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CONTRIBUTED PAPER

Simulating the efficacy of wolf–dog hybridization management with individual-based modeling

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Abstract

Introgressive hybridization between wolves and dogs is a conservation concern due to its potentially deleterious long-term evolutionary consequences. European legislation requires that wolf–dog hybridization be mitigated through effective management. We developed an individual-based model (IBM) to simulate the life cycle of gray wolves that incorporates aspects of wolf sociality that affect hybridization rates (e.g., the dissolution of packs after the death of one/both breeders) with the goal of informing decision-making on management of wolf–dog hybridization. We applied our model by projecting hybridization dynamics in a local wolf population under different mate choice and immigration scenarios and contrasted results of removal of admixed individuals with their sterilization and release. In several scenarios, lack of management led to complete admixture, whereas reactive management interventions effectively reduced admixture in wolf populations. Management effectiveness, however, strongly depended on mate choice and number and admixture level of individuals immigrating into the wolf population. The inclusion of anthropogenic mortality affecting parental and admixed individuals (e.g., poaching) increased the probability of pack dissolution and thus increased the probability of interbreeding with dogs or admixed individuals and boosted hybridization and introgression rates in all simulation scenarios. Recognizing the necessity of additional model refinements (appropriate parameterization, thorough sensitivity analyses, and robust model validation) to generate management recommendations applicable in real-world scenarios, we maintain confidence in our model’s potential as a valuable conservation tool that can be applied to diverse situations and species facing similar threats.

KEYWORDS

Canis lupus, hybridization, individual-based model, management, population dynamics, projection modeling

INTRODUCTION

Although natural hybridization (the intermixing of 2 distinct related taxa [Gompert & Buerkle, 2016]) is a positive evolutionary force because it introduces beneficial adaptive genetic variation (Abbott et al., 2016), anthropogenic hybridization is considered a threat to biodiversity (Ottenburghs, 2021; Todesco et al., 2016). Anthropogenic hybridization can threaten parental species persistence through the waste of reproductive effort if first-generation hybrids are sterile (demographic swamping) or through the replacement of parental populations

by hybrid swarms (genetic swamping; Allendorf et al., 2001) if the first-generation hybrids are fertile. Hybridization between domesticated forms and their wild ancestors is a specific case of anthropogenic hybridization, and it can be exacerbated by human pressures, including encroachment of wildlife habitat and the widespread occurrence of domesticated species (Boivin et al., 2016; Smith et al., 2022). Anthropogenic hybridization is occurring between gray wolves (*Canis lupus*) and dogs (*Canis lupus familiaris*) (Hindrikson et al., 2017). As for other species within the genus *Canis* (e.g., Galov et al., 2015), wolves and dogs can interbreed and their fertile hybrids can backcross with both

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parental populations, leading to the introgression of domesticated genes into the wolf gene pool (Vilà & Wayne, 1999). Cubaynes et al. (2022) found that in North American wolf populations, one introgressed dog allele can increase individuals' fitness by conferring resistance to the canine distemper virus. However, the potentially deleterious consequences of consistent gene flow from dogs to wolves could lead to the loss of adaptive combinations of genes and unique genotypes with a distinctive evolutionary history and the reduction in fitness and adaptive potential due to the introgression of maladaptive traits (Bohling, 2016; Hindrikson et al., 2017; Smith et al., 2022; Wayne & Shaffer 2016).

Although hybridization between wolves and dogs occurred repeatedly since the domestication of dogs (Pilot et al., 2018, 2021), the phenomenon may be occurring at an increasing rate, especially where wolves are recolonizing human-dominated landscapes (e.g., Europe) where free-ranging dogs are the most abundant carnivore (Ritchie et al., 2014). The presence of ongoing hybridization has been confirmed by large-scale surveys that detected recently occurring hybridization (i.e., up to 3 generations [Caniglia et al., 2020]) in several Eurasian wolf populations (Hindrikson et al., 2017; Salvatori et al., 2020). If no effective and timely management reactions are put in place, high levels of admixture prevalence (i.e., proportion of individuals of mixed wolf–dog ancestry, hereafter admixed individuals) could be reached. Accordingly, intensive noninvasive genetic surveys of local admixed wolf populations show prevalence values up to 50% (Salvatori et al., 2019) or 70% (Santostasi et al., 2021), percentages that exclude introgressed individuals of third or older backcross generations to wolves.

To mitigate the threat represented by wolf–dog anthropogenic hybridization, the European Union Council Directive 92/43/EEC and Recommendation 173, 2014 of the Bern Convention mandate member countries to counter wolf–dog hybridization through effective management. The implementation of hybridization management is, however, controversial on practical grounds (Pacheco et al., 2017). This is due to the unclear legal status of admixed individuals (Trouwborst, 2014), a lack of agreement about how to intervene (Donfrancesco et al., 2019), and a lack of reliable data on the effectiveness of alternative management strategies (Salvatori et al., 2020). Although this situation tends to delay management decisions and implementation (Donfrancesco et al., 2019; Salvatori et al., 2020), simulation work indicates that in the absence of management, ongoing hybridization may lead to genomic extinction (Fredrickson & Hedrick, 2006; Santostasi et al., 2020; Wolf et al., 2001).

Increasing evidence shows that individuals' behaviors associated with long-term monogamy, territorial defense, group living, and social cohesion (Kleiman, 2011) serve as behavioral reproductive barriers that prevent hybridization among sympatric *Canis* taxa (Hinton et al., 2018). Assortative mating based on similarity in body size and behavior can also limit the extent of hybridization between red wolves (*Canis rufus*) and coyotes (*Canis latrans*; Hinton et al., 2018). Long-term studies on the hybridization of coyote with red wolf (Bohling & Waits, 2015) and coyote with eastern wolf (*Canis lyciae*; Rutledge et al., 2011) in North America show that such barriers are

disrupted when recurrent anthropogenic mortality (e.g., poaching) of wolf breeders causes pack disruption. In the presence of a large availability of nonconspecific mates, this situation corresponds to likely opportunities for hybridization and facilitates the successful raising of admixed litters (Bohling & Waits, 2015; Rutledge et al., 2011). Although preventive and proactive management measures are generally meant to prevent such situations (Donfrancesco et al., 2019), reactive management aimed at reducing the number and diffusion of admixed individuals represents a fundamental tool to limit anthropogenic introgression from further spreading into a hybrid swarm (e.g., Senn et al., 2019; Stoskopf et al., 2005). Two main reactive strategies have been applied to canids to reduce the extent of hybridization: removal of admixed individuals from the population (i.e., either through culling or capture [Stoskopf et al., 2005]) or their sterilization and release. The latter intervention, assuming hormone-sparing sterilization (i.e., vasectomy and tubal ligation) does not affect social and territorial behavior (Gese & Terletzky, 2015), is based on the placeholder concept. According to this principle, long-term monogamy and territorial defense of the admixed (sterilized) individuals would ensure sterile territories, thereby reducing reproductive opportunities for admixed individuals dispersing across the landscape (Bromley & Gese, 2001a, 2001b; Gese & Terletzky, 2015). Although both removal and sterilization approaches are effective in reducing introgression in the red wolf–coyote case (Gese & Terletzky, 2015), these methods have not been assessed in the wolf–dog case and their relative efficacy has not been evaluated formally.

