RESOURCE ARTICLE

MOLECULAR ECOLOGY RESOURCES WILEY

simRestore: A decision-making tool for adaptive management of the native genetic status of wild populations

Flor Hernández[1] | Thijs Janzen[2,3] | Philip Lavretsky[1]

[1]Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas, USA

[2]Department of Ecological Genomics, Carl von Ossietzky University Oldenburg, Oldenburg, Germany

[3]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

Correspondence
Flor Hernández, Department of Biological Sciences, University of Texas at El Paso, El Paso, TX 79668, USA.
Email: fbhernandez2@miners.utep.edu

Abstract

Anthropogenic hybridization, or higher and non-natural rates of gene flow directly and indirectly induced by human activities, is considered a significant threat to biodiversity. The primary concern for conservation is the potential for genomic extinction and loss of adaptiveness for native species due to the extensive introgression of non-native genes. To alleviate or reverse trends for such scenarios requires the direct integration of genomic data within a model framework for effective management. Towards this end, we developed the simRestore R program as a decision-making tool that integrates ecological and genomic information to simulate ancestry outcomes from optimized conservation strategies. In short, the program optimizes supplementation and removal strategies across generations until a set native genetic threshold is reached within the studied population. Importantly, in addition to helping with initial decision-making, simulations can be updated with the outcomes of ongoing efforts, allowing for the adaptive management of populations. After demonstrating functionality, we apply and optimize among actionable management strategies for the endangered Hawaiian duck for which the current primary threat is genetic extinction through ongoing anthropogenic hybridization with feral mallards. Simulations demonstrate that supplemental and removal efforts can be strategically tailored to move the genetic ancestry of Hawaii's hybrid populations towards Hawaiian duck without the need to completely start over. Further, we discuss ecological parameter sensitivity, including which factors are most important to ensure genetic outcomes (i.e. number of offspring). Finally, to facilitate use, the program is also available online as a Shiny Web application.

KEYWORDS
anthropogenic hybridization, conservation, decision-making tool, genomic extinction, management strategy

1 | INTRODUCTION

Classically, gene flow or the interbreeding of individuals from genetically distinct taxonomic units is often expected to result in outbreeding depression (Abbott et al., 2013; Barton, 2013; Mallet, 2007), with sustained exchange of genetic material eventually leading to the loss of either one (i.e. loss of taxa) or both (i.e. formation of a hybrid swarm) interacting species (Kearns et al., 2018; Seehausen et al., 2008). However, secondary contact between taxa can also lead to the formation and maintenance of hybrid zones, which can cause reproductive reinforcement, and perhaps eventual completion of the speciation process (Abbott et al., 2013; Grant & Grant, 1992; López-Caamal & Tovar-Sánchez, 2014; Rhymer, 2006; Todesco et al., 2016). While gene flow is now recognized as an important

natural phenomenon in the evolutionary history of many animal species, human activities have dramatically increased the rates of hybridization worldwide (Allendorf et al., 2001; Mallet, 2005; Nolte & Tautz, 2010). Specifically, direct and indirect human activities (e.g. increased urbanization, augmenting wild lands and the intentional and unintentional release of invasive and often domestic species) are leading to unnaturally high rates of secondary contact among historically allopatric species (Crispo et al., 2011; McFarlane & Pemberton, 2019). Such anthropogenic hybridization has become a focal cause of concern for the conservation of many species (Crispo et al., 2011; Lavretsky et al., 2023; Leitwein et al., 2018; McFarlane & Pemberton, 2019; Wells et al., 2019). Among activities that result in such human-mediated gene flow is the common practice of using captive-reared populations for conservation or restocking purposes in forestry, fisheries and game management (Brennan et al., 2014; Söderquist et al., 2017). However, the selective pressures on wild (i.e. natural selection) versus domestic (i.e. artificial selection) individuals often results in contrasting trait selection, with those specific to human-modified environments often being maladaptive in the wild (Christie et al., 2012; Crispo et al., 2011). Thus, the interbreeding between domestic and wild counterparts has frequently been found to lead to outbreeding depression or reduced local adaptation in the wild (Crispo et al., 2011). Increasing incidence of such interactions has brought understanding the impacts of anthropogenic hybridization on wild populations to the forefront of conservation science (Hirashiki et al., 2021).

