



Assessing the dynamics of hybridization through a matrix modelling approach

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1 **Title**

2 Assessing the dynamics of hybridization through a matrix modelling approach

3

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25 **Highlights**

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

32 **Abstract**

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

51 **Keywords**

52 Genomic extinction, hybrids, hybridization, matrix models, Mediterranean common dolphin,
53 population projections, prevalence, sensitivity analysis, striped dolphin, wolf

55 **1. Introduction**

56 Hybridization, defined as the interbreeding of individuals from genetically distinct populations,
57 regardless of their taxonomic status (Allendorf et al., 2001) is recognized as a relatively common
58 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 anthropogenic 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 (Seehausen 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 hybridization 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 classifying 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

possible management actions can also be used to provide management recommendations (Crouse et al 1987; Cross and Beissinger 2001).

The first attempts to model hybridization-extinction dynamics had a genetic focus and were based on changes in allelic frequencies at one or more loci (Huxel, 1999; Ferdy and Austerlitz, 2002). Compared to genetic models, ecological models place a greater emphasis on life-history traits, by explicitly examining the effects of fitness parameters (e.g., survival and reproductive rates) on the hybridization outcome. Within the ecological approach, two types of model have been used to model hybridization dynamics (Hall and Ayres, 2008): 1) individual-based models that simulate the contribution of each individual to the hybridization dynamics of the entire population (e.g., Thompson et al., 2003; Hooftman et al., 2007), and 2) population-based models that can be used when the mean fitness parameters of the main demographic stages are available (e.g., Wolf et al., 2001; Campbell et al., 2002). Both modelling approaches were applied to hybridization in plant species (Hall and Ayres, 2008; Todesco et al., 2016). However, to our knowledge, few studies used individual-based models (Fredrickson and Hedrick, 2006; Nathan et al., 2019) and none used population-based models to simulate hybridization dynamics in animal species.

Here, we develop a population-based approach to project the dynamics of animal hybridization. By using a stage-based matrix model, and grouping individuals into genealogical categories, each described by their mean fitness parameters (i.e., age-specific survival, per capita fertility rate), our approach overcomes the need of realistic and accurate data at the individual level. To provide a practical example of this modeling approach, we illustrate its application to two case studies. The first refers to two delphinid species belonging to different genera, that interbreed in the Gulf of Corinth, Greece (Bearzi et al., 2016; Antoniou et al., 2019): the striped dolphin *Stenella coeruleoalba* and the common dolphin *Delphinus delphis*. The Mediterranean subpopulation of the former species is classified as Vulnerable, and the latter as Endangered in the IUCN Red List (Bearzi et al., 2003; Aguilar and Gaspari, 2012). Within the Gulf of Corinth, however, the subpopulation of common dolphin would qualify as Critically Endangered due to its small size (point estimate 22 individuals; Santostasi et al., 2016) and high ($\geq 50\%$) probability of extinction in three generations (Santostasi et al., 2018). Recently confirmed hybridization with the much more abundant striped dolphin population (point estimate 1331 individuals; Santostasi et al., 2016) threatens the persistence of common dolphins in the Gulf of Corinth (Antoniou et al., 2019; Santostasi et al., 2018). We regard this as a case of anthropogenic hybridization, considering that the steep decline of common dolphins due to anthropogenic impacts (Bearzi et al., 2003) locally 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 possible 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 ≥ 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

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

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

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

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

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

We assume that the probability of reproduction between adult females belonging to one group and adult males belonging to one of the three other groups, is proportional to the relative abundances of adult males $\alpha(t)$, $\beta(t)$ and $\gamma(t)$ which are given by the ratio between adult males (A_m) of one group divided by the total number of adult males $TOT_m(t)$:

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

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

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

Therefore, the number of offspring belonging to the parental group 1 produced at time $t+1$ is given by the number of females surviving to time $t+1$, $A_{1f}(t)Sa_1$, multiplied by their per capita fertility rate (f_1) multiplied by the relative abundance of adult males of group 1 $\alpha(t)$. The number of offspring belonging to the parental group 2 produced at time $t+1$ is therefore:

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

The number of admixed offspring produced by e.g., the crossing between females of the group 1 and males of the group 2 is calculated as $A_{1f}(t)f_1Sa_1\beta(t)$ and the total number of admixed offspring at time $t+1$ is given by the sum of the contribution of all the possible crosses (Table 1):

