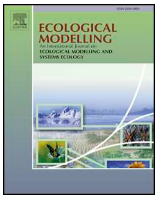
Ecological Modelling 431 (2020) 109120

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Assessing the dynamics of hybridization through a matrix modelling approach

Nina Luisa Santostasi[a,b,c,*], Paolo Ciucci[a], Giovanni Bearzi[c,d], Silvia Bonizzoni[c,d], Olivier Gimenez[b]

[a] Dept. Biology and Biotechnologies, University of Rome La Sapienza, Rome, Italy
[b] CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France
[c] Dolphin Biology and Conservation, Cordenons (PN), Italy
[d] OceanCare, Wädenswil, Switzerland

ARTICLE INFO

Keywords:
Genomic extinction
Hybrids
Hybridization
Matrix models
Mediterranean common dolphin
Population projections
Prevalence
Sensitivity analysis
Striped dolphin
Wolf

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 admixed 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 the admixed individuals is lower than that of parentals, hybridization can reinforce reproductive isolation between incompletely isolated species (Barton and Hewitt, 1989), but it can also cause extinction through demographic swamping (Allendorf et al., 2001; Wolf et al., 2001). If the fitness of the admixed individuals 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

---

[*] Corresponding author: Nina Luisa Santostasi
E-mail address: n.santostasi@gmail.com (N.L. Santostasi).

https://doi.org/10.1016/j.ecolmodel.2020.109120
Received 25 September 2018; Received in revised form 5 January 2020; Accepted 6 May 2020

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, 2016) based *inter alia* on admixed individuals fitness and relative abundance (i.e., 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 admixed individuals removal and/or sterilization to the management of the human disturbances that cause hybridization in the first place (Allendorf et al., 2001; Bohling, 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 recommmendatios (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 only 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 subpopulations of both species are classified as Vulnerable and as Endangered respectively in the IUCN Red List (Bearzi et al., 2003; Aguilar and Gaspari, 2012). Within the Gulf of Corinth, however, the subpopulation of common dolphin qualifies as Critically Endangered due to its small size (point estimate 22 individuals; Santostasi et al., 2016) and high (≥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 (Santostasi et al., 2018; Antoniou et al., 2019). 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, 2002; Antoniou et al., 2019). The possible hybridization outcomes for the two isolated dolphin subpopulations in the Gulf of Corinth have not been previously explored (Antoniou et al., 2019).

In the second case study we evaluate the possible outcomes of hybridization between the wolf (*Canis lupus*) and its domestic counterpart, the dog (*Canis lupus familiaris*). Hybridization between wolves and dogs has been documented in several European countries and represents a well-known threat to wolf conservation (Boitani, 2000; 2003). Still, little is known about the possible outcomes of hybridization between wolves and dogs. Hybridization with dogs may represent a problem for recovering wolf populations expanding into human-dominated landscapes, where few potential wolf mates compete with free-ranging dogs that are abundant and widespread (Randi, 2008; Galaverni et al., 2017). Although reproductive isolation due to behavioral or physiological barriers has been often assumed to contrast introgressive hybridization (Vilà and Wayne, 1999; Randi and Lucchini, 2002; Galaverni et al., 2017), admixed wolf populations are increasingly being reported where wolves live in close contact with free-ranging dogs population (e.g., Italy: Caniglia et al., 2013; Galaverni et al., 2017; Salvatori et al., 2019).

The matrix model presented here allows to quantitatively assess the possibles outcomes of hybridization (i.e., genomic extinction vs. persistence) under different fitness scenarios. Providing management recommendations is beyond the scope of this study, but our model represents a valuable tool to inform management once appropriately customized and parametrized. While our focus is on mammalian species, the analytical approach described here is valid for other taxa, and it could be adopted to project the dynamics of admixed populations for situations entailing both natural and anthropogenic hybridization.

2. Methods

2.1. General model

We consider a system in which there are two parental groups (T1 and T2) that interbreed and produce an admixed progeny (H). We regard the admixed progeny as an absorbing state encompassing all offspring produced by pairs of different parental groups, where at least one of the parents is an admixed individual (Wolf et al., 2001). The possible crosses considered and the produced progeny are listed in Table 1. Based on the assumed dynamics of interbreeding and production of offspring, we project the future abundance of the three mixing groups over time. We present the projections step by step with linear equations and we introduce the equivalent matrix formulation to calculate the asymptotic growth rate and perform sensitivity analyses. Finally, we discuss the behavior of the model by applying it to our case studies.

2.1.1. Model equations

We assume that parental and admixed groups have similar life cycles, with three age classes: offspring (C individuals up to 1 year old), juveniles (J non-reproductive individuals up to 3 years old) and adults (A reproductive individuals ≥ 3 years old). The transitions among age

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

classes are described by survival parameters (S) and the reproductive parameters are described by per capita fertility rates (f). At time t, the total number of individuals of the different groups (the parentals and the admixed) is:

$$N_{\mathrm{TOT}} = N_1 + N_2 + N_h,$$

where N_1 is the total number of individuals in group 1, N_2 is the total number of individuals in group 2 and N_{h} is the total number of admixed individuals.

We model the dynamics of females and males separately. Below, we show the equations for females. Each group at time t is composed by females (f) and males (m) belonging to the three different age classes:

$$\begin{aligned}
N_{1\mathrm{f}}(t) &= C_{1\mathrm{f}}(t) + J_{1\mathrm{f}}(t) + A_{1\mathrm{f}}(t),\\
N_{2\mathrm{f}}(t) &= C_{2\mathrm{f}}(t) + J_{2\mathrm{f}}(t) + A_{2\mathrm{f}}(t),\\
N_{\mathrm{hf}}(t) &= C_{\mathrm{hf}}(t) + J_{\mathrm{hf}}(t) + A_{\mathrm{hf}}(t).
\end{aligned}$$

We assume that the rate 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 ($\mathrm{A_m}$) of one group divided by the total number of adult males $TOT_{\mathrm{m}}(t)$:

$$\begin{aligned}
\alpha(t) &= A_{1\mathrm{m}}(t)/TOT_{\mathrm{m}}(t),\\
\beta(t) &= A_{2\mathrm{m}}(t)/TOT_{\mathrm{m}}(t),\\
\gamma(t) &= A_{\mathrm{hm}}(t)/TOT_{\mathrm{m}}(t).
\end{aligned}$$

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, $A_{1f}(t)\mathrm{Sa}_1$, 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:

$$C_2(t+1) = \mathrm{A}_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\beta(t).$$

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 $A_{1f}(t)\mathrm{f}_1\mathrm{Sa}_1\beta(t)$ 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):

$$\begin{aligned}
C_h(t+1) = \; & A_1(t)\mathrm{f}_1\mathrm{Sa}_1\beta(t) + A_2(t)\mathrm{f}_2\mathrm{Sa}_2\alpha(t) + A_1(t)\mathrm{f}_1\mathrm{Sa}_1\gamma(t)\\
& + A_2(t)\mathrm{f}_2\mathrm{Sa}_2\gamma(t)\\
& + A_h(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\alpha(t) + A_h(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\beta(t) + A_h(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\gamma(t),
\end{aligned}$$

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:

$$\begin{aligned}
C_{1f}(t+1) &= C_{1m}(t+1) = C_1(t+1)0.5,\\
C_{2f}(t+1) &= C_{2m}(t+1) = C_2(t+1)0.5,\\
C_{hf}(t+1) &= C_{hm}(t+1) = C_h(t+1)0.5.
\end{aligned}$$

Depending on the species mating system, hybridization can be modelled in different ways. For example, for species in which only the dominant individuals reproduce, it can be convenient to model hybridization at the level of the formation of the reproductive pairs. We consider this situation when dealing with the wolf x dog case study (section 3.2).