Demographic simulations are a valuable and cost-effective tool to project population dynamics in hybridizing populations, and they can inform management decisions (Santostasi et al., 2020). Individual-based models (IBMs) are bottom-up models simulating the fate of individuals according to behavioral rules depending on their characteristics (Grimm & Railsback, 2005). Results at the population level emerge from the individual-level simulations. Due to their flexibility, IBMs have been increasingly used for the projection of population dynamics in complex systems, such as the management of social species (Hrascky et al., 2019) and hybridization dynamics (Fredrickson & Hedrick, 2006; Nathan et al., 2019). With an IBM, Fredrickson and Hedrick (2006) suggested that sterilization is an effective short-term strategy to mitigate introgression between red wolves and coyotes in expanding red wolf populations, and their predictions were successively validated by empirical data (Gese & Terletzky, 2015). IBMs mimicking aspects of gray wolves' social behavior and ecology have also been developed (e.g., Chapron et al., 2016; Marucco & McIntire, 2010). More recently, a multifaceted model meant to account for the inherent complexity of wolf social behavior and dynamics has been produced (Bauduin et al., 2020) that included processes such as inbreeding avoidance, pack dissolution following the loss of a breeder, adoption of dispersers by existing packs, establishment of new packs through budding, and different modalities of breeder replacement (Bauduin et al., 2020). By expanding on Bauduin et al.'s (2020) model, we integrated a hybridization module into the IBM to project wolf–dog hybridization dynamics. We then provided a theoretical application of the

TABLE 1 Individual characteristics used in the individual-based model of wolf–dog hybridization.

Parameter	Explanation
Individual identity (ID)	Individual identification code
Age class	Pup (1–11 months) Yearling (12–23 months) Adult (≥ 24 months)
Mother ID and father ID	Identity of the parents
Residency status	Disperser versus pack member
Pack ID	Pack identification code for pack members
Social status	Breeder versus subordinate (i.e., nonbreeder)
Percentage of wolf genomic content	50% wolf genomic content from the mother plus 50% wolf genomic content from the father
Percentage of dog genomic content	100%—percentage of wolf genomic content
Sex	Female versus male
If female	Has bred before versus has never bred before
Breeder experience	
Cohort	Year of birth

final IBM wolf–dog hybridization model by comparing of the relative efficacy of alternative management interventions in mitigating the prevalence of admixture in a simulated wolf population. As a case study, we illustrated the potential application of this model to explore management alternatives for a protected wolf population. Due to the lack of case-specific parameterization and independent data to validate the model, our focus was not on generating management recommendations. Instead, our aim was to explore broader questions that we deemed pertinent to the ongoing discourse surrounding wolf–dog hybridization management. Specifically, by simulating the wolf population dynamics over 10 generations under different demographic, connectivity, and management scenarios, our specific objectives were to project the dynamics of introgression under a no-management regime, simulate the effect of additive anthropogenic mortality on introgression dynamics with no management, and explore the relative efficacy of alternative reactive management strategies (i.e., removal vs. sterilization and release).

METHODS

General model description and parametrization

Following Bauduin et al. (2020), the time step of the simulations was 1 year, during which the individuals went through life-history processes (i.e., submodels) with outcomes dependent on individual demographic, social, and genetic attributes (Table 1). The first 4 submodels simulated the wolf's life cycle: reproduction, aging, natural mortality, and change of social status. The fifth submodel simulated management interventions or anthropogenic mortality (Figure 1). The change of social status submodel in turn comprised several submodules mimicking social behavior events and dynamics, including pack dissolution,

replacement of dead breeders, dispersal, immigration, permanent emigration, adoption, and pack establishment through various mechanisms (Figure 1). The model calculated a relatedness coefficient between individuals (r) by keeping track of the individuals' genealogy. We used a relatedness threshold of $r \geq 0.125$ (i.e., first cousins) to model inbreeding avoidance between closely related individuals (Caniglia et al., 2014; von-Holdt et al., 2008). We programmed the model in R (R Core Team, 2014) with the package NetLogoR (Bauduin et al., 2019). The R script to run the model is available on GitHub (<https://github.com/Nina86/WolfDogHybridizationIBM>).

Submodels describing wolf life cycle

A detailed description of the model is provided in Appendix S1 and Bauduin et al. (2020). We briefly describe the core submodels 1–4 (Figure 1) here. The rationale behind each parameter choice is detailed in Appendix S2, and model parameters, their values, and corresponding references are listed in Table 2.

Each year, any pack with a breeding pair produced a litter (reproduction submodel). We allowed one breeding pair per pack. At the turn of each year, the age of the individuals was increased by 1 (aging submodel). We recognized 3 age classes: pups (0–11 months old), yearlings (12–23 months old), and adults (≥ 24 months old). Only individuals who entered their third year of age were sexually mature (Wikenrose et al., 2021).

In the natural mortality submodel, individuals' natural mortality probabilities varied according to age and social status (residents vs. dispersers) (Blanco & Cortés, 2007; Smith et al., 2010) (Table 2; Appendix S2). We also modeled density-dependent mortality rates for resident adults in packs that had high mortality due to territorial strife when carrying capacity was reached (Cubaynes et al., 2014) (Appendices S1 & S2). We equated these mortality rates with natural mortality, whereas