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

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 survival values, f_1 and f_2 are the group-specific per capita fertility rates. Because we model separately males and females, the number of offspring of each sex produced every year by each group is obtained by multiplying the total number of offspring by 0.5, assuming a 50:50 sex ratio at birth:

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

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

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

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

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

$$= \begin{pmatrix} 0 & 0 & f_1 S a_1 \alpha(t) 0.5 & 0 & 0 & 0 & 0 & 0 & 0 \\ S c_1 & S j_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S a_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & f_2 S a_2 \beta(t) 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & S c_2 & S j_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S a_2 & 0 & 0 & 0 \\ 0 & 0 & f_1 S a_1 (\beta(t) + \gamma(t)) 0.5 & 0 & 0 & f_2 S a_2 (\alpha(t) + \gamma(t)) 0.5 & 0 & 0 & f_h S a_h (\alpha(t) + \beta(t)) \\ 0 & 0 & 0 & 0 & 0 & 0 & S c_h & S j_h & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S a_h \end{pmatrix}$$

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 reproductively mature later (having the oldest age of first reproduction between the two parental
276 species).

277

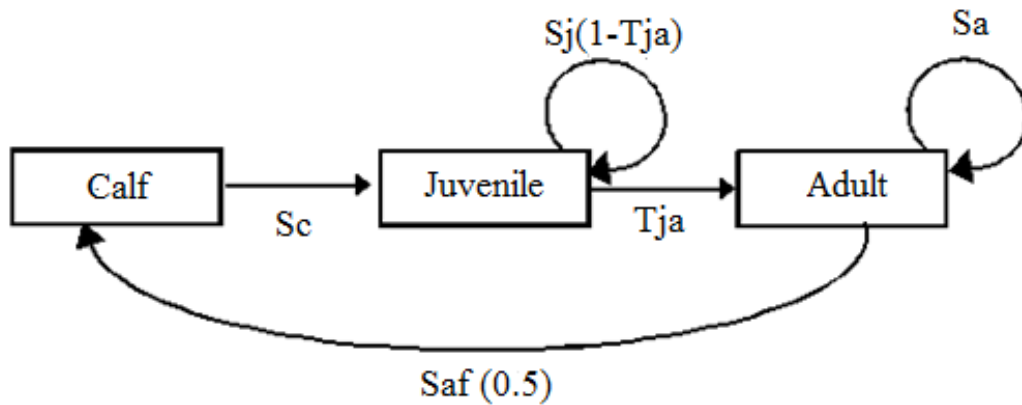


Figure 1. Life cycle used for the dolphin case study. Parameters are: Sc = survival of calves, Tja = transition probability from the juvenile to the adult stage modelled as the survival of juveniles (Sj) raised power of age of first reproduction - 1, Sa = survival of adults, f = per capita fertility rate, approximated as the annual pregnancy rate.

Table 2. Demographic parameters used for projecting the abundance of striped and common dolphins in the presence of hybridization using alternative parental and admixed individual fitness 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

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

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

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

(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

$$\begin{pmatrix} 0 & 0 & f_{Sc}Sa_{Sc} \alpha(t)0.5 & 0 & 0 & 0 & 0 & 0 & 0 \\ Sc_{Sc} & (1 - Tja_{Sc})Sj_{Sc} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & Tja_{Sc} & Sa_{Sc} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & f_{Dd}Sa_{Dd} \beta(t)0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & Sc_{Dd} & (1 - Tja_{Dd})Sj_{Dd} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & Tja_{Dd} & Sa_{Dd} & 0 & 0 & 0 \\ 0 & 0 & f_{Sc}Sa_{Sc}(\beta(t) + \gamma(t))0.5 & 0 & 0 & f_{Dd}Sa_{Dd}(\alpha(t) + \gamma(t))0.5 & 0 & 0 & f_hSa_h(\alpha(t) + \beta(t)) \\ 0 & 0 & 0 & 0 & 0 & 0 & Sc_h & (1 - Tja_h)Sj_h & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & Tja_h & Sa_h \end{pmatrix}$$