The number of female adults and juveniles at time t + 1 for the three groups are obtained as follows (the equations are showed only for group 1):

$$\begin{aligned}
J_{1\mathrm{f}}(t+1) &= C_{1\mathrm{f}}(t)\mathrm{Sc}_1\\
A_{1\mathrm{f}}(t+1) &= J_{1\mathrm{f}}(t)\mathrm{Sj}_1 + A_{1\mathrm{f}}(t)\mathrm{Sa}_1
\end{aligned}$$

where Sc, Sj and Sa are respectively survival rates for offspring, juveniles and adults. The total number of females at time t + 1 is therefore:

$$\begin{aligned}
N_{1\mathrm{f}}(t+1) &= A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\alpha(t)0.5 + C_{1\mathrm{f}}(t)\mathrm{Sc}_1 + J_{1\mathrm{f}}(t)\mathrm{Sj}_1 + A_{1\mathrm{f}}(t)\mathrm{Sa}_1\\
N_{2\mathrm{f}}(t+1) &= A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\beta(t)0.5 + C_{2\mathrm{f}}(t)\mathrm{Sc}_2 + J_{2\mathrm{f}}(t)\mathrm{Sj}_2 + A_{2\mathrm{f}}(t)\mathrm{Sa}_2\\
N_{\mathrm{hf}}(t+1) &= [A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\beta(t) + A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\alpha(t) + A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\gamma(t)\\
&\quad + A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\gamma(t) + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\alpha(t) + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\beta(t)\\
&\quad + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\gamma(t)]0.5 + C_{\mathrm{hf}}\mathrm{Sc}_\mathrm{h} + J_{\mathrm{hf}}(t)\mathrm{Sj}_\mathrm{h} + A_{\mathrm{hf}}(t)Sa_h
\end{aligned}$$

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

$$\begin{aligned}
N_{1\mathrm{m}}(t+1) &= A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\alpha(t)0.5 + C_{1\mathrm{m}}\mathrm{Sc}_1 + J_{1\mathrm{m}}(t)\mathrm{Sj}_1 + A_{1\mathrm{m}}(t)\mathrm{Sa}_1\\
N_{2\mathrm{m}}(t+1) &= A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\beta(t)0.5 + C_{2\mathrm{m}}\mathrm{Sc}_2 + J_{2\mathrm{m}}(t)\mathrm{Sj}_2 + A_{2\mathrm{m}}(t)\mathrm{Sa}_2\\
N_{\mathrm{hm}}(t+1) &= [A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\beta(t) + A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\alpha(t) + A_{1\mathrm{f}}(t)\mathrm{f}_1\mathrm{Sa}_1\gamma(t)\\
&\quad + A_{2\mathrm{f}}(t)\mathrm{f}_2\mathrm{Sa}_2\gamma(t)\\
&\quad + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\alpha(t) + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\beta(t) + A_{\mathrm{hf}}(t)\mathrm{f}_\mathrm{h}\mathrm{Sa}_\mathrm{h}\gamma(t)]\\
&\quad 0.5 + C_{\mathrm{hm}}\mathrm{Sc}_\mathrm{h} + J_{\mathrm{hm}}(t)\mathrm{Sj}_\mathrm{h} + A_{\mathrm{hm}}(t)\mathrm{Sa}_\mathrm{h}
\end{aligned}$$

2.1.2. Matrix formulation

The model above can be conveniently formulated as $\boldsymbol{N}(\mathrm{t}+1) = \boldsymbol{AN}(\mathrm{t})$ where:

$$\boldsymbol{N}(t) = [C_1(t)J_1(t)A_1(t)C_2(t)J_2(t)A_2(t)C_h(t)J_h(t)A_h(t)]^{\mathrm{T}}$$

and

$$\boldsymbol{A} = \begin{pmatrix}
0 & 0 & \mathrm{f_1Sa_1}\alpha(\mathrm{t})0.5 & 0 & 0 & 0 & 0 & 0 & 0\\
\mathrm{Sc_1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & \mathrm{Sj_1} & \mathrm{Sa_1} & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & \mathrm{f_2Sa_2}\beta(\mathrm{t})0.5 & 0 & 0 & 0\\
0 & 0 & 0 & \mathrm{Sc_2} & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & 0 & \mathrm{Sj_2} & \mathrm{Sa_2} & 0 & 0 & 0\\
0 & 0 & \mathrm{f_1Sa_1}(\beta(\mathrm{t}) + \gamma(\mathrm{t}))0.5 & 0 & 0 & \mathrm{f_2Sa_2}(\alpha(\mathrm{t}) + \gamma(\mathrm{t}))0.5 & 0 & 0 & \mathrm{f_hSa_h}(\alpha(\mathrm{t}) + \beta(\mathrm{t}) + \gamma(\mathrm{t}))0.5\\
0 & 0 & 0 & 0 & 0 & 0 & \mathrm{Sc_h} & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathrm{Sj_h} & \mathrm{Sa_h}
\end{pmatrix}$$

In the following section, we consider two real-world scenarios illustrating the relevance of the model described above. All the analyses are performed with the software R (R core team, 2018).

2.2. Applications

2.2.1. Dolphin model

We built stage-based matrices (Fig. 1; Taylor et al., 2007) for the two parental species and the admixed individuals with the following stages: calf (individuals up to 1 year old), juveniles (non-reproductive individuals up to species-specific age of first reproduction reported by Taylor et al., 2007) and adults (individuals that reached the age of first reproduction). We used the available stage-specific demographic parameters for the target populations in the Gulf of Corinth, Greece (Santostasi et al., 2016) and we used parameters estimated for other populations of the same species for the non available stage-specific demographic parameters (see Table 2 and Appendix A for details about model parametrization). We built three fitness scenarios for admixed individuals (Table 2): i) in the Null Model we assumed that admixed individuals had intermediate demographic traits between the two species, ii) in the Hybrid Vigour scenario we assumed that hybrids have higher survival (the upper 95% confidence limit estimated for the population by Santostasi et al., 2016) and annual per capita fertility rate (the highest annual pregnancy rate reported for Atlantic common dolphin subpopulations reported in Murphy et al., 2009) and that they