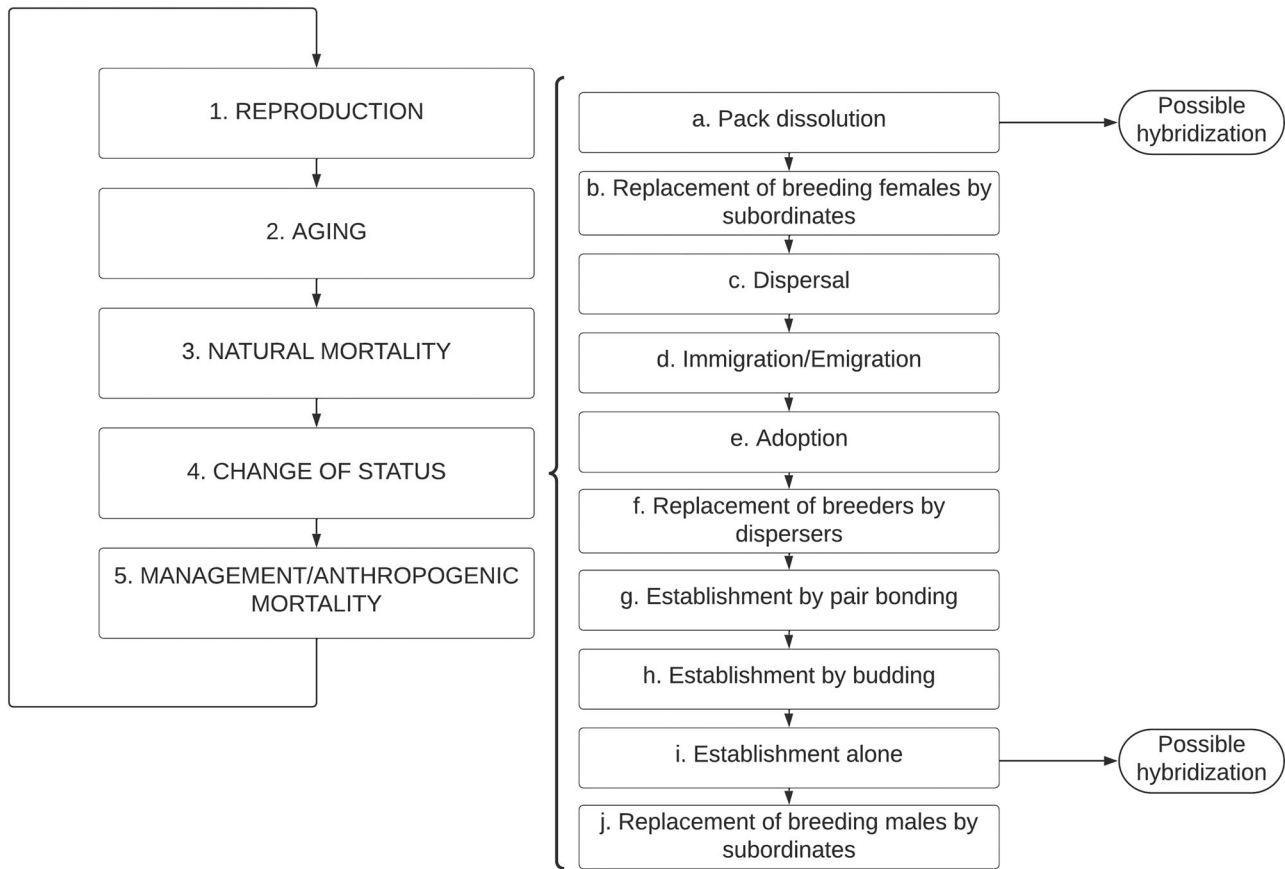


FIGURE 1 General structure of the individual-based model used to simulate individual wolves' life cycle (Bauduin et al., 2020), hybridization dynamics, and management options (left, 5 main submodels representing the wolf life cycle; right, detailed structure of the change of social status submodel).

additive anthropogenic mortality (due to management or other causes) was considered in submodel 5.

In the change of social status submodel, we allowed for 10 different possibilities based on known wolf biology (Figure 1). Individuals' social status could change from resident to disperser if their pack dissolved following the death of one or both breeders. Small packs (≤ 4 members) may dissolve (Brainerd et al., 2008) according to the following rules: packs composed of pups only dissolved with certainty (Bauduin et al., 2020), and packs with one missing breeder had a lower probability of dissolving than packs where both breeders were missing (Brainerd et al., 2008). Adult subordinate females could become breeders by replacing a dead breeding female in their pack (Caniglia et al., 2014; vonHoldt et al., 2008). In this case, if the breeding male was closely related to the selected female, it would lose its breeder status and become a subordinate (Appendix S1).

Resident individuals could become dispersers if their pack became larger than the maximum size allowed (Table 2; Appendix S1), and the excess nonbreeders would disperse (Gese & Mech, 1991). Individual probability to disperse is age specific, mimicking an increase of dispersal probability with the onset of sexual maturity so that most adult wolves did not remain in their natal pack (Haight & Mech, 1997; Jimenez et al., 2017) (details in Appendix S2).

Each year a variable number of immigrants (Table 2; Appendix S1) entered the population as dispersers, unrelated to the individuals in the population. The sex of immigrants was randomly assigned, and their age was drawn from a truncated Poisson distribution (bounded between 1 and 15) with a mean of 2 because dispersers are most commonly yearlings (Mech & Boitani, 2003). A variable number of individuals permanently emigrated from the population each year (Table 2; Appendix S1).

Dispersers could become residents by being adopted in packs that were not yet at their maximum size (Mech & Boitani, 2003). Pups, yearlings, and 3-year-old males had a higher probability of becoming adoptees (Mech & Boitani, 2003).

Adult male and female dispersers could become breeders by replacing a dead breeder of the same sex unless they were closely related to the remaining breeder (Appendix S1). Dispersers could become breeders by occupying vacant territories and establishing new packs. We modeled the probability of new pack establishment (i.e., occupation of available territories) as a decreasing function related to the number of occupied territories (Appendix S1). We imposed a maximum number of available territories in the study area (Caniglia et al., 2014) (Table 2) as a proxy of carrying capacity. We calculated the

TABLE 2 Parameters used to project hybridization dynamics under different biological and management scenarios in the individual-based model of wolf–dog hybridization.

Submodel	Parameter	Value	Reference	
Reproduction	Mean litter size	6.1	Sidorovich et al., 2007	
	Pups sex ratio	50:50		
Natural mortality	Annual pup mortality	0.602	Smith et al., 2010	
	Yearling true mortality	0.18 (SD 0.04)	Marucco et al., 2009	
	Adult mortality when vacant territories are available	0.18 (SD 0.04)	Marucco & McIntire, 2010; Marucco et al., 2009	
	Adult mortality at carrying capacity	$\text{logit}(\text{survival}_{\text{adult}}) = 1.196 - (0.505 / ((\text{density}_{\text{adult\&yearling}} - 53.833) / 17.984))$		Cubaynes et al., 2014
	Territory size for calculating density	104 km ²		Mancinelli & Ciucci, 2018
	Dispersing pup survival	0		
Pack dissolution	Disperser survival (yearlings and adults)	0.7	Blanco & Cortés, 2007	
	Probability of dissolution for small packs with 1 breeder	0.258	Brainerd et al., 2008	
	Probability of dissolution for small packs with no breeder	0.846	Brainerd et al., 2008	
	Pack size threshold for potential dissolution	4.055	Brainerd et al. 2008	
Dispersal	Mean pack size	5.6 (SD 1.251, min 3, max 8)	Caniglia et al., 2014	
	Pup dispersal probability	0.25	Haight & Mech, 1997	
	Yearling dispersal probability	0.5	Haight & Mech 1997	
	Adult dispersal probability	0.9	Haight & Mech 1997	
Establishment	Probability of successful adoption	0.5	Bauduin et al., 2020	
	Carrying capacity	50 packs	Caniglia et al., 2014	
	Relatedness threshold above which mating is avoided	0.125	Caniglia et al., 2014	
Hybridization	Probability of successful budding	0.5	Bauduin et al., 2020	
	P_{min} (minimum value for probability of mating with dogs, R_{WD})	0.5	Defined by user	
	P_{max} (maximum value for R_{WD})	0.7	Defined by user	
Migration	N_{thresh} (threshold of population abundance for which $R_{\text{WD}} = P_{\text{min}}$)	100	Defined by user	
	Proportion of dispersing individuals that emigrate outside the study area	0.1	Defined by user	
Management	Number of immigrants	1–5	Defined by user	
	Admixed individuals to be managed	20%		
	Minimum threshold of dog ancestry for admixed individuals to be managed	0.25%, first generation backcrosses	Caniglia et al., 2020	
	Breeders among the managed individuals for adults only management	60%	Defined by user	
	Adult nonbreeders for adults only management	40%	Defined by user	

probability of new pack establishment before each submodule involving the occupation of available territories.

We defined 3 types of new pack establishments: establishment by pair bonding (Mech & Boitani, 2003) (not closely related dispersers could establish a new pack by pair bonding), establishment by budding (dispersers could pair with resident subordinates of the opposite sex from an existing pack and establish a new pack), and establishment alone (Morales-

González et al., 2022) (dispersers that did not find a mate could establish alone in a vacant territory and at the next time step form a breeding pair with an adult disperser).

Finally, if no adult male disperser replaced the missing breeding male in a pack, one of the male adult subordinates could become a breeder. In this case, we removed the inbreeding threshold and allowed the formation of closely related pairs in the absence of alternative mates (vonHoldt et al., 2008)

(Appendix S1). If there were several adult subordinate males in the pack, one was randomly selected among those least related to the breeding female.