305

2.2.2. Wolf x dog model

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

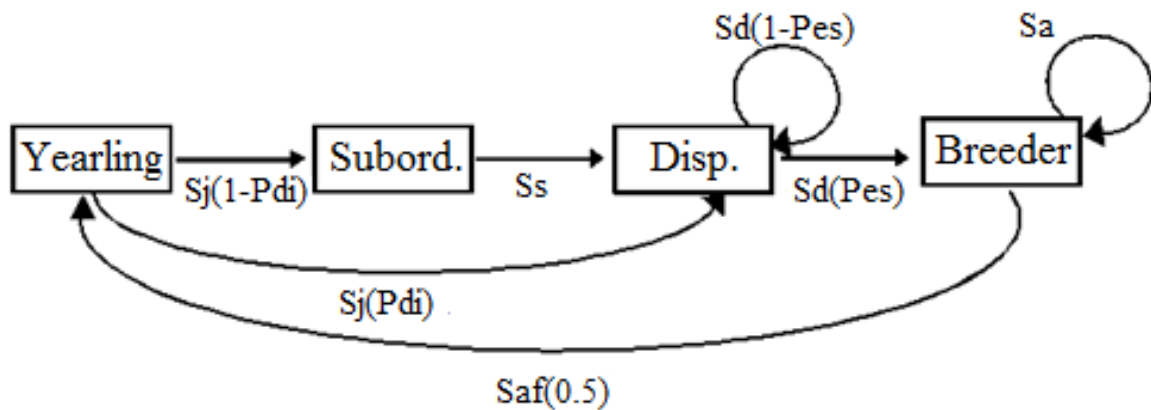


Figure 2. Life cycle for the wolf case study. Parameters are: S_j = survival of yearlings, S_s = survival of subordinates (yearlings and adults), S_d = survival of dispersers (yearlings and adults), S_a = survival of breeders, f = annual per capita fertility rate approximated as the litter size, P_{di} = probability of going in dispersal, P_{es} = probability of establishing a pack.

We modeled hybridization at the level of the formation of the reproductive pairs. Hybridization was documented in the almost totality of cases to occur between female wolves and male dogs (Randi et 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

$$\begin{pmatrix} 0 & 0 & 0 & f_w Sa_w 0.5 & 0 & 0 & 0 & 0 \\ S_j p d_w & 0 & S s_w & 0 & 0 & 0 & 0 & 0 \\ S_j (1 - p d_w) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S d_w p e s_w \alpha(t) & 0 & S a_w & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & f_h S a_h 0.5 \\ 0 & 0 & 0 & 0 & S_j p d_h & 0 & S s_h & 0 \\ 0 & 0 & 0 & 0 & S_j (1 - p d_h) & 0 & 0 & 0 \\ 0 & S d_w p e s_h (f r d + \gamma(t)) & 0 & 0 & 0 & S d_h p e s_h (\alpha(t) + \gamma(t)) & 0 & S a_h \end{pmatrix}$$

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 ¹Marucco et al., 2010; ²Blanco and Cortés 2007; ³Marucco et al., 2009; ⁴Mech and Boitani, 2003;
368 ⁵Marescot et al., 2012.

369

370 **3. Sensitivity analysis**

371 We performed a sensitivity 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 (McCarthy et al., 1995; Cross
374 and Beissinger, 2001). Here, we use “genomic extinction” to refer to the disappearance 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 checked 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 perform 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}

	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 establishing 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 establishing a pack	0-0.7 ⁶
Dog	Frequency of mating with dogs	0-1