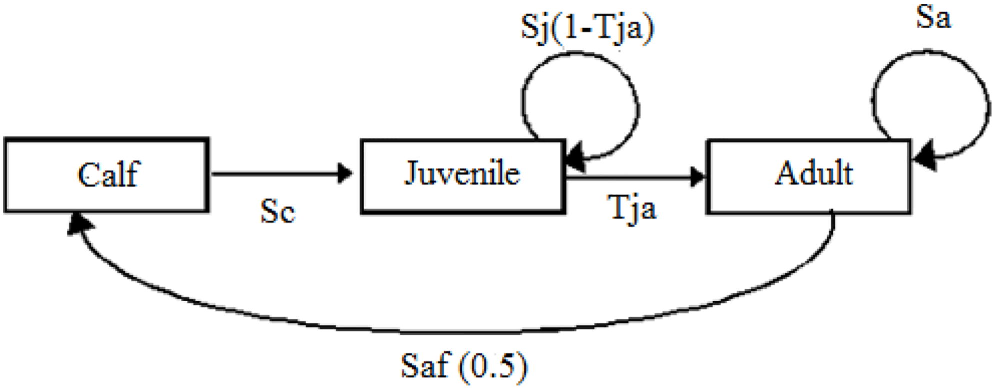


Figure 1. Life cycle used for the dolphin case study. Parameters are: Sc = survival of calves, Tja = transition rate from the juvenile to the adult stage modelled as the survival of juveniles (Sj) raised to the power of age of first reproduction - 1, Sa = survival of adults, f = per capita fertility 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
	Striped dolphin	Common dolphin	Admixed dolphin	Admixed dolphin	Admixed dolphin
Initial abundance	1331[a]	22[a]	55[a]	55[a]	55[a]
Per capita fertility rate (f)	0.25[b]	0.26[c]	0.26	0.19[d]	0.33[e]
Age of first reproduction	11[b]	9[c,f]	10	11	9
Calf survival (Sc)	0.80[g]	0.80[g]	0.80	0.80[g]	0.80[g]
Juvenile survival (Sj)	0.94[a]	0.94[a]	0.94	0.92[a]	0.96[a]
Transition rate 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}

[a] Gulf of Corinth, Greece (Santostasi et al., 2016).
[b] Western Mediterranean (Calzada et al., 1997).
[c] Atlantic (Murphy et al., 2009)
[d] Iberian (Murphy et al., 2009).
[e] control group (Murphy et al., 2009).
[f] Eastern North Atlantic (Mannocci et al., 2012).
[g] Theoretical calculation by Taylor et al., (2007).

become reproductively mature earlier (having the youngest age of first reproduction between the two parental species), iii) in the Outbreeding Depression scenario we assumed that admixed individuals have lower survival (the lower 95% confidence limit estimated for this population by Santostasi et al., 2016) and annual per capita fertility rate (the lowest annual pregnancy rate reported for Atlantic common dolphin subpopulations reported in Murphy et al., 2009), and that they become reproductivley mature later (having the oldest age of first reproduction between the two parental species).

The mating systems of odontocete cetaceans (toothed whales) have been reported as either polygynous (some males with multiple partners) or polygynandrous (both males and females with multiple partners; Murphy et al., 2005). We assumed that mature females belonging to one species would reproduce with mature males belonging to the same species, the other species or the admixed individuals, proportionally to their relative abundance. We used deterministic projections (i.e., with constant parameters) to compare the predicted time of extinction for the two species with and without the hybridization effect. The matrix formulation corresponding to the dolphin model is presented below. The subscript Sc refers to striped dolphin, the subscript Dd refers to common dolphins the subscript h refers to admixed individuals. In the Appendix A we show the corresponding R code, the linear equations, and we describe how to incorporate demographic stochasticity.

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

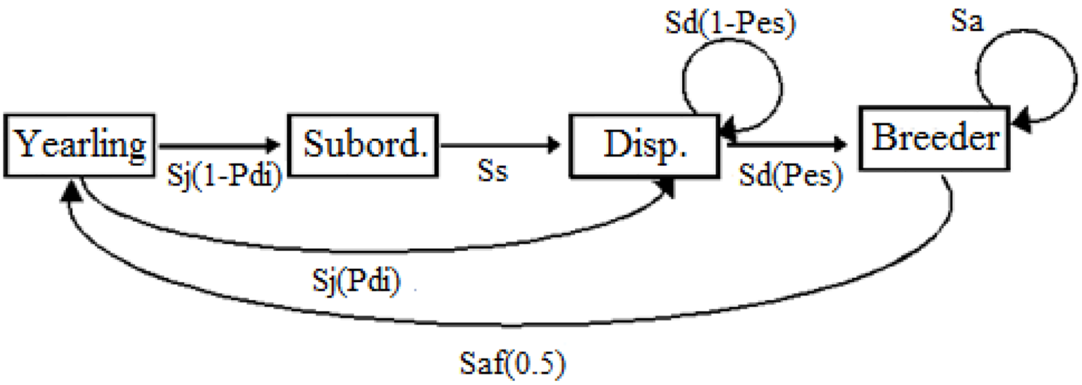


Figure 2. Life cycle for the wolf case study. Parameters are: Sj = survival rate of yearlings, Ss = survival rate of subordinates (yearlings and adults), Sd = survival rate of dispersers (yearlings and adults), Sa = survival rate of breeders, f = annual per capita fertility rate approximated as the litter size, Pdi = dispersal rate, Pes = transition rate to the breeder stage.

Table 3
Rates of formation of the reproductive pairs considered in the model.

Female parent	Male parent	Rate
W	W	$Df_w \mathrm{sd_w Pes_w} \alpha(\mathrm{t})$
W	D	$Df_w \mathrm{sd_w Pes_h} frd(\mathrm{t})$
W	H	$Df_w \mathrm{sd_w Pes_h} \gamma(\mathrm{t})$
H	W	$Df_w \mathrm{Sd_h Pes_h} \gamma(\mathrm{t})$
H	H	$Df_w \mathrm{Sd_h Pes_h} \gamma(\mathrm{t})$

Df_w = abundance of wolf females in dispersal, $\mathrm{Pes_w}$ = transition rate to the breeder stage for wolf females, $\mathrm{Pes_h}$ = transition rate to the breeder stage for admixed females, *frd* = constant annual frequency of reproductive events between female wolves and male dogs, α(t) = relative abundance of male wolves in dispersal, γ(t) = relative abundance of admixed males in dispersal.

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 pair breeds, producing a single litter of pups every year. The pups that survived their first year (yearlings), may survive their second year (with survival rate Sj) and disperse (with dispersal rate Pdi), or they may remain in the natal pack (with non-dispersal rate 1 - Pdi) 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 survival rate Ss) one year in the natal pack they will then leave and become individuals in dispersal by their third year of age; 2) the subordinates never directly transition to being breeders; 3) individuals in dispersal can either die or survive (with survival rate Sd), and gain access to reproduction by establishing a new pack (with transition rate to the breeder stage Pes) or remain dispersers (1-Pes); 4) breeders never lose their status remaining in the breeder stage and surviving with survival rate Sa. 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; Marucco and McIntire, 2010 in which hybridization has not been detected yet (Fabbri et al., 2007). The details about model parametrization are shown in Appendix B.

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 between male wolves and female dogs appears to be rare (Hindrickson et al., 2012). Therefore, in the model we did not consider reproductive pairs formed by male wolves and female dogs. For simplicity, we did not model the occurrence of backcrossing to dogs (the reproduction of admixed individuals and dogs; Table 3). We assumed that a constant number of reproductive events happens every year between female wolves and male dogs (parameter *frd*). The rate of the formation of reproductive pairs between a female wolf and male wolf at time t +1 is therefore expressed as the product between the abundance of wolf females in dispersal (Df_w) by their survival ($\mathrm{Sd_w}$) by the probability that a female reaches the breeder stage by establishing a new pack ($\mathrm{Pes_w}$) by the relative abundance of wolf males in dispersal *α(t)*. The rates of formation of wolf-dog reproductive pairs, and of reproductive pairs in which at least one individual is admixed are formulated in Table 3.