Submodels describing hybridization and its management

In our IBM, we integrated a module accounting for a wolf–dog hybridization process. We modeled female-based, directional hybridization (i.e., only female wolves hybridizing with male dogs) because cases of hybridization between male wolves and female dogs are rarely reported and not well documented (Hindrickson et al., 2012). Bohling and Waits (2015) showed that red wolf–coyote admixed pairs are more likely to form after the death of one breeder in the presence of high availability of heterospecific mates and that young, first-time female breeders are responsible for a significant proportion of hybridization events. Similar mechanisms have also been hypothesized for gray wolves hybridizing with dogs in Europe (Godinho et al., 2011; Salvatori et al., 2019).

We integrated hybridization between wolves and dogs in the pack dissolution and the establishment alone submodules (Figure 1). Following either pack dissolution or establishment as single wolves, adult females of 3–4 years old that never bred before could mate with dogs. The event of a nonadmixed female wolf mating with dogs (WD) was simulated with Bernoulli trials with the probability of mating a dog equal to P_{WD} (Appendix S2), calculated as (Fredrickson & Hedrick, 2006):

$$P_{WD} = P_{\max} e^{-Nr_w}, \quad (1)$$

where N is the number of wolves and hybrids (i.e., potential mates) in the population, P_{\max} is the maximum value for P_{WD} (when $N \rightarrow 0$, $P_{WD} \rightarrow P_{\max}$), $r_w = \frac{\ln(P_{\min}/P_{\max})}{N_{\text{thresh}}}$ is a constant affecting the rate of change in P_{WD} , and N_{thresh} is the threshold value of N for which P_{\min} is reached (Fredrickson & Hedrick, 2006). We assumed that when $N > N_{\text{thresh}}$, $P_{WD} = 0$, indicating that hybridization between wolves and dogs stops when potential conspecific mates (i.e., admixed and nonadmixed wolves) availability increases to a given threshold. Following Fredrickson and Hedrick (2006), the probability of an admixed female (H) to mate with a dog (D) (P_{HD}) is

$$P_{HD} = P_{WD} + (1 - A_H) \times (P_{DD} - P_{WD}), \quad (2)$$

where A_H is the proportion of dog ancestry of the admixed individual (Fredrickson & Hedrick, 2006) and P_{DD} is the probability of a dog mating with a dog (details in Appendix S2).

The females who mated with dogs were not available for any following pairing with a male wolf and could not be adopted; established alone in a vacant territory; and produced a hybrid litter (i.e., reproduction submodel) in the following year. The dog genomic content of each of the hybrid pups was $\geq 50\%$, accounting for contributions from the father (100% dog) and from the mother who could be either admixed or

not. We assumed that there were no differences in survival and reproductive rates between wolves and admixed individuals.

We simulated removal and sterilization and release for management of introgressive hybridization because these have been applied to mitigate introgressive hybridization in canids (Gese & Terletzky, 2015; Salvatori et al., 2020). To account for the inherent uncertainty in hybrid identification (Caniglia et al., 2020), admixed individuals potentially targeted by management were those with a dog genomic content $\geq 25\%$ (i.e., from first-generation hybrids to first-generation backcrosses) (Table 2; Appendix S1). We also arbitrarily set the percentage of the admixed individuals to be managed each year at 20% to conservatively account for logistics and management constraints. Finally, for each of the 2 management interventions, we also simulated targeting admixed individuals either selectively (only adults were removed or sterilized) or unselectively (all individuals, regardless of age, were removed or sterilized) (details in Appendix S1).

Composite modeling scenarios

We simulated the dynamics of hybridization in our study population over 10 generations (i.e., 30 years with a 3-year generation time) (Skoglund et al., 2011) starting from its known composition of nonadmixed (min = 13, max = 19) and admixed (min = 25, max = 31) wolves distributed in 7 packs (Santostasi et al., 2021). We considered uncertainty in the genetic composition of immigrants and in mate choice behavior with a set of 24 hierarchical scenarios (Figure 2) (model parametrization in Table 2 & Appendix S1). First, we considered 2 immigration scenarios (i.e., all immigrants were nonadmixed wolves vs. all immigrants were admixed) and, then, for each of these, we simulated 2 mate-choice alternatives: wolves and admixed individuals that were available for mating at each time step pair-bonded randomly (i.e., random mating) or selectively according to their similarity in dog genomic content (i.e., assortative mating) (Fredrickson & Hedrick, 2006). For each of these 4 scenarios, we further simulated the 2 management interventions (i.e., removal vs. sterilization), each implemented through 2 targeting approaches (i.e., all age classes vs. adults only). Moreover, we contrasted the effect of the abovementioned management interventions with 2 additional scenarios, both simulating the lack of management of anthropogenic hybridization: one in which only natural mortality occurred, and the other in which an additional 20% of the population affected each year by anthropogenic mortality. The latter scenario represented situations where wolf populations, even if protected, are exposed to accidental mortality and poaching (e.g., wolves in Italy; Musto et al., 2021). We stress that this proportion is applied to the entire population (including wolves and admixed individuals); therefore, it results in a higher number of removed individuals than the 20% recently admixed individuals' removal (where the proportion is applied to a smaller portion of the population). Because we wanted to disentangle the effects of additive mortality from the effect of management, the management scenarios only included natural mortality.

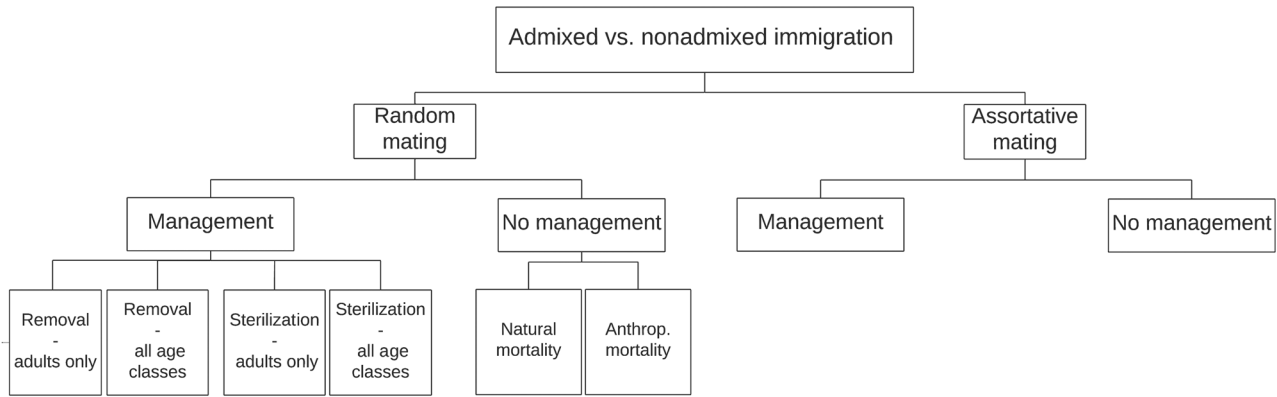


FIGURE 2 Modeling scenarios used to assess the relative efficacy of alternative management interventions to prevent genetic swamping in admixed wolf populations, while accounting for uncertainty in immigration and mate choice behavior. Management and no-management scenarios are shown only for random mating scenario for figure readability.