Gene flow is both perceived as a problem and heralded as a potential solution, depending on the taxonomic organism of interest within conservation science (Flanagan et al., 2018). On the one hand, a species under threat of genetic extinction can require management involving the removal of the invading species, translocation of the threatened population, or habitat improvement (Rieseberg & Gerber, 1995; Wolf et al., 2001). Conversely, gene flow has been used to a limited extent as a conservation strategy to rescue the viability (i.e. improve the fitness) of small, inbred populations, known as 'genetic rescue' (Frankham, 2015; Hedrick & Fredrickson, 2010; Miller et al., 2012; Todesco et al., 2016). Traditional methods for evaluating these conservation actions have been based on increases in positive (e.g. population size, reproductive success and survival rates) and decreases in negative (e.g. deleterious traits and mortality rate) ecological factors of the species to be conserved (Frankham, 2015; Hedrick & Fredrickson, 2010; Miller et al., 2012). Advances in next-generation DNA sequencing technologies along with novel analytical methods have been useful to provide genetic information, such as rates of hybridization, to complement conservation plans (Anderson & Thompson, 2002; Flanagan et al., 2018; Hohenlohe et al., 2021; van Wyk et al., 2017). However, integrating genomic data into conservation management requires significant genetic knowledge and bioinformatics expertise, which is often lacking (Flanagan et al., 2018; Hoban et al., 2013; Hohenlohe et al., 2021).

To reach policymakers and managers, the development of more user-friendly programs and clear guidelines for applying genetic information to wildlife biology and management is needed.

In particular, methodologies in which molecular and/or ecological data can be annually updated would provide a means for adaptive management planning. Towards this end, we developed simRestore, a decision-making R-based program that simulates the time (in generations) until a population may attain genetic native status under differing management strategies. The program makes use of backcrossing and admixture as a mechanism to establish genetic integrity (Lavretsky et al., 2016, 2019), and provides users a framework to incorporate management actions (e.g. augmenting and removal efforts) in combination with ecologically informative variables (e.g. survival rate) and genetic information (e.g. ancestry assignment) to simulate the expected time in generations to achieve the native status of the threatened species. Thus, the program consists of two intertwined models covering ecological and genetic data (Table 1). Importantly, as most conservation programs are resource-limited, the program is also designed to simulate under those limitations, including the total number of individuals that can be released and/or removed, as well as any temporal restrains for project completion. Finally, in addition to helping with initial decision making, simulations can be updated with the outcomes of ongoing efforts, allowing for the adaptive management of populations. Here, we demonstrate software functionality, as well as its utility through optimization of actionable management strategies for the endangered Hawaiian duck (*Anas wyvilliana*) for which the current primary threat is genetic extinction through ongoing anthropogenic hybridization with feral mallards (*Anas platyrhynchos*) (USFWS, 2012; Wells et al., 2019).

1.1 | Study system

Once found across the main Hawaiian Islands, Hawaiian ducks once again only reside on the Island of Kauai (Wells et al., 2019). Although habitat loss and overhunting were in part responsible for their decline (Engilis & Pratt, 1993), it is the establishment of feral mallard populations that appear to be the proximate cause of conservation concern today (Engilis Jr. et al., 2020, see also Wells et al., 2019). Although captive-rearing programs and reintroductions were attempted from the1960s to the 1980s (Browne et al., 1993; Engilis & Pratt, 1993), these efforts ultimately failed due to not handling the burgeoning feral mallard populations that eventually interbred with translocated Hawaiian ducks to form feral mallard×Hawaiian duck hybrid populations across Islands (Wells et al., 2019). Although the conservation of the Hawaiian duck could move forward with restarting all populations from Kauai stock after the extirpation of existing feral mallard×Hawaiian duck hybrids, such efforts are often not financially sustainable but also are complicated by human dimensions (Stronen & Paquet, 2013). Instead, there is potential to maximize management strategies by varying restocking and partial removal efforts optimized for each wetland's characteristics. Given that sequential backcrossing into the same gene pool has the potential to re-establish the genetic signature of the backcrossed parental population within only a few generations (Lavretsky et al., 2016, 2019), the genetics of a hybrid population can thus be artificially