For wolves, we used the probability of establishing a pack calculated by Marescot et al., (2012) as the transition rate to the breeder stage (Pes). Such annual rate varies uniformly between 0.3 to 0.7. For the Null Model, we assigned the the same average value (Pes = 0.5) to wolves and admixed individuals. We produced two alternative scenarios of reproductive isolation by simulating a reduced probability of establishing a pack for admixed females. In one scenario (Reproductive Isolation 1), we attributed the average value (0.5) to wolves and the minimum value (0.3) to the admixed individuals. In the second scenario (Reproductive Isolation 2) we assigned the maximum probability of establishing a pack to wolves (0.7) and the minimum probability (0.3) to the admixed individuals (Table 4). We used the prevalence of hybrids as a measure to define the type of hybridization reached at the end of the projection time-frame. The matrix formulation corresponding to the wolf x dog model is presented below:

$$\begin{pmatrix}
0 & 0 & 0 & \mathrm{f_w Sa_w} 0.5 & 0 & 0 & 0 & 0 \\
\mathrm{Sj_w}\, Pdi_w & 0 & \mathrm{Ss_w} & 0 & 0 & 0 & 0 & 0 \\
\mathrm{Sj_w}\,(1 - Pdi_w) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathrm{Sd_w} Pes_w \alpha(t) & 0 & \mathrm{Sa_w} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathrm{f_h Sa_h} 0.5 \\
0 & 0 & 0 & 0 & \mathrm{Sj_h}\, Pdi_h & 0 & Ss_h & 0 \\
0 & 0 & 0 & 0 & \mathrm{Sj_h}\,(1 - Pdi_h) & 0 & 0 & 0 \\
0 & \mathrm{Sd_w} Pes_h(frd + \gamma(t)) & 0 & 0 & 0 & \mathrm{Sd_h} Pes_h(\alpha(t) + \gamma(t)) & 0 & \mathrm{Sa_h}
\end{pmatrix}$$

Table 4

Demographic parameters used for projecting the abundance of wolves and admixed 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[a]	0	6[a]	0	6[a]	0
Average litter size (f)	3.387[a]	3.387[a]	3.387[a]	3.387[a]	3.387[a]	3.387[a]
Juvenile survival (Sj)	0.551[a]	0.551[a]	0.551[a]	0.551	0.551[a]	0.551
Subordinate survival (Ss)	0.82[a]	0.82[a]	0.82[a]	0.82[a]	0.82[a]	0.82[a]
Disperser Survival (Sd)	0.69[b]	0.69[b]	0.69[b]	0.69[b]	0.69[b]	0.69[b]
Breeder survival (Sa)	0.82[c]	0.82[c]	0.82[c]	0.82[c]	0.82[c]	0.82[c]
Dispersal rate (Pdi)	0.25[d]	0.25[d]	0.25[d]	0.25[d]	0.25[d]	0.25[d]
Transition rate to the breeder stage (Pes)	0.5[d,e]	0.5[d,e]	0.5[d,e]	0.3[d,e]	0.7[d,e]	0.3[d,e]

[a] Marucco and McIntire, 2010.
[b] Blanco and Cortés 2007.
[c] Marucco et al., 2009.
[d] Mech and Boitani, 2003.
[e] Marescot et al., 2012.

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

2.3. Sensitivity analysis

We performed a sensitiviy analysis to explore the relationship between the hybridization outcome (genomic extinction vs. persistence of parental and admixed populations after 50 years) and the demographic parameters of parental species and admixed individuals (Mc Carthy et al., 1995; Cross and Beissinger, 2001). Here, we use "genomic extinction" to refer to the disappearence of parental individuals from the population (Allendorf et al., 2001). We generated 15,000 parameter sets by drawing them from uniform distributions (Table 5) to emphasize the effects of variability in vital rates on model sensitivity (Cross and Beissinger, 2001). We projected population abundance with each parameter set and checked if the population went extinct or not using a quasi-extinction threshold of 5 parental mature females. We conducted logistic regressions to explore the relationship between the probability of genomic extinction of the two parental species as response variables and demographic parameters used in the projections as independent explanatory variables. For each regression we built full models including all the parameters and used a backward stepwise selection procedures to identify the sets of parameters of potential importance (Fredrickson and Hedrick, 2006). From those sets of parameters we ranked their relative importance in affecting the probability of genomic extinction of the parental species based on their standardized regression coefficients which are the regression coefficient divided by their standard error (Cross and Beissinger, 2001). In the Appendix A and B we show the code to perform the logistic regression sensitivity analysis and how to perform a sensitivity analysis of the asymptotic growth rate using the matrix formulation for the two case studies (R codes are also reported there).

3. Results

3.1. Striped x common dolphin model

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

3.2. Wolf x dog model

Depending on the scenario, hybridization had different final outcomes. In the Null Model all the scenarios reached complete admixture (prevalence of admixed individuals = 1) after 50 years and prevalence increased more rapidly at the increasing of the recurrent gene flow from dogs (Fig. 5, upper-left panel). The reproductive isolation scenarios showed different outcomes. In the scenario with the weakest reproductive isolation (Reproductive Isolation 1) the prevalence increased less rapidly compared to the Null Model (Fig. 5, upper-right panel) but did not reach an asymptote, heading towards a final outcome of complete admixture (Allendorf et al., 2001). In the scenario of strongest reproductive isolation (Reproductive Isolation 2), prevalence reached an asymptote whose final value increased at the increasing of the intensity of the recurrent gene flow from dogs (Fig. 5, lower-left panel). In this last case the final outcome is the co-existence of admixed and parental individuals with a constant prevalence (assuming that all the demographic parameters remain constant over time). This last scenario falls into the definition of "widespread introgression" (Allendorf et al., 2001).

3.3. 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).

For the wolf x dog case study, our sensitivity analysis showed that wolf genomic extinction probability was mostly affected by wolf breeder survival (Sa_w), followed by annual frequency of mating with dogs (*frd*), wolf access to reproduction (i.e., transition rate to the breeder stage, Pes_w) and annual wolf per capita fertility rate f_w, with the same relative importance (Table 7).

4. Discussion

Identifying the demographic factors affecting the outcome of hybridization helps both understanding evolutionary mechanisms and developing meaningful management and conservation measures when

Table 5
Demographic parameters range used for drawing the demographic parameters from uniform distributions to project the abundance of parental and admixed individuals in the sensitivity analyses.

Striped x common dolphin

Taxon	Parameter	Range
Common dolphin	Initial abundance	16-32[a]
	Age of first reproduction	9-11[b,c,d]
	Calf survival	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility rate	0-0.33[b,c]
Admixed dolphins	Initial abundance	36-84[a]
	Age of first reproduction	9-11[b,c,d]
	Calf survival	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility rate	0-0.33[b,c]
Striped dolphin	Initial abundance	1331-1578[a]
	Age of first reproduction	9-11[b,c,d]
	Calf	0.2-1
	Juvenile survival	0.2-1
	Adult survival	0.2-1
	Annual per capita fertility rate	0-0.33[b,c]

Wolf x dog

Taxon	Parameter	Range
Wolf	Annual per capita fertility rate	0-4.5[e]
	Juvenile survival	0.2-1
	Subordinate survival	0.2-1
	Disperser Survival	0.2-1
	Breeder survival	0.2-1
	Dispersal rate	0-0.4[e]
	Transition rate to the breeder stage	0-0.7[f]
Admixed	Annual per capita fertility rate	0-4.5[e]
	Juvenile survival	0.2-1
	Subordinate survival	0.2-1
	Disperser Survival	0.2-1
	Breeder survival	0.2-1
	Dispersal rate	0-0.4[e]
	Transition rate to the breeder stage	0-0-7[f]
Dog	Frequency of mating with dogs	0-1

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

[a] Gulf of Corinth, Greece (Santostasi et al., 2016).

