555 (50%) probability of extinction after 15 years. Although the two predictions are not entirely

556 comparable due to the different methodologies, our results suggest that hybridization may pose an

557 additional and important threat that must be considered when evaluating the conservation status of

558 common dolphins. This is particulatly relevant at larger scales, considering that, in the

559 Mediterranean Sea common dolphins occurr in simpatry with the more abundant striped dolphins

560 and mixed-species groups are not rare (Frantzis & Herzing, 2002; Giménez et al., 2017; Espada et

561 al., 2019).

562

563 Interestingly, the population growth rate of the most abundant species, the striped dolphin, was also

564 affected and hybridization could eventually lead this population to genomic extinction, under

565 scenarios in which the fitness of admixed individuals is equal to or greater than that of parentals

566 (i.e., the Null Model and the Outbreeding Depression scenario). However, striped dolphins are

567 predicted to persist and even increase in the next 100 years, if the fitness of admixed individuals is

568 lower than that of parentals (i.e., the Outbreeding Depression scenario). More research on the

569 fitness of admixed individuals would help understand which scenario represents the most likely

570 alternative. Research on the genetic composition and ecology of admixed individuals would help

571 understand if the predicted "hybrid swarm" may: 1) lead to a new species (Lamichhaneey et al.,

572 2017; Larsen et al., 2010); 2) preserve the integrity of the striped dolphin species by backcrossing

573 and dilution of the common dolphin genetic contribution; or 3) allow for the persistence of adaptive

574 common dolphin alleles in the striped dolphin, as suggested by other cases of adaptive introgression

575 (Figueirò et al., 2017).

576

For the wolf x dog case study, our results confirm that hybridization with dogs should be expected
to be a serious threat to the wolf genomic integrity, at least under weak reproductive isolation
and/or frequent breeding with dogs. The sensitivity analysis pointed out that the most influential
parameters decreasing the chances of genomic extinction are linked to social and reproductive
integrity (i.e., survival of wolf breeders and the per capita fertility rate) and the annual frequency of
mating with dogs. These results are in agreement with observations of hybridization in eastern
wolves (*Canis lycaon*) and coyotes in Canada (Rutledge et al., 2011), and of red wolves and coyotes
in North Carolina (Bohling and Waits, 2015). In both cases, high levels of mortality coupled with a
large availability of coyotes have been identified as the main causes of hybridization. Our results
offer further evidence that human-related factors contributing to hybridization (i.e., increased wolf
mortality and dog presence) must be managed to avoid the risk of genomic extinction of wild
wolves (Rutledge et al., 2011; Bohling and Waits, 2015).

In conclusion, our model provides estimates of genomic extinction risk in presence of hybridization
by using data obtained during demographic monitoring programs of threatened populations. This
model allows to link demographic parameters and environmental variables, therefore predicting
hybridization dynamics under changing environments. Population projection models clearly
represent a valuable tool to predict the outcome of hybridization, therefore contributing to
management decision (Kelly et al., 2010).

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