To take stochasticity into account, we performed 50 replicates (population trajectories) per scenario, averaging 4 descriptive measures of relative management performance over 30 years. The first measure was prevalence (i.e., proportion of admixed individuals in the population). In calculating prevalence, we considered as detectable admixed individuals those whose genomic content was $\geq 6.25\%$. Therefore, they comprised first-generation hybrids and their backcrosses to wolves up to the third generation (Caniglia et al., 2020). The second measure was admixture structure. In describing admixture structure, we differentiated among recently admixed individuals (i.e., dog genomic content $\geq 25\%$, comprising first-generation hybrids and first-generation backcrosses to wolves); introgressed individuals (i.e., dog genomic content $> 6.25\%$ and $< 25\%$, comprising second and third backcrosses [Caniglia et al., 2020]); and wolves (dog genomic content $< 6.25\%$, notably; fourth generation of backcrossing individuals classified as nonadmixed wolves). The third measure was the extent of admixture (i.e., the average individual's dog genomic content) (McFarlane & Pemberton, 2019). The fourth measure was the number of admixed dispersers produced in the absence of management, which was used to quantify the potential for hybridization to spread beyond the local population.

Sensitivity analyses

To assess whether the demographic parameters specified in the model had a significant effect on the models' main output (i.e., the prevalence of admixture in the population after 10 generations), we ran a sensitivity analysis increasing or decreasing by 5% the value of one parameter at a time and quantifying the departure of the results compared with the baseline value (Bauduin et al., 2020; Ovenden et al., 2019). We considered the model sensitive to uncertainty in each parameter if the output varied more than 20% from the results obtained with the baseline parameter's value (Ovenden et al., 2019). We repeated the sensitivity analysis for each of the 4 no-management–natural-

mortality scenarios (i.e., wolf immigration–random mating, wolf immigration–assortative mating, admixed immigration–random mating, and admixed immigration–assortative mating). Details are in Appendix S3.

RESULTS

Immigration by nonadmixed wolves

In the scenarios with immigration by nonadmixed wolves and random mating, the prevalence of admixed individuals increased over time under the no-management–natural-mortality regime (Figure 3a); extent of admixture remained constant (Figure 4a); and introgressed individuals (i.e., dog genomic content $> 6.25\%$ and $< 25\%$) represented the most abundant admixed category in the population (Figure 5a). Concurrently, nonadmixed wolves steadily decreased through time, indicating conditions of genetic swamping (Figures 3a & 5a). Under the same simulated conditions, any management strategy was more effective in addressing wolf–dog hybridization than doing nothing because all management interventions caused a reduction in prevalence (ranging from 38% for all age classes sterilization to 66% for adult-only removal) (Figure 3a). All management strategies also prevented an increase in the extent of admixture (Figure 4a) and favored nonadmixed wolves that became the most abundant category (Figure 5c–f) in the population. However, the sterilization strategy decreased the numbers of both admixed and nonadmixed wolves (Figure 5e,f), causing a lower overall reduction in prevalence than the removal strategy (Figure 5c,d).

Compared with random mating, assortative mating tended to decrease the overall prevalence of admixed individuals, even under the no-management–natural-mortality regime, and reduced the differences between the management strategies (Figure 3b). Although the relatively low precision of the projections did not allow us to draw firm conclusions, assortative mating also affected the relative efficacy of the alternative management options; adult-only sterilization and release were the

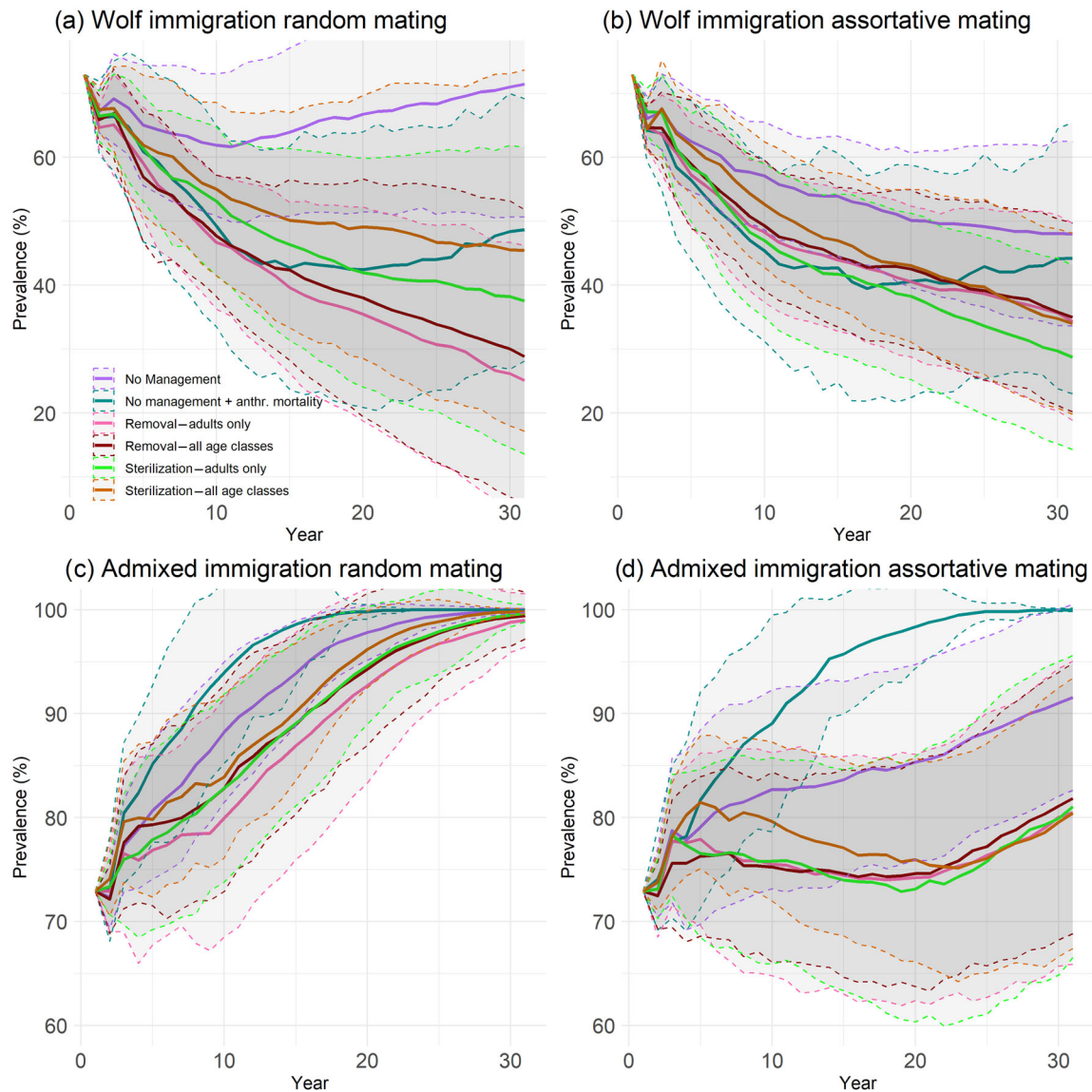


FIGURE 3 (a–d) Prevalence of admixed individuals under different immigration and mate choice scenarios and management interventions (lines, projection over 30 years of annual prevalence averaged across simulation replicates of 50; shaded area, 25th–75th interquartile range). The management scenarios involved only natural mortality.

most effective strategies over the long term (62% reduction in prevalence) (Figure 3b).

Under the no-management–anthropogenic-mortality regime, irrespective of mate choice assumptions, anthropogenic mortality produced a decrease in prevalence during the first 10–15 years, comparable to the effect of reactive management (Figure 3a,b). However, anthropogenic mortality induced an increase in prevalence from 20 years onward (Figure 3a,b) and a regular increase in the extent of admixture (Figure 4a,b), which was in line with the increase in abundance of the recently admixed individuals (Figure 5b; Appendix S4b).