[b] Western Mediterranean (Calzada et al., 1997).

[c] Control group (Murphy et al., 2009).

[d] Eastern North Atlantic (Mannocci et al., 2012).

[e] Mech and Boitani, 2003.

[f] Marescot et al., 2012.

hybridization is a threat (Bohling, 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 Wyck et al., (2016) considered that backroses 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 Wyck 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 overcame 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 unavailable in many studies. In such cases, one would need to make assumptions regarding admixed individuals survival and fertility rates. However, sensitivity analysis showed that genomic extinction probability was largely affected by the demographic parameters of parentals, whereas the parameters of admixed individuals had a lower relative importance. Nonetheless, the sensitivity of model predictions to unknown parameters should be tested through sensitivity analyses, and should be taken into account by considering different scenarios. Moreover, the comparison of alternative simulated scenarios with empirical data (i.e., the observed prevalence trends) can provide insight into the evolutionary mechanism shaping the observed patterns.

Another important limitation is that, for simplicity and for the absence of species-specific information, we assumed random mating and did not model more complex mating choice scenarios that could lead to assortative mating. If information about assortative mate choice is available, it can be modelled by changing the reproduction coefficients (α, β and γ in paragraph 2.1.1) from being proportional to the relative abundance of mature males to reflecting the observed percentage of conspecific and heterospecific matings.

At the moment, our projections cannot be validated due to the absence of long-term data on the quantitative evaluation of hybridization for the two case-studies. However, the predicted outcomes are consistent with previous studies showing that hybridization can lead to rapid genomic extinction in the absence of reproductive isolation (Huxel, 1999) or other forms of segregation (Wolf et al., 2001; Fredrickson and Hedrick, 2006). Two studies on wolf x dog hybridization (Salvatori et al., 2019; Santostasi et al., 2019) showed that the prevalence of hybrids can locally reach high levels (around 50%) where reproductive isolation between wolves and dogs is disrupted by anthropogenic disturbance (e.g., presence of free ranging dogs, food provisioning, high wolf anthropogenic mortality), supporting the results of our projections. We suggest that, given the importance of reproductive isolation mechanisms in determining the wolf x dog hybridization outcome, more research should be addressed to understand to what extent and in which circumstances those mehcanisms are effective in contrasting hybridization. In absence of such information, the lack of strong reproductive isolation should be assumed as a precautionary measure.

Studies on hybridization dynamics in cetaceans that could be used to validate our projections are not available. However, our finding that

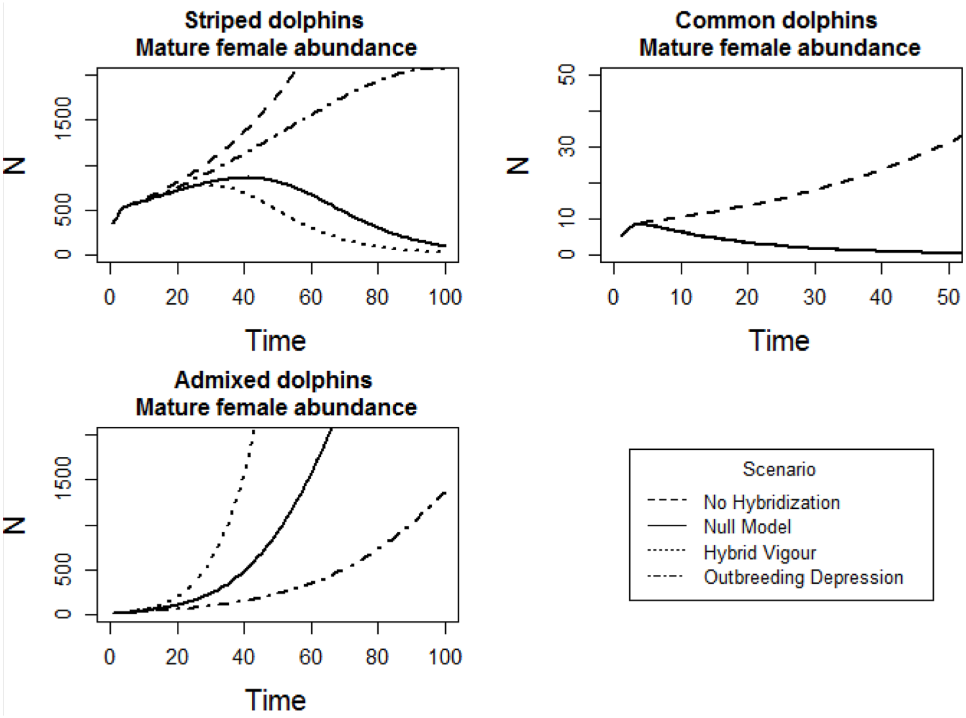


Figure 3. Population trajectories of striped, common and admixed dolphins under different parental and admixed individuals fitness scenarios (the continuos line represents the Null Model while the different types of dashed lines represent the model in absence of hybridization, the Outbreeding Depression Scenario and the Hybrid Vigour Scenario).

the genomic extinction risk for the parental population increases as their initial frequency decreases, making the least abundant species particularly vulnerable, is consistent with previous studies (Allendorf et al., 2001; Epifanio and Philipp, 2001).

We stress that the interest of our model is not the production of absolute predictions of population fate. Being long term hybridization dynamics otherwise difficult to test empirically, the practical value of our model is to illustrate the expected relative outcomes of alternative biological and managament scenarios. The comparison of those outcomes can be useful to highlight future research priorities and to inform