TABLE 1 Overview of available parameters available in the simRestore R package as well as their range of values to modify depending the studies species.

Function	Function description	Range of values	Hawaiian duck simulation input values
Morgan	Size of the chromosome in Morgan	0+	1 (Lavretsky et al., 2019)
K	Carrying capacity	1+	400 (Robinson et al., 2017)
Reproductive success rate	Frequency of females that yield offspring at the end of the breeding season (e.g. a fraction of 1 – reproduction_success_rate of females). This is a joint effect of breeding females getting killed (see female_death_rate) and other sources of failure to complete a clutch. Other sources of failure are calculated from nest_success_rate and female_death_rate, such that reproduction failure rate=1–reproduction_success_rate/(1–female breeding risk)	From 0 to 1	0.387 (Malachowski & Dugger, 2018)
Reproductive risk	Additional death rate of females or males because of breeding (e.g. as a result of protecting the offspring against predators). Provide as a vector where the first index indicates the risk for females, the second the risk for males	From 0 to 1	0.2 for females (Malachowski (personal communication, November 2020))
Mean number of offspring	Mean number of offspring per female	1+	6 (Malachowski & Dugger, 2018)
Sd offspring size	Standard deviation of number of offspring per female (assuming the number of offspring is always 0 or larger)	1+	1 (Malachowski & Dugger, 2018)
Extra pair copulation	Probability per offspring to be the result of extra pair copulation	From 0 to 1	0
Maximum age	Organisms maximum age (Default 6)	0+	6 (Malachowski (personal communication, November 2020))
S_{min}	Minimum survival rate	0+	0.5 (Robinson et al., 2017)
S_{max}	Maximum survival rate	0+	0.9 (Robinson et al., 2017)
b	Steepness of the survival rate	From −3 to 0	−2 (Robinson et al., 2017)
p	Density at which the survival rate changes most relative	From 0 to 2	0.5 (Robinson et al., 2017)
Number of generations	Number of generations to simulate	From 2 to 100	20
Target frequency	Target ancestry	From 0 to 1	0.99
Optimize supplementation	When set to 0, FALSE or a negative number, it will not be optimized. When negative, the absolute value will be taken as a fixed contribution to each generation (but will not be optimized)	User preference	TRUE
Optimize REMOVAL	When set to 0, FALSE or a negative number, it will not be optimized. When negative, the absolute value will be taken as a fixed contribution to each generation (but will not be optimized)	User preference	TRUE
Number of replicates	Number of replicates (bootstraps)	From 0 to 10	100
Verbose	provides verbose output if TRUE	User preference	User preference
Initial population size	Starting Population size	From 0 to 1000	100
Starting frequency	Initial focal population ancestry frequency in the population	From 0 to 1	Wetland specific (Table S1)

TABLE 1 (Continued)