In the no-management–natural-mortality scenarios, the percentage of admixed individuals in the dispersers pool reached a plateau at about 70% ($n = 57$) for random mating and 50%

($n = 42$) for assortative mating (Appendix S5). The addition of anthropogenic mortality did not allow the population to reach carrying capacity; therefore, the total number of individuals was smaller than in the scenarios with natural mortality (Figure 5b) and the number of dispersers was low (about 4 per year) (Appendix S6). The percentage of admixed individuals in the dispersers pool was about 50% ($n = 2$) for both assortative and random mating scenarios (Appendix S6a,b).

Immigration by admixed wolves

In the scenarios simulating immigration by admixed individuals, the prevalence increased regardless of the management

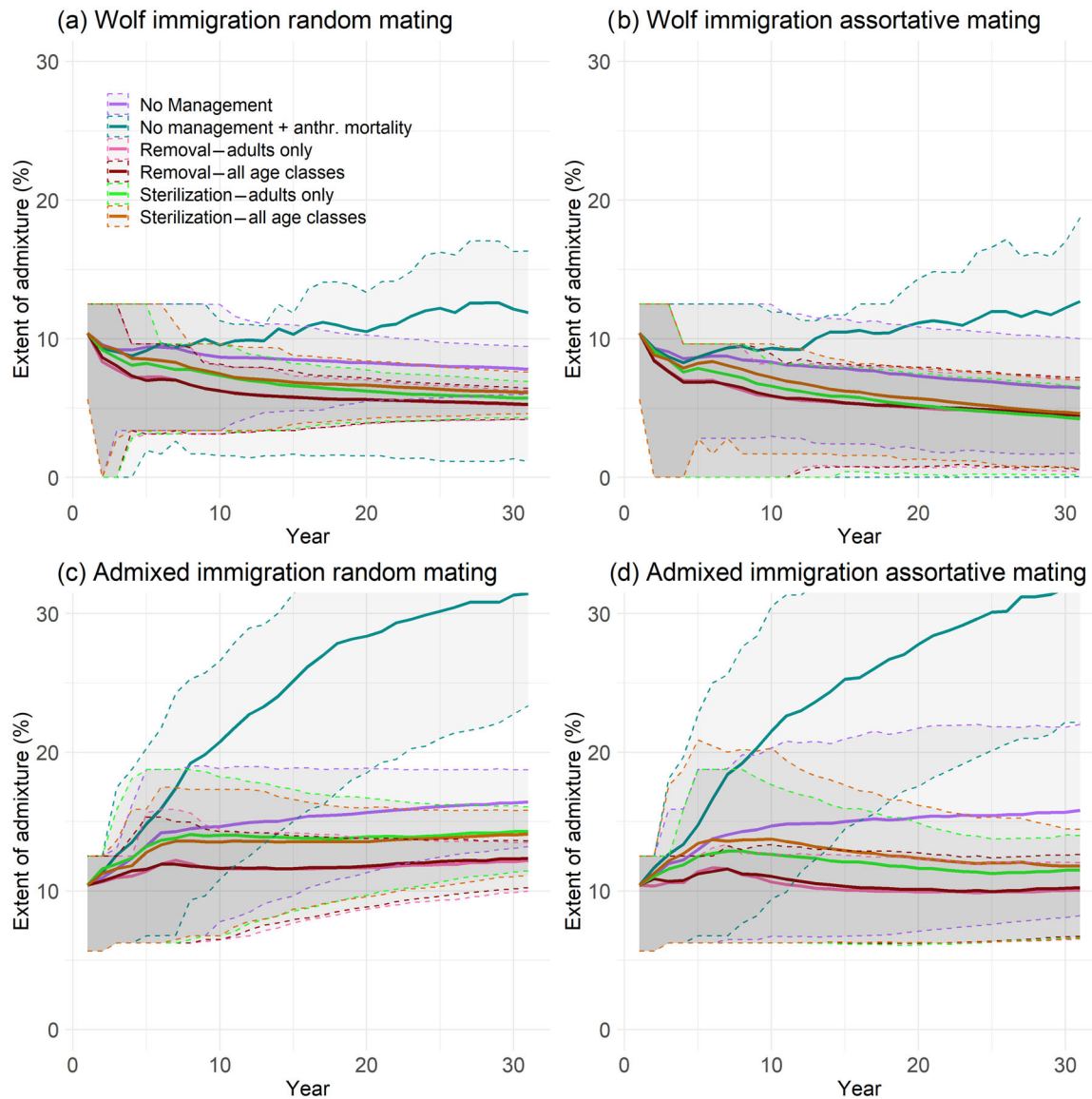


FIGURE 4 (a–d) Individuals’ average extent of admixture simulated under different immigration and mate choice scenarios and management interventions (lines, projection over 30 years of annual prevalence averaged across simulation replicates of 50; shaded area, 25th–75th interquartile range). The management scenarios only involved natural mortality.

strategy, although at a slower rate under the assumption of assortative mating compared with random mating (Figure 3c,d). Expectedly, the no-management regimes led to faster rates of increase in prevalence and extent of admixture compared with the other management scenarios (Figures 3c,d & 4c,d). The addition of anthropogenic mortality further accelerated the increase in prevalence, leading to complete admixture under both mate choice assumptions; this was especially noticeable in the assortative mating scenario (Figures 3c,d & 4c,d).

Under both mate choice scenarios, management slowed the increase in prevalence and extent of admixture, and wolves remained the least abundant category (Appendices S7 & S8). However, under the assumption of assortative mating, management succeeded in preserving about 20% of nonadmixed wolves (Appendix S8).

In the no-management–natural-mortality scenarios, the percentage of admixed individuals in the dispersers pool reached a plateau at about 100% for random mating ($n = 83$) and 84% for assortative mating ($n = 70$) (Appendix S7). In the presence of anthropogenic mortality, the percentage of admixed individuals in the dispersers pool was about 100% ($n = 4$) for both assortative and random mating scenarios (Appendix S8).

Sensitivity analyses

Under the wolf immigration–random mating and wolf immigration–assortative mating scenarios, the model was robust to the variations in demographic parameters, with the sole exception of the simulated number of immigrants