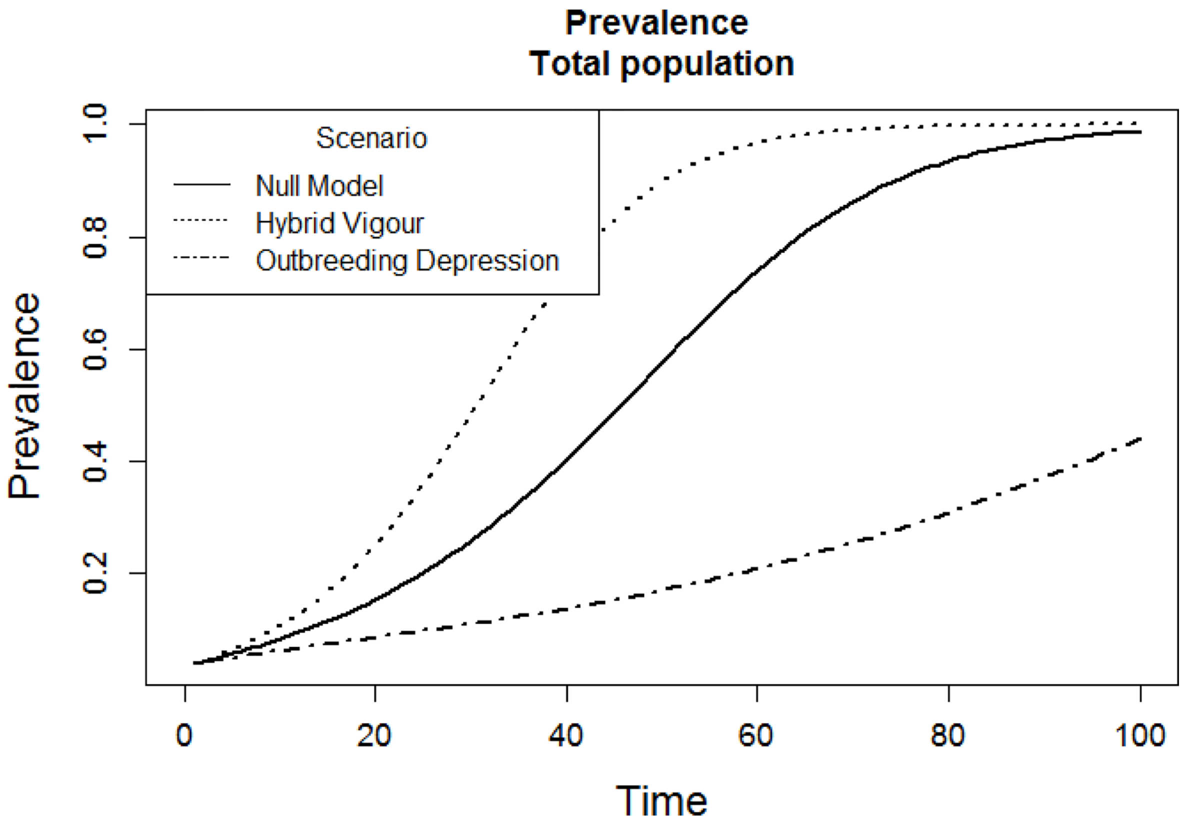


Figure 4. Projected prevalence of striped x common dolphin admixed individuals in the mixed dolphin population of the Gulf of Corinth, Greece under different parental and admixed individuals fitness scenarios (the continuos line represents the Null Model while the different types of dashed lines represent the Outbreeding Depression Scenario and the Hybrid Vigour Scenario).

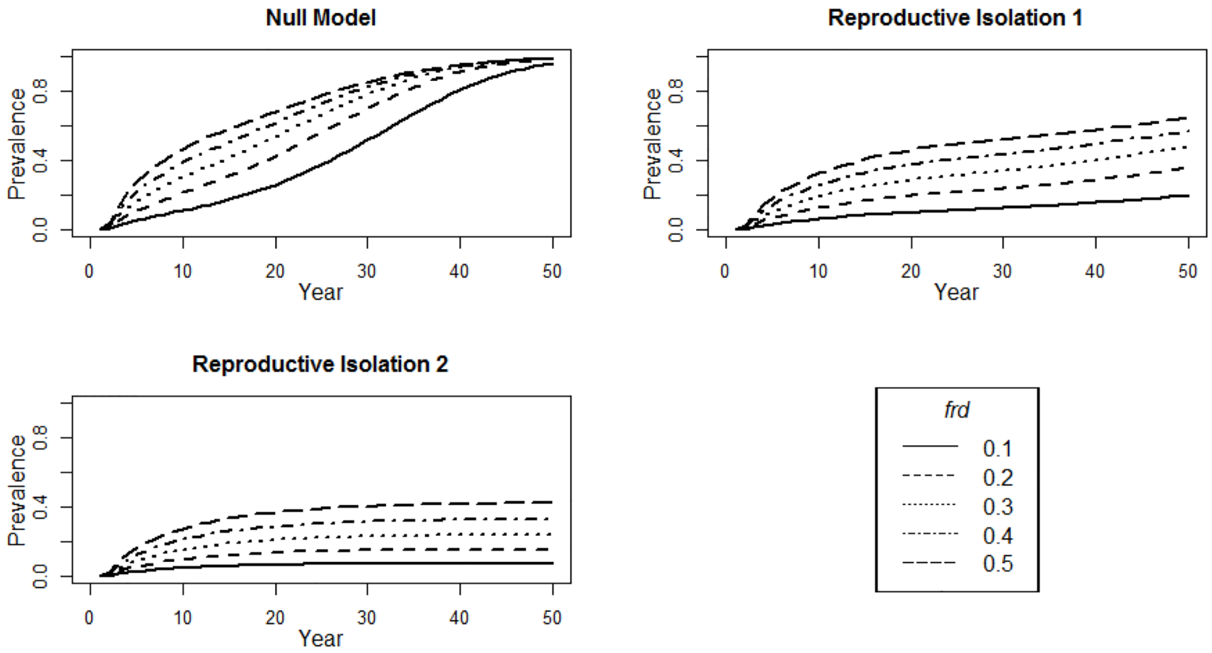


Figure 5. Projected prevalence of wolf x dog admixed individuals under increasing levels of recurrent gene flow from dogs (parameter *frd*) and under different reproductive isolation scenarios: the Null Model (upper-left panel), the Reproductive Isolation 1 scenario (upper-right panel) and the Reproductive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

Table 6

Logistic regression sensitivity analysis results for striped and common dolphin population projections in the presence of hybridization.

Parameter	Coefficient	Standard Error	Standardized Coefficient	p value
Striped dolphin genomic extinction				
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				
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

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 capita 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.

decision-making in a context of uncertainty (Gervasi and Ciucci, 2018).

In alternative, not acknowledging hybridization in the projections may lead to underestimating the risk of genomic extinction. The common dolphin (the least abundant species) had a 100% probability of going extinct after a relatively short time (16 years) regardless the fitness scenario. A previous count-based projection (Santostasi et al., 2018) did not include the effect of hybridization (although it included the effect of demographic stochasticity) and estimated a considerably lower (50%) probability of demographic extinction after 15 years.

Table 7

Logistic regression sensitivity analysis results for the wolf population projections in the presence of hybridization with dogs.

Parameter	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

The parameters are sorted in descending order of relative importance, evaluated by looking at the standardized regression coefficients. Sa = annual breeder survival, f = fertility rate (approximated as litter size), Pes (transition rate to the breeder stage), *frd* = annual frequency of mating with dogs, Sj = annual juvenile survival, Sd = annual disperser survival, Ss = annual subordinate survival, Pdi = annual dispersal rate. The subscript w indicates wolf demographic parameters and the subscript h indicates admixed individuals' demographic parameters.

Although the two predictions are not entirely comparable due to the different methodologies, our results suggest that hybridization may pose an additional and important threat that must be considered when evaluating the conservation status of common dolphins. This is particularly relevant at larger scales, considering that, in the Mediterranean Sea common dolphins occurr in simpatry with the more abundant striped dolphins and mixed-species groups are not rare (Frantzis and Herzing, 2002; Giménez et al., 2017; Espada et al., 2019).

Interestingly, the population growth rate of the most abundant species, the striped dolphin, was also affected and hybridization could eventually lead this population to genomic extinction, under scenarios in which the fitness of admixed individuals is equal to or greater than that of parentals (i.e., the Null Model and the Hybrid Vigour scenario). However, striped dolphins are predicted to persist and even increase in the next 100 years, if the fitness of admixed individuals is lower than that of parentals (i.e., the Outbreeding Depression scenario). More research on the fitness of admixed individuals would help understand which scenario represents the most likely alternative. Research on the genetic composition and ecology of admixed individuals would help understand if the predicted "hybrid swarm" may: 1) lead to a new species (Larsen et al., 2010; Lamichhaney et al., 2018); 2) preserve the integrity of the striped dolphin species by backcrossing and dilution of the common dolphin genetic contribution; or 3) allow for the persistence of adaptive common dolphin alleles in the striped dolphin, as suggested by other cases of adaptive introgression (Figueiró et al., 2017).