Function	Function description	Range of values	Hawaiian duck simulation input values
Genetic model	The model can either use a simplified model ('point') of underlying genetics, which speeds up simulation considerably, but underestimates genetic variation. Alternatively, a more detailed genetic model is available, making use of the theory of junctions, this can be accessed using the option 'junctions'. Default is 'simplified'	• Point • Junctions	Junctions
Ancestry put	Average ancestry of individuals being used for supplementation. If the target is high focal ancestry (e.g. aiming for focal ancestry of 1.0), ancestry put should reflect this and be set to 1.0 (which is the default value). When supplementing with non-native individuals, this value can consequently be lowered	From 0 to 1	1
Ancestry pull	Maximum ancestry of individuals used for pulling	From 0 to 1	1
Sex ratio put	The sex ratio of individuals that are added (if any) to the population. Sex ratio is expressed as males/(males+females), such that 0.5 indicates an even sex ratio, 0.9 indicates a male biased sex ratio and 0.1 indicates a female biased sex ratio	From 0 to 1	0.5
Sex ratio pull	The sex ratio of individuals that are removed (if any) from the population. The sex ratio is expressed as males/(males+females), such that 0.5 indicates an even sex ratio, 0.9 indicates a male biased sex ratio and 0.1 indicates a female biased sex ratio	From 0 to 1	0.5
Sex ratio offspring	Sex ratio of newly born offspring. The sex ratio is expressed as males/(males+females), such that 0.5 indicates an even sex ratio, 0.9 indicates a male biased sex ratio and 0.1 indicates a female biased sex ratio	From 0 to 1	0.5
Establishment burn-in	Number of generations since admixture or population establishment	User preference	30

Note: All values used across functions for Hawaiian duck simulations are also provided.

FIGURE 1 Overview of the simRestore shiny app display. (Left) Display of the main variables to modify, and (Right) the three graphs using a simple simulation.

moved towards a target parental through directed management efforts. However, the number of individuals required to be added and/or removed is dependent on many ecological factors (see Table 1; Hennessy et al., 2022). Fortunately, continued conservation efforts surrounding Hawaiian ducks have resulted in in-depth biological and genetic knowledge for the species that can be used to optimize management strategies among populations.

2 | METHODS

Simulation code for the simRestore package can be accessed directly via the R programming language, and can be incorporated into analysis scripts. It is available as an R package, accessible via CRAN, or via www.github.com/thijsjanzen/simRestore. However, for those unfamiliar with the R programming language the simulation code can also be used via a Shiny Web application (Chang et al., 2022); which can be run either locally, or hosted online. The Shiny Web application presents a user-friendly graphical interface (GUI) in which the user can manipulate conditions through direct value input, buttons and sliders to adjust chosen parameters (Figure 1). Once the parameters are set, the user is then presented with direct graphical feedback indicating the required supplementation or removal efforts, resulting change in focal ancestry and population size change. The Shiny Web application is publicly available at https://thijsjanzen.shinyapps.io/simRestoreApp/.

2.1 | Life-history model

Life-history model simulations are implemented using a population with overlapping generations and explicit sexes, where offspring may compete next year for mating opportunities and superfluous males or females may be excluded from mating. We assumed density-dependent population growth, such that over time, an equilibrium density of individuals is reached. The model proceeds through 'seasons' during which the following events occur in sequence: (1) survival, (2) human intervention, (3) mating and offspring survival and (4) offspring recruitment (Figure 2a).

Each season of the life cycle, survival is assumed to be the same and irrespective of sex. However, survival is density-dependent such that at higher densities, individuals have a lower survival rate due to a shortage of resources (Gunnarsson et al., 2013). We model density dependence of survival following Robinson et al. (2017), who model survival in American Black Duck (*Anas rubripes*) using the following equation:

$$S = S_{max} + \frac{S_{min} - S_{max}}{1 + \left(\frac{D}{p}\right)^b} \tag{1}$$

where S is the survival probability (and max and min indicate the maximum and minimum survival probabilities), D is the density (e.g. N/K, where N is the number of individuals, and K is the carrying capacity), p is a variable that indicates the reflection point (e.g. the point at which survival is 50% of $S_{max} - S_{min}$), and b is a variable that indicates the steepness of the curve (Figure 2b). In addition to annual survival probability, we also include the capacity for users to include additional mortality for either or both sexes, as breeding animals often have higher rates of mortality (Lima, 2009; Norrdahl & Korpimäki, 1998; Simmons & Kvarnemo, 2006).