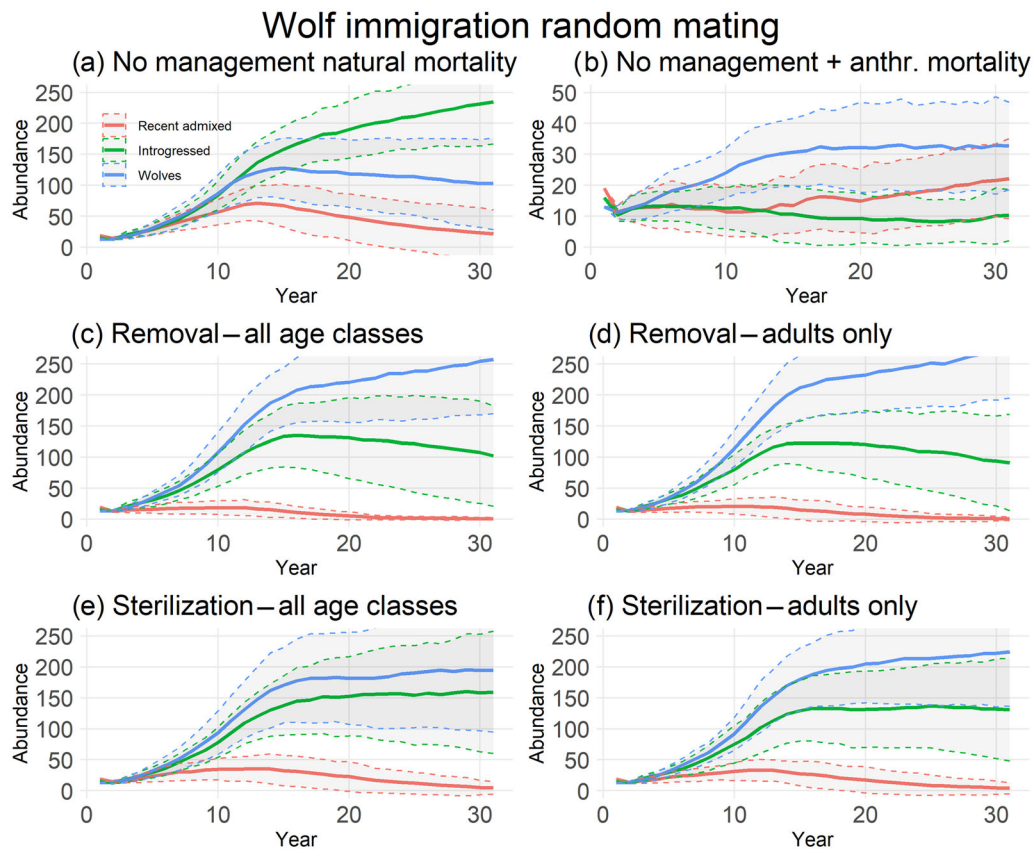


FIGURE 5 (a–f) Population composition in terms of recently admitted individuals (i.e., dog genomic content $\geq 25\%$), introgressed individuals of later generations of backcross (i.e., dog genomic content $>6.25\%$ and $<25\%$), and wolves (dog genomic content $<6.25\%$) over time under different management strategies for the nonadmixed wolf immigration and random mating scenario (lines, projection over 30 years of the abundance of each population category across 50 simulation replicates; shaded area, 25th–75th interquartile range). Management scenarios involved only natural mortality.

(Appendices S9 & S10). Specifically, both in the random and the assortative mating scenarios, the final prevalence decreased by $>20\%$ when the number of immigrants increased by 50% (Appendix S9). Under the admixed immigration–random mating and admixed immigration–assortative mating, both the random and the assortative mating models were insensitive to variations in demographic parameters (Appendices S10 & S11).

DISCUSSION

To our knowledge, ours is the first attempt to compare the relative efficacy of alternative management interventions to mitigate wolf–dog hybridization. Although we could not validate the results due to the lack of independent data from our case study, our results are consistent with previous simulation studies on canids (Fredrickson & Hedrick, 2006; Santostasi et al., 2020) and other taxa (Wolf et al., 2001) in showing that, given our simulated initial conditions (i.e., high initial prevalence and ongoing hybridization), failing to provide a management response leads to an increase of prevalence of admixed individuals over time in most of the simulated scenarios.

Our simulations identified some mechanisms that naturally reduced the prevalence of admixed individuals (e.g., assortative mating and immigration of nonadmixed wolves). Although assortative mating mainly slowed down the increase of admix-

ture, immigration of nonadmixed wolves had a potentially strong effect in reducing prevalence, depending on the number of immigrants per year (Appendix 4). Other potential scenarios that we did not simulate, such as different initial conditions (e.g., a lower initial prevalence or a lower probability of interbreeding with dogs P_{WD}) or selective pressures favoring the fitness of wolf-like phenotypes, may naturally prevent the spread of admixture in wolf populations. However, such mechanisms do not seem to apply to our study population, where the estimated prevalence of admixed individuals reached high levels (70%) (Santostasi et al., 2021). We believe that our simulations offer useful insights into the potential hybridization and introgression dynamics of wolf populations where introgression of dog genes has been recently deemed an issue of increasing concern (Galaverni et al., 2017; Hindrikson et al., 2017; Salvatori et al., 2020). Consistent with previous studies (Fredrickson & Hedrick, 2006; Santostasi et al., 2020; Wolf et al., 2001), our findings further emphasized that, under given environmental and anthropogenic conditions (e.g., high anthropogenic mortality, occurrence of free-ranging dogs), neglecting the management of hybridization may substantially contribute to the spread of introgression, possibly leading to the genetic swamping of parental wolf populations.

We modeled a potential mechanism through which additive anthropogenic mortality (affecting admixed and nonadmixed wolves) could determine an increase in hybridization and

introgression rates. Anthropogenic mortality may disrupt social cohesion within wolf packs (Borg et al., 2015; Brainerd et al., 2008; Cassidy et al., 2023), a condition that in the red wolf–coyote and the eastern wolf–coyote systems led to increased opportunities of hybridization (Bohling & Waitts, 2015; Rutledge et al., 2011). This mechanism was reproduced in our simulations, where pack dissolution increased the chances of hybridization events by making subordinates available for reproduction and created establishment and reproduction opportunities for dispersing individuals by vacating occupied territories. In the admixed immigration scenario, this resulted in additive anthropogenic mortality producing a larger surge in recently admixed individuals and in the extent of admixture than in the scenarios with natural mortality only. Although these dynamics have not yet been documented or quantified in wolf–dog hybridization systems, they are nonetheless expected based on demographic and behavioral grounds. From a strictly demographic standpoint, matrix modeling (Santostasi et al., 2020) shows that the survival of adult wolf breeders is inversely proportional to the probability of genetic swamping in wolf populations hybridizing with dogs. From a behavioral perspective, the stability of packs reduces the chance of hybridization by limiting the access to reproduction in the red wolf–coyote hybridization system (Bohling & Waitts, 2015).

Under the nonadmixed wolves' immigration scenario, anthropogenic mortality caused an initial decline in prevalence, up to about the fifth generation (Figure 3a,b). In our original population, admixed wolves were more numerous than nonadmixed ones (Santostasi et al., 2021), exposing the former to a proportionally higher risk of human-related mortality. However, once admixed individuals decreased to about 40% of the population, anthropogenic mortality was more likely to target the more abundant nonadmixed wolves, reversing the trend (Figure 3a,b). In contrast, additive anthropogenic mortality in wolf populations receiving admixed immigrants caused the largest surge in the prevalence of admixed individuals, a projection that was little affected by uncertainty in mating choice behavior (Figure 3c,d). Overall, these results concur with previous studies (Fredrickson & Hedrick, 2006; Santostasi et al., 2020) in indicating that pack persistence and high survival of adult, nonadmixed wolves are of paramount importance in reducing the spreading of introgression, especially where poor or no management of hybridization is in place.

Accounting for uncertainty in mate choice (i.e., random vs. assortative) and type of immigration (admixed vs. nonadmixed), any of the 2 reactive management interventions we simulated was more effective in reducing the prevalence of admixed individuals than the no-management regime. In addition, even though the relatively low precision of our projections did not allow us to draw any firm conclusion, removal seemed slightly more effective than sterilization under the wolf immigration and random mating assumption (Figure 3a), but the opposite was true in the case of wolf immigration and assortative mating (Figure 3b). In both cases, however, targeting the individuals with the greater reproductive potential (i.e., adults) was more effective in reducing prevalence than unselective management. Assuming nonadmixed immigration and random mating, the

efficacy of sterilization was lower than that of removal, with the difference being in the reproductive behavior of mixed breeding pairs (i.e., admixed and nonadmixed breeders) affected by management. Removal of an admixed breeder in mixed breeding pairs did not preclude the other (nonadmixed) breeder from finding another nonadmixed mate and eventually reproducing. However, sterilization of an admixed breeder will maintain a sterile breeding pair (i.e., the placeholder concept [Gese & Terletzky, 2015]), thereby precluding the (nonadmixed) wolf breeder from reproducing again. In the long term, sterilization slowed the increase in the proportion of nonadmixed wolves in the population compared with removal (Figure 5c,d).