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., 2012), 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., 2012; 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 decisions (Kelly et al., 2010).

Declaration of Competing Interest

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

Acknowledgements

OG and NLS were supported by the French National Research Agency with a Grant ANR-16-CE02-0007. NLS was supported by a PhD grant by Sapienza University of Rome. We thank the Editor and two anonimous reviewers for their insightful suggestions during the editorial process. We thank Dr. Federico Manna for his help with the matrix formulations.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109120.

Literature cited

Abbott, R.J., Barton, N.H., Good, J.M., 2016. Genomics of hybridization and its evolutionary consequences. Mol. Ecol. 25, 2325–2332.

Antoniou, A., Frantzis, A., Alexiadou, P., Paskou, N., Poulakakis, N., 2019. Evidence of introgressive hybridization between *Stenella coeruleoalba* and *Delphinus delphis* in the Greek Seas. Mol. Phylogenet. Evol. 129, 325–337.

Allendorf, F.W., Leary, R.F., Spruell, P., Wenburg, J.K., 2001. The problems with hybrids: setting conservation guidelines. Trends Ecol. Evol. 16, 613–622.

Barton, N.H., Hewitt, G.M., 1989. Adaptation, speciation and hybrid zones. Nature 341, 497–503.

Aguilar, A., Gaspari, S., 2012. *Stenella coeruleoalba* (Mediterranean subpopulation). The IUCN Red List of Threatened Species.

Bearzi, G., Bonizzoni, S., Santostasi, N.L., Furey, N.B., Eddy, L., Valavanis, V.D., Gimenez, O., 2016. Dolphins in a scaled-down Mediterranean: the Gulf of Corinth's odontocetes. Mediterranean Marine Mammal Ecology and Conservation. Adv. Mar. Biol. 75, 297–331.

Bearzi, G., Reeves, R.R., Notarbartolo di Sciara, G., Politi, E., Cañadas, A., Frantzis, A., Mussi, B., 2003. Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. Mammal. Rev. 33, 224–252.

Bohling, J.H., 2016. Strategies to address the conservation threats posed by hybridization and genetic introgression. Biol. Conserv. 203, 321–327.

Bohling, J.H., Waits, L.P., 2015. Factors influencing red wolf–coyote hybridization in eastern North Carolina, USA. Biol. Conserv. 184, 108–116.

Boitani, L., 2000. Action plan for the conservation of Wolves in Europe (*Canis lupus*). Council of Europe Publishing, Strasbourg, France, pp. 1–84.

Boitani, L., 2003. Wolf conservation and recovery. In: Mech, L.D, Boitani, L. (Eds.), Wolves, Behaviour Ecology and Conservation. University of Chicago Press, Chicago, United States of America, pp. 317–340.

Calzada, N., Aguilar, A., Lockyer, C., Grau, E., 1997. Patterns of growth and physical maturity in the western Mediterranean striped dolphin, *Stenella coeruleoalba*. Can. J. Zool. 75, 632–637.

Campbell, D.R., Waser, N.M., Pederson, G.T., 2002. Predicting patterns of mating and potential hybridization from pollinator behavior. Am. Nat. 159, 438–450.

Caniglia, R., Fabbri, E., Greco, C., Galaverni, M., Manghi, L., Boitani, L., Sforzi, A., et al., 2013. Black coats in an admixed wolf dog pack is melanism an indicator of hybridization in wolves? Eur J Wildl Res 59, 543–555.

Crispo, E., Moore, J., Lee-Yaw, J.A., Gray, S.M., Haller, B.C., 2011. Broken barriers: human-induced changes to gene flow and introgression in animals. BioEssays 33, 508–518.

Cross, P.C., Beissinger, S.R., 2001. Using logistic regression to analyze the sensitivity of PVA models: a comparison of methods based on African wild dog models. Conserv. Biol. 15, 1335–1346.

Crossman, C.A., Taylor, E.B., Barrett-Lennard, L.G., 2016. Hybridization in the Cetacea: widespread occurrence and associated morphological, behavioral, and ecological factors. Ecol. Evol. 6, 1293–1303.

Crouse, D., Crowder, L., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68, 1412–1423.

DeMarais, B.D., Dowling, T.E., Douglas, M.E., Minckley, W.L., Marsh, P.C., 1992. Origin of *Gila seminuda* (Teleostei: Cyprinidae) through introgressive hybridization: implications for evolution and conservation. Proc. Natl. Acad. Sci. U.S.A 89, 2747–2751.

Epifanio, J., Philipp, D., 2001. Simulating the extinction of parental lineages from introgressive hybridization: the effects of fitness, initial proportions of parental taxa, and mate choice. Rev. Fish Biol. Fish. 10, 339–354.

Espada, R., Olaya-Ponzone, L., Haasova, L., Martín, E., García-Gómez, J.C., 2019. Hybridization in the wild between *Tursiops truncatus* (Montagu 1821) and *Delphinus delphis* (Linnaeus 1758). PLoS ONE 14(4).

Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., Weber, J.M., et al., 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (*Canis lupus*) population. Mol. Ecol. 16, 1661–1671.

Ferdy, J., Austerlitz, F., 2002. Extinction and introgression in a community of partially cross-fertile plant species. Amer. Nat. 160, 74–86.

Figueiró, H.V., Li, G., Trindade, F.J., Assis, J., Pais, F., Fernandes, G., Santos, S.H.D., et al., 2017. Genome-wide signatures of complex introgression and adaptive evolution in the big cats. Sci. Adv. 3.

Frantzis, A., Herzing, D.L., 2002. Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece. Mediterranean Sea). Aquat. Mamm. 28, 188–197.

Fredrickson, R.J., Hedrick, P.W., 2006. Dynamics of hybridization and introgression in red wolves and coyotes. Conserv. Biol. 20, 1272–1283.

Galaverni, M., Caniglia, R., Pagani, L., Fabbri, E., Boattini, A., Randi, E., 2017. Disentangling timing of admixture, patterns of introgression, and phenotypic indicators in a hybridizing wolf population. Mol. Biol. Evol. 34, 2324–2339.

Gervasi, V., Ciucci, P., 2018. Demographic projections of the Apennine brown bear population *Ursus arctos marsicanus* (Mammalia: Ursidae) under alternative management scenarios. The European Zoological Journal 85, 242–252.

Gese, E.M., Knowlton, F.F., Adams, J.R., Beck, K., Fuller, T., Murray, D.L., Steury, T.D., et al., 2015. Managing hybridization of a recovering endangered species: the red wolf *Canis rufus* as a case study. Curr. Zool. 61, 191–205.

Giménez, J., Cañadas, A., Ramírez, F., Afán, I., García-Tiscar, S., Fernández-Maldonado, Castillo, J.J., et al., 2017. . Intra- and interspecific niche partitioning in striped and common dolphins inhabiting the southwestern Mediterranean Sea. Mar. Ecol. Progr. Ser. 567, 199–210.

Godinho, R., Llaneza, L., Blanco, J.C., Lopes, S., Álvares, F., García, E.J., Palacios, V., et al., 2011. . Genetic evidence for multiple events of hybridization between wolves and domestic dogs in the Iberian Peninsula. Mol. Ecol. 20, 5154–5166.