Human intervention is modelled as the supplementation or removal of individuals from the population. When supplementing, individuals are by default added in an equal sex ratio (50% males,
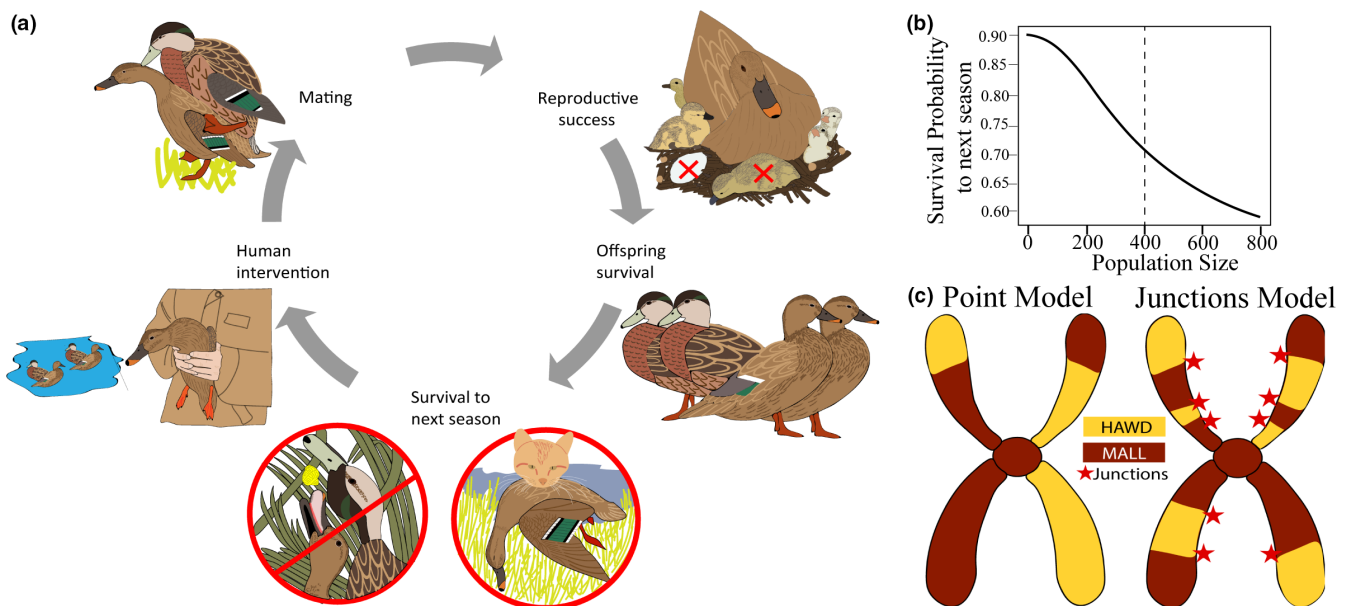

FIGURE 2 Overview of the ecological and genomic information used in the simRestore program. (a) Schematic of annual life-history of Hawaiian duck, (b) Survival curve based on Robinson et al. (2017) equation, dashed line indicating calculated carrying capacity $K = 400$, (c) Genetic model: Point ancestry model and Junction ancestry model using genetic ancestry of Hawaiian duck (yellow) and mallard (brown).

50% females), and assuming that the added individuals carry the ancestry of the focal system of interest. When removing, individuals are removed irrespective of sex and can be removed depending on their maximum genetic ancestry. For example, if this variable is chosen to be 0.5, only individuals with less than 50% native species ancestry are removed. By default, the value is chosen to be 1, which means individuals are removed irrespective of their native species ancestry. Additionally, the sex ratio of individuals added or removed can be changed by the user, as can the ancestry of the individuals supplemented.