When assuming assortative mating, however, the sterilization of admixed breeders selectively affected the reproductive potential of mostly admixed–admixed breeding pairs, contributing at least as efficiently as removal to reducing admixture in the population, under both immigration scenarios (Figure 3b–d). Overall, these findings confirm the use of sterile placeholders to reduce the reproductive potential of admixed individuals (Gese & Terletzky, 2015), especially if mate choice is assortative. This approach, however, has been evaluated only in the red wolf–coyote hybridization system. Differences in body size and behavior among red wolves, coyotes, and their hybrids, however, are not necessarily comparable to those expected in wolves and wolf–dog hybrids, an important topic that should be further investigated. We nevertheless believe the placeholder approach holds promise as a management intervention to mitigate wolf–dog hybridization, especially where lethal removal or capture and placement in captivity of hybrids are not allowed, affordable, or deemed socially acceptable.

According to our simulated conditions, regardless of the implementation of any management intervention, continuous immigration of admixed individuals in the population rendered any management strategy largely ineffective when mating was random, converging to complete admixture in 30 years (Figure 3c). Although this corresponds to the scenario in which all immigrants were admixed and realizing that the corresponding projections were highly sensitive to parametrization of the immigration rate, our findings underline how the management of local wolf populations ought to be designed and implemented at the landscape scale and that management should account for metapopulation dynamics (Benson et al., 2012). Wolves can disperse over long distances (e.g., Ciucci et al., 2009), and admixed individuals may disperse as well (Caniglia et al., 2013). Therefore, any locally well-managed wolf population that is part of a large metapopulation is at risk of admixture if any subpopulation within dispersal distance is admixed. Notably, our results showed that the no-management option, especially under anthropogenic mortality, corresponded in the long term not only to widespread admixture, but also to the high availability of admixed dispersers (Appendices S5 and S6), thereby increasing the risk of admixture spreading to other connected subpopulations.

The aim of our work was not to provide specific management recommendations but to provide preliminary understanding of the interactions between wolf demographics and management in the wolf–dog hybridization system. However, some

general considerations about management can be drawn from our results. First, the no-management policy seemed to have the poorest outcome from a conservation perspective because it allowed the spread of admixture and led to genetic swamping in the parental wolf population in the majority of the scenarios. Second, although we simulated management at a relatively low intensity (i.e., 20% of recently admixed individuals each year), the placeholder strategy (i.e., hormone-sparing sterilization and release) seemed to be a viable alternative to the removal of admixed individuals. Applicability of the placeholder strategy to the wolf–dog hybridization case, however, is pending on additional research about mating strategies. Third, the management of wolf–dog hybridization in local populations necessitates an assessment of admixture at wider scales (Matias et al., 2022). Its implementation needs to be coordinated across the landscape, involving transjurisdictional and transboundary cooperation among local, regional, and national administrations and agencies (Salvatori et al., 2020). Wolf populations that are sources of admixed individuals should become management priorities. Small, admixed populations susceptible to human-related mortality, connected through immigration to other admixed populations, and for which there is no management in place are at high risk of genetic swamping. Fourth, because the death of nonadmixed wolves greatly increased hybridization and introgression rates, we also warn against any source of human-related mortality of nonadmixed wolves in populations affected by widespread introgression or where there is a high hybridization risk due to the presence of free-ranging dogs. The prevention of any form of human-related mortality of nonadmixed wolves should be a priority when planning wolf–dog hybridization management. This aspect is also relevant for those wolf populations in which hybridization has been documented and that are also subjected to lethal population control or exploitation. In these cases, efforts should be made to understand the wolf removal costs in terms of the spread of admixture and to explicitly address the status of admixed individuals in control or exploitation programs.

Although illustrating in detail and critically comparing the effectiveness and feasibility of alternative reactive management interventions is out of the scope of this work, it should be recognized that lethal control, though more practical, can be controversial because it relies only on apparent phenotypical (i.e., morphological) cues of introgression that are generally considered unreliable to discriminate between admixed and nonadmixed wolves (Caniglia et al., 2020; Galaverni et al., 2017; Stronen et al., 2022). Instead, both the removal through capture and placement in captivity and sterilization and release allow for more reliable detection of admixed individuals through genetic or genomic means (Galaverni et al., 2017). In both cases, allegedly admixed individuals need to be live trapped and, although they are temporarily held in captivity, their genotype needs to be determined from high-quality DNA extracted from a blood sample. This procedure, however, may be less practical and more costly.

By simulating a management efficiency of 20%, we realistically accounted for the low effectiveness expected through targeted removal or sterilization of specific admixed individuals. It should be emphasized, however, that our analysis of

the relative performance evaluation of alternative management interventions did not include an assessment of their implementation costs and relative feasibility. Nevertheless, the costs and lower practicality of establishing sterile territories in admixed wolf populations may be offset by higher costs in terms of social conflict and controversy stemming from lethal control measures. Besides considerations concerning the practicality, social acceptability, and cost-effectiveness of such interventions, we believe it is nevertheless valuable to assess their expected relative efficacy.

In our simulations, we assumed an unsaturated, introgressed, core wolf population in a suitable landscape offering several available territories. In a saturated population scenario, however, we would expect the spatial spread of introgression to be slowed by a reduced probability of success in establishing new packs and the final prevalence in the population to be strongly affected by the genetic composition of the packs surrounding the introgressed core. The scenarios that we evaluated could be modified to match specific initial conditions (e.g., population size, structure, dynamics, and connectivity) and management strategies (e.g., intensity, frequency, and duration of management interventions) or to accommodate additional biological complexity, such as more flexible immigration scenarios or changes in the environment affecting vital rates that would increase simulation realism, especially for long-term projections.

Our individual-based approach allowed us to include wolf behavioral processes that were not considered in previous wolf–dog hybridization modeling attempts (Fredrickson & Hedrick, 2006; Santostasi et al., 2021) and to consider realistic thresholds for the detection of admixed individuals based on noninvasive genetic sampling (Caniglia et al., 2020). However, such complexity has the downside of relying on a high number of parameters that are expected to vary greatly depending on population characteristics and environmental conditions (Johnston et al., 2019). We were forced to resort to parameters from other populations (e.g., litter size) (Table 2) and to arbitrarily defined parameters (e.g., maximum and minimum R_{WD} , probability for a female wolf of mating with a dog [Table 2]). Moreover, we could not perform any model validation of the predictions due to the general lack of long-term estimates of wolf–dog hybridization dynamics. These limitations confine the interpretation of our results to an initial exploration of the possible interplay among wolf population dynamics, hybridization mechanisms, and management strategies. We nonetheless believe that, with the necessary precautions (i.e., appropriate parametrization, extensive sensitivity analysis, exploration of an exhaustive number of scenarios), our modeling approach can still improve the management decision process, which is highly controversial and lacks empirical testing (Donfrancesco et al., 2019). Ideally, we advocate for the use of our model in an adaptive management framework (Holling, 1978; Walters, 1986), where the monitoring of management outcomes (i.e., trends in prevalence) would be used for model validation and improvement.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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