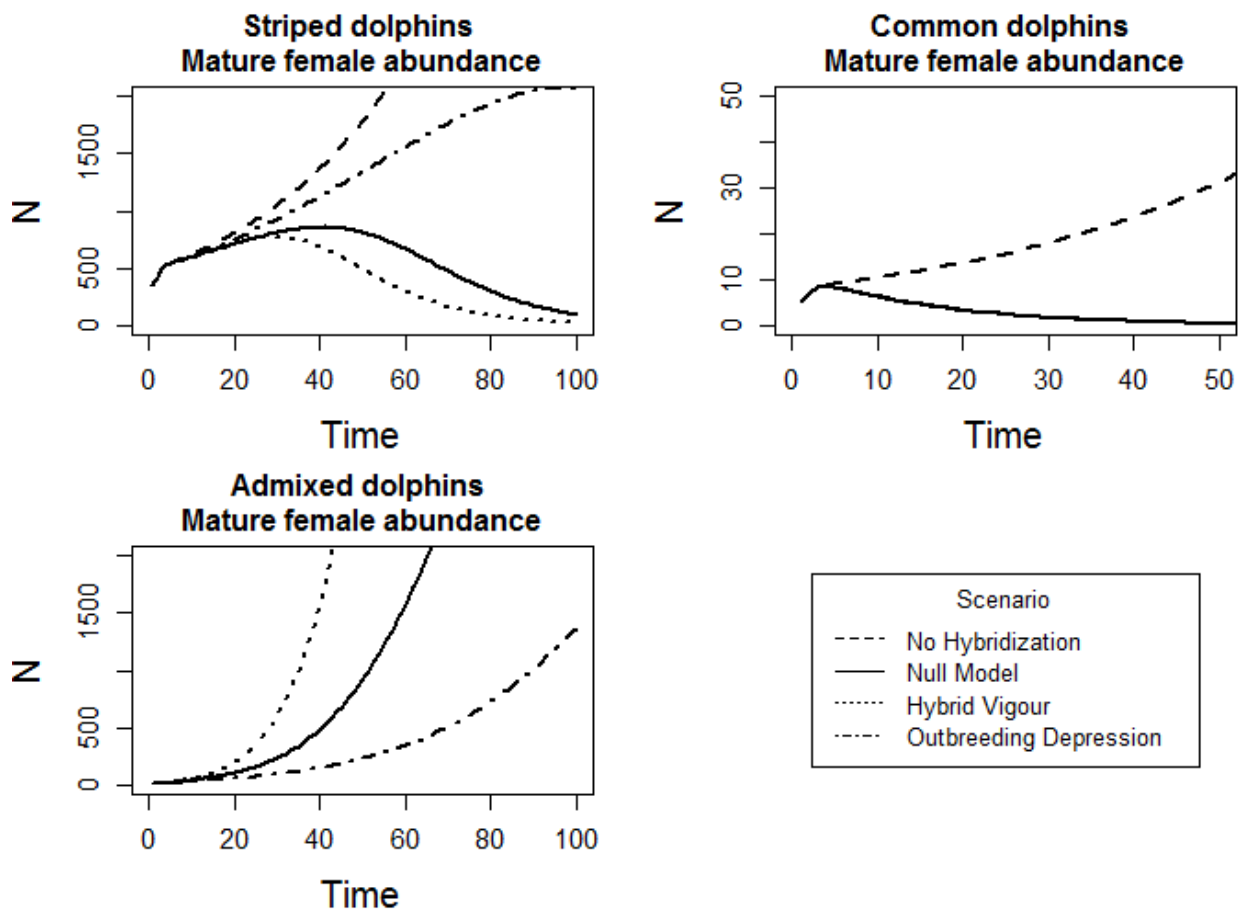
¹Gulf of Corinth, Greece (Santostasi et al., 2016); ²Western Mediterranean (Calzada et al., 1995);
³control group (Murphy et al., 2009); ⁴Eastern North Atlantic (Mannocci et al., 2012); ⁵Mech and
Boitani, 2003; ⁶Marescot et al., 2012