To simulate mating, we consider two models designed to emulate the diverse range of social and behavioural aspects of reproductions observed across species: (1) 'Strict Pair Bonding', where females and males pair up in such a way that each female mates with one available male. If there are fewer males than females, some females remain unmated (and vice versa). (2) 'Random mating', characterized by mating probabilities being equal among all individuals in a population. Additionally, we introduced a variable accounting for the probability of offspring resulting from EPC (i.e. extra-pair copulation), a behaviour primarily observed in birds but also present in other species (Brouwer & Griffith, 2019; Soulsbury, 2010; Uller & Olsson, 2008). Furthermore, we do not model multi-season pair bonding to retain simplicity of the model. Thus, in smaller populations, offspring of a pair might mate with one of their parents in the next season (albeit this chance is relatively low, in the order of $1/N$, which is usually less than 1%). Other factors affecting population growth are also considered in the model, such as reproductive success (i.e. the probability of successfully breeding; Table 1).

After mating, offspring recruitment is lower than the total number of offspring produced due to a multitude of factors such as predation (natural and human), parasitism and deteriorating environmental conditions like food abundance (Bortolotti et al., 2011; Gaillard et al., 2008; Hoover & Reetz, 2006; Knights et al., 2012; Rigby, 2008). Thus, we modelled the contribution of variation in recruitment to changes in the population growth as density dependence. For simplicity, we have chosen to make recruitment identical to adult survival and use the same equation (see above Equation 1) with identical parameters (Robinson et al., 2017).

2.2 | Genetic model

The implementation of the genetic model assumes a diploid genome (Zhang et al., 2020), where each chromosome undergoes crossover during meiosis, and the user can specify the total number of chromosomes to be simulated. Upon creation of new offspring, both mother and father provide a single copy of the genome, which are combined to form the diploid offspring genome. Sex is determined randomly (Trivers & Willard, 1973), independent of the genetic makeup and ignoring any potential processes driving sex determination or sex skew. Two models are implemented to track ancestry in the genome:

(1) an explicit crossover model tracking 'junctions', and (2) a point ancestry model (Figure 2c).

In the explicit crossover model, local ancestry is explicitly tracked along the genome and we explicitly model crossovers, resulting recombination events and the effect this has on changes in ancestry. The effects on ancestry are tracked by keeping account of the number of switches in ancestry along the genome, coined 'junctions' by Fisher (1954). Junctions inherit similar to point mutations, provide a computationally efficient method to track changes in ancestry (Baird, 1995) and are well studied mathematically (Janzen et al., 2018; Janzen & Miró Pina, 2022 and references therein). Furthermore, using junctions to track local ancestry (in contrast to, for instance, using high-density SNP maps), allows us to retain high-resolution tracking of Linkage Disequilibrium, while retaining high computational efficiency (see Janzen & Diaz, 2021 for more expansive scenarios utilizing junctions). Changes in ancestry and the resulting junctions arise from crossover events, and we draw the number of crossovers per chromosome from a Poisson distribution, with the mean rate equal to the size of each chromosome expressed in Morgan, with a default value of 1. The location of each crossover on a chromosome is assumed to be independent of the location of other crossovers on the same chromosome, and crossovers are assumed to be distributed uniformly across the genome. Crossovers are independent between chromosomes. Crossovers on locations with differing ancestry between chromosomes result in recombination and the formation of a junction in the resulting recombined chromosome. Over time, the accumulation of recombinations then creates the ancestry-mosaic observed in admixed individuals.

Alternatively, in the point ancestry model, we only track the average ancestry along the genome and each copy of the genome is represented by a single floating-point number per chromosome, indicating the average proportion of ancestry belonging to either of the two parental species. To create a new copy, the average genome ancestry of both copies per chromosome existing in the parent is used. For example, if the parent has one chromosome copy with 20% focal ancestry, and one chromosome copy with 80% focal ancestry, the resulting single chromosome copy that is being given to the offspring has 50% focal ancestry. Thus, this model assumes that recombination acts as a process that uniformly mixes the two genomes. Although this model assumes an overly simplistic representation of the underlying ancestry dynamics, it provides a computationally efficient method to obtain results that, on average, behave very closely to the junctions method. The reason these two methods are so similar, is that although the accumulation of junctions changes the spatial arrangement of ancestry along a genome, it does not change the average ancestry along the genome, as this is mainly driven by population size effects such as drift. To test whether the genetic ancestry means estimated using the point ancestry and junction genetic model are different, we performed statistical tests using R Statistical Software (v 4.1.3, R Core Team, 2023). Shapiro tests were used to evaluate the normal distribution of the data; however, this assumption was not met to perform a parametric test. Therefore, we

performed the Wilcoxon rank-sum test to compare our two independent samples.