Grabenstein, K.C., Taylor, S.A., 2018. Breaking barriers: causes, consequences, and experimental utility of human-mediated hybridization. Trends Ecol. Evol. 2342, 1–15.

Grant, P.R., Grant, B.R., 1992. Hybridization of bird species. Science 256, 193–197.

Hall, R.J., Ayres, D.R., 2008. What can mathematical modeling tell us about hybrid invasions? Biol. Invasions 11, 1217–1224.

Hewitt, G.M., 1988. Hybrid zones: natural laboratories for evolutionary studies. Trends Ecol. Evol. 3, 158–167.

Hindrickson, M., Mannil, P., Ozolins, J., Krzywinsky, A., Saarma, U., 2012. Bucking the trend in wolf-dog hybridization between female dogs and male wolves. PLoS ONE 7(10).

Hooftman, D.A.P., De Jong, M.J., Oostermeijer, J.G.B., den Nijs, H.C.M., 2007. Modelling the long-term consequences of crop-wild relative hybridization: a case study using four generations of hybrids. J. Appl. Ecol. 44, 1035–1045.

Huxel, G.R., 1999. Rapid displacement of native species by invasive species: effects of hybridization. Biol. Cons. 89, 143–152.

Kelly, B., Whiteley, A., Tallmon, D.A., 2010. The Arctic melting pot. Nature 468, 891.

Lamichhaney, S., Han, F., Webster, M.T., Andersson, L., Grant, B.R., Grant, P.R., 2018. Rapid hybrid speciation in Darwin's finches. Science 359, 224–228.

Larsen, P.A., Marchán-Rivadeneira, M.R., Baker, R.J., 2010. Natural hybridization generates mammalian lineage with species characteristics. Proc. Natl. Acad. Sci. USA. 107 11447–1152.

Mannocci, L., Dabin, W., Augeraud-Véron, E., Dupuy, J-F., Barbraud, C., Ridoux, V., 2012. Assessing the impact of bycatch on dolphin populations: the case of the common dolphin in the Eastern North Atlantic. PLoS ONE 7(2).

Marescot, L., Gimenez, O., Duchamp, C., Marboutinc, E., Chapron, G., 2012. Reducing matrix population models with application to social animal species. Ecol. Model. 232, 91–96.

Marucco, F., McIntire, E.J.B., 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. J. Appl. Ecol. 47, 789–798.

Marucco, F., Pletscher, D.H., Boitani, L., Schwartz, M.K., Pilgrim, K.L., Lebreton, J-D., 2009. Wolf survival and population trend using non-invasive capture–recapture techniques in the Western Alps. J. Appl. Ecol. 46, 1003–1010.

McCarthy, M.A., Burgman, M.A., Ferson, S., 1995. Sensitivity analysis for models of population viability. Biol. Cons. 73, 93–100.

Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, United States of America, pp. 1–447.

Murphy, S., Collet, A., Rogan, E., 2005. Mating strategy in the male common dolphin (*Delphinus delphis*): what gonadal analysis tells us. J. Mammal. 86, 1247–1258.

Murphy, S., Winship, A., Dabin, W., Jepson, P., Deavill, R., Reid, J.R., Spurrie, C., et al., 2009. Importance of biological parameters in assessing the status of *Delphinus delphis*. Mar. Ecol-Prog. Ser. 388, 273–291.

Nathan, L.R., Mamoozadehb, N., Tumasc, H.R., Gunselmand, S., Klasse, K., Metcalfef, A., Edgeg, C., et al., 2019. A spatially-explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics. Ecol. Modell. 401, 40–51.

Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. Trends Ecol. Evol. 19, 18–24.

Pacheco, C., López-bao, J.V., García, E.J., Lema, F.J., Llaneza, L., Palacios, V., Godinho, R., 2017. Spatial assessment of wolf-dog hybridization in a single breeding period. Sc. Rep. 7, 1–10.

R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randi, E., 2008. Detecting hybridization between wild species and their domesticated relatives. Mol. Ecol. 17, 285–293.

Randi, E., Lucchini, V., 2002. Detecting rare introgression of domestic dog genes into wild wolf (*Canis lupus*) populations by Bayesian admixture analyses of microsatellite variation. Conserv. Genet 3, 31–45.

Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. Annu. Rev. Ecol. Syst. 27, 83–109.

Rutledge Y., L., White N., B., Row R., J., Patterson R., B., 2012. Intense harvesting of eastern wolves facilitated hybridization with coyotes. Ecol. Evol. 2, 19–33.

Santostasi, N.L., Bonizzoni, S., Bearzi, G., Eddy, L., Gimenez, O., 2016. A robust design capture-recapture analysis of abundance, survival and temporary emigration of three odontocete species in the Gulf of Corinth, Greece. PLoS ONE 11(12).

Santostasi, N.L., Bonizzoni, S., Gimenez, O., Eddy, L., Bearzi, G., 2018. Common dolphins in the Gulf of Corinth are Critically Endangered. Aquat. Conserv. 1–9.

Santostasi, N.L., Ciucci, P., Caniglia, R., Fabbri, E., Molinari, L., Reggioni, W., Gimenez, O., 2019. Use of hidden Markov capture–recapture models to estimate abundance in the presence of uncertainty: application to the estimation of prevalence of hybrids in animal populations. Ecol Evol 9, 744–755.

Salvatori V., Godinho, R., Braschi, C., Boitani, L., Ciucci, P., 2019. High levels of recent wolf × dog introgressive hybridization in agricultural landscapes of central Italy. Eur. J. Wildlife Res. 65, 73.

Taylor, B.L., Chivers, S.J., Larese, J., Perrin, W.F., 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01 National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA, United States of America, pp. 1–24.

Thompson, C.J., Thompson, B.J.P., Ades, P.K., Cousens, R., Garnier-Gere, P., Landman, K., Newbigin, E., et al., 2003. Model-based analysis of the likelihood of gene introgression from genetically modified crops into wild relatives. Ecol. Model. 162, 199–209.

Todesco, M., Pascual, M.A., Owens, G.L., Ostevik, K.L., Moyers, B.T., Hübner, S., Heredia, S.M., et al., 2016. Hybridization and extinction. Evol. Appl. 9, 892–908.

Vähä, J.P., Primmer, C.R., 2006. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. Mol. Ecol. 15, 63–72.

van Wyk, A.M., Dalton, D.L., Hoban, S., Bruford, M.W., Russo, I.R.M., Birss, C., Grobler, B., et al., 2016. Quantitative evaluation of hybridization and the impact on biodiversity conservation. Ecol. Evol. 7, 1–11.

Verhoeven, K.J.F., Macel, M., Wolfe, L.M., Biere, A., 2011. Population admixture, biological invasions and the balance between local adaptation and inbreeding depression. Proc. R. Soc. Lond. [Biol] 278, 2–8.

Vilà, C., Wayne, R.K., 1999. Hybridization between wolves and dogs. Conservat. Biol. 13, 195–198.

Wolf, D.E., Takebayashi, N., Rieseberg, L.H., 2001. Predicting the risk of extinction through hybridization. Conservat. Biol. 15, 1039–1053.

Zimen, E., 1975. Social dynamics of the wolf pack. In: Fox, M.V. (Ed.), The Wild Canids: their Systematics, Behavioural Ecology and Evolution. Van Nostrand Reinhold, New York, United States of America, pp. 336–363.