Results

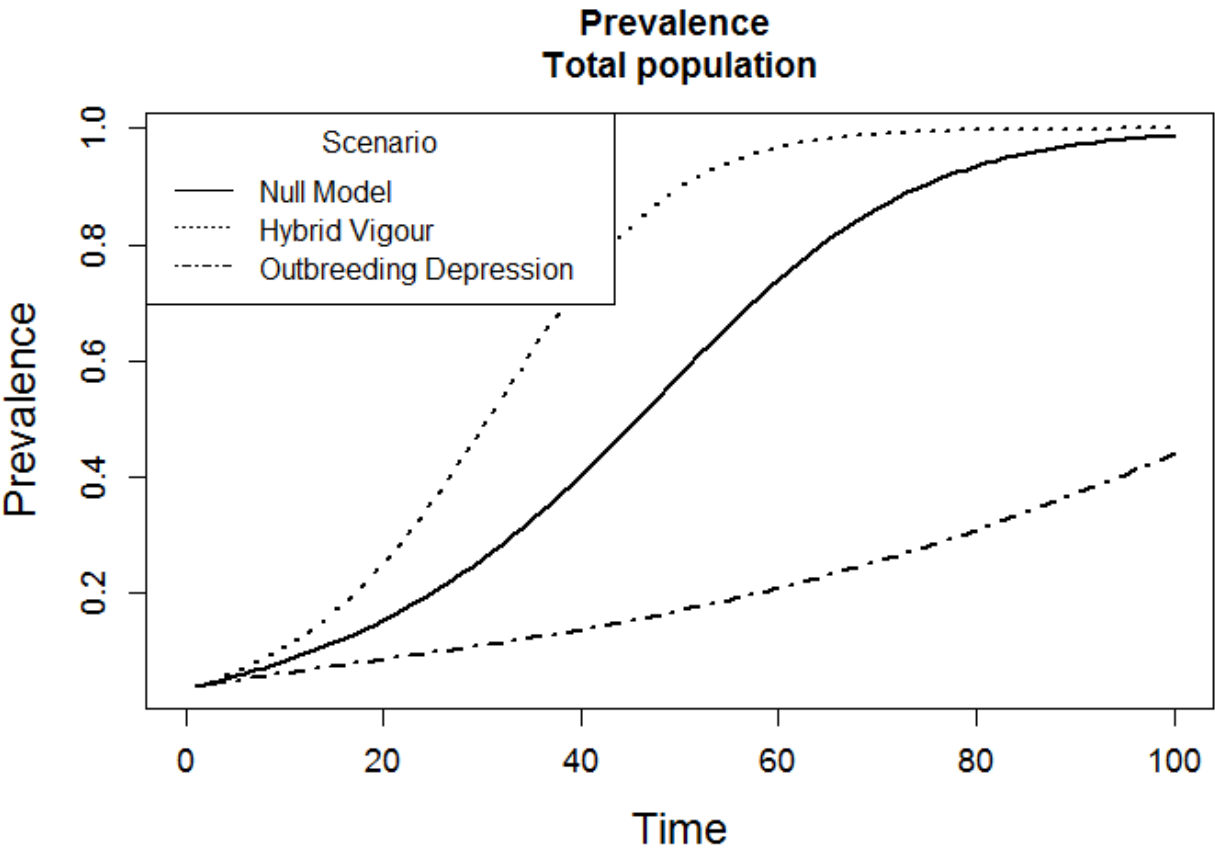
3.1 Striped x common dolphin model

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 continuous 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).

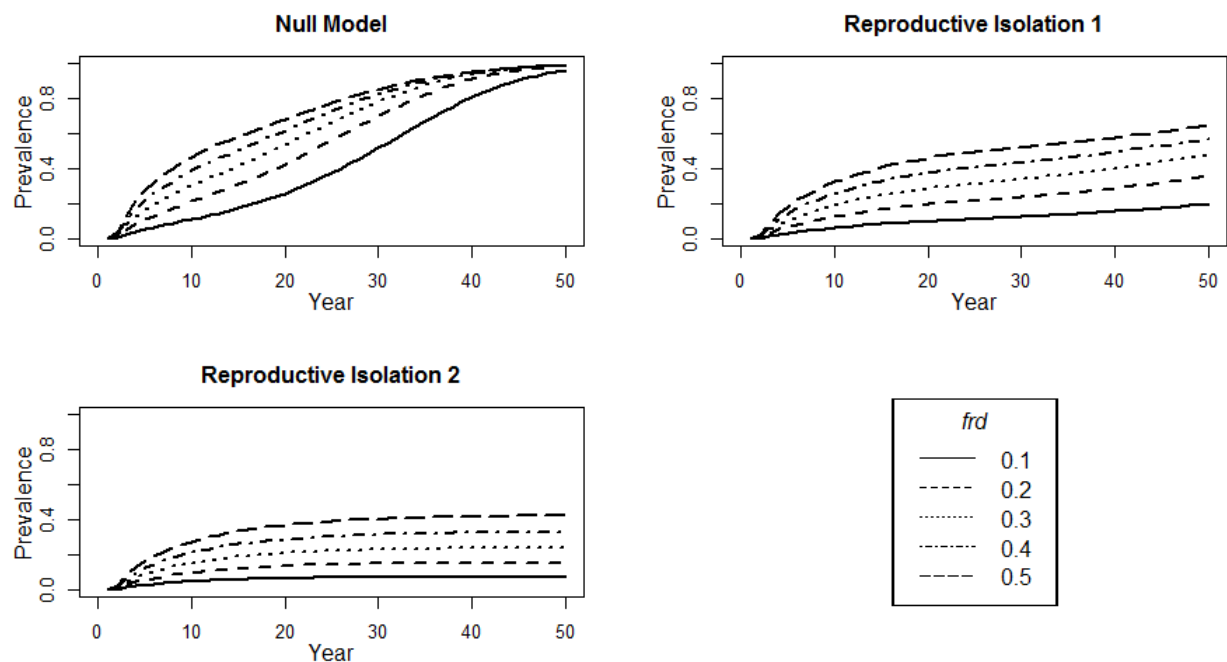


420
421 **Figure 4.** Projected prevalence of striped x common dolphin hybrids in the mixed dolphin
422 population of the Gulf of Corinth, Greece under different parental and admixed individuals fitness
423 scenarios (the continuous line represent the Null Model while different type of dashed lines represent
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

437 individuals with a constant prevalence of hybrids (assuming that all the demographic parameters
 438 remain constant over time). This last scenario falls into the definition of “widespread introgression”
 439 (Allendorf et al., 2001).
 440



441
 442 **Figure 5.** Projected prevalence of wolf x dog hybrids under increasing levels of recurrent gene flow
 443 from dogs (parameter *frd*) and under different reproductive isolation scenarios: the Null Model
 444 (upper-left panel), the Reproductive Isolation 1 scenario (upper-right panel). and the Reproductive
 445 Isolation 2 scenario (lower-left panel).
 446

447 **Sensitivity analysis**

448 For the dolphin case study the probability of genomic extinction of both striped and common
 449 dolphins was most affected by the survival of mature individuals followed by juvenile survival with
 450 almost the same relative importance (Table 6). However, for common dolphins, the initial
 451 abundance was also important (Table 6).
 452

453 **Table 6.** Logistic regression sensitivity analysis results for striped and common dolphin population
 454 projections in the presence of hybridization. The parameters are sorted in descending order of
 455 relative importance, evaluated by looking at the standardized regression coefficients. Sa = adult
 456 survival, Sj = juvenile survival, Sc = calf survival, f = annual per capita fertility rate, ia = initial
 457 abundance. The subscript Sc refers to striped dolphin parameters, the subscript Dd refers to
 458 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
<i>frd</i>	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

474 3. Discussion

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

483
484 On the other hand, ignoring genetic processes can be an important limitation (Hall and Ayres,
485 2008). In its present formulation, our model does not make a distinction between ancient (later
486 generations backcrosses) and recent hybrids (first and second generation hybrids), which raises two
487 issues. First, because later generations backcrosses have a limited mixed genomic content, in
488 several cases they are indistinguishable from parentals with the current diagnostic techniques (Vähä
489 and Primmer, 2006). Second, later generations backcrosses are often considered as parentals from a
490 management perspective. For example, in the management of the anthropogenic hybridization
491 between bontebok *Damaliscus pygargus pygargus* and blesbok *D. p. phillipsi* in South Africa, van
492 Wick et al., (2016) considered that backcrosses to parental bonteboks with $\geq 90\%$ of bontebok genes
493 are not to be removed from the population. In the management of the red wolf and coyote, canids
494 with $> 87.5\%$ of red wolf genes are classified as red wolves and not sterilized or culled (Gese et al.,
495 2015). To overcome this limitation, it may be desirable to split the “admixed” group into recent and
496 ancient hybrids, and pool the ancient hybrids together with the parental populations. The threshold
497 between the two groups could be set according to the defined acceptable threshold of admixture in
498 the parentals, while also considering the power of the diagnostic system (Vähä and Primmer, 2006;
499 van Wick et al., 2016). Despite these limitations, our modelling framework provides a clear way to
500 make explicit the assumptions underlying the definition of hybrids (Thompson et al., 2003).

501
502 Even though population-based approaches like the one described here require less-detailed
503 information compared to individual-based approaches (Hall and Ayres, 2008), one still needs to
504 know the survival and reproductive rates for all the population stages, and these may be unavailable
505 for the target population. In this study, we overcome such limitation by resorting to parameters
506 estimated for other populations, which may introduce an unknown level of uncertainty. Moreover,
507 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 mechanisms are effective in contrasting wolf x dog hybridization. In absence of such information,
536 the absence of strong reproductive 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 management scenarios. The comparison of those outcomes can be useful to highlight 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 particularly relevant at larger scales, considering that, in the
559 Mediterranean Sea common dolphins occur in sympatry with the more abundant striped dolphins
560 and mixed-species groups are not rare (Frantzis & Herzog, 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 (Lamichhane 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 (Figueiró et al., 2017).

576

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

589

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

596

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