To initialize simulations, an ancestry mosaic is derived by performing 30 generations of Wright-Fisher admixture (e.g. non-overlapping generations, random mating, constant population size) using the known genetic ancestry of an admixed population as a starting point. We use Wright-Fisher admixture instead of the life-history model previously described to generate the starting mosaic to save computation time, and to constrain the population size such that it matches the initial population size. For example, if the current frequency is 80/20, then we start the Wright-Fisher admixture with 80% focal ancestry and 20% non-focal ancestry, allowing this 'population' to then inbreed over 30 generations to obtain an approximate ancestry mosaic previously shown to generate ancestry blocks of correct size and distribution (Janzen et al., 2018; Janzen & Miró Pina, 2022).

2.3 | Static versus adaptive simulation model optimizations

Apart from providing functionality to forward simulate a chosen set of parameters, the package also provides functionality to optimize parameters to reach a target level of focal ancestry. First, static optimization attempts to find a fixed per-generation amount of input and removal efforts to reach the target level of genetic integrity. Alternatively, an adaptive optimization model provides more specific information by attempting to optimize the distribution of individuals to be added or removed over a set of generations to reach the target level of genetic integrity. To reduce the degrees of freedom for fitting such a distribution, adaptive optimization does not directly fit the number of individuals per generation (keeping the total constant), but rather fits two parameters of a beta distribution, which is used to determine the number of individuals per generation. Optimization can be performed for supplementation, for removal, or for the joint effort of both supplementation and removal.

2.4 | Ecological parameter sensitivity analysis

We wanted to understand how the accuracy of the ecological data may impact modelling outputs, and thus, also determine how each ecological parameter influences management strategies. To do so, we tested and ranked how supplementation estimates were affected by successively varying each ecological parameter (Table 1). Sensitivity analyses were based on the static optimization of supplementation, assuming a population (N) size of 400, a starting genetic ancestry of 20:80 for parental A versus B, with a target ancestry of 99% for focal parental A, and using the junction as the genetic model. Each analysis was run 100 times with optimized supplementation and estimated population sizes following management strategy summarized as boxplots and including the mean value of the percent change in optimized value given a starting value per ecological parameter.

In our sensitivity analysis, we first explored the impact of density dependence by varying the steepness/slope of the survival curve (varied as −4, −3.5, …, −0.5; see parameter b in Table 1). Similarly, we explored sensitivity of results to the mean number of offspring (i.e. varied as 1, 2, …, 10), maximum individual age (i.e. varied as 1, 2, …, 10), reproductive risk of females and males (i.e. varied as 0, 0.05, …, 0.4) and reproductive success (i.e. varied as 0.0, 0.1, …, 1.0). Specifically, sensitivity ranking of ecological parameters was based on the magnitude of changes in estimated supplementation number and population size for each assessed parameter value expressed as percentage. In short, the magnitude of change was based on the subtraction of the current estimated number (CE) of individuals/ population size and previous estimates (PE), divided by the current value, and all multiplied by 100% [((CE-PE)/CE)*100%]. For example, to understand differences between the mean numbers of offspring of two compared to one, the magnitude of change was determined for estimated supplementation and population size as the PE and CE values under the mean number of offspring of one versus two respectively. In the end, ecological parameters with the largest magnitude of changes between values were considered more sensitive. We plotted and visualized percent change of the absolute values as boxplots using R.

2.5 | Case study: Simulating potential conservation strategies for Hawaiian duck

To illustrate the performance of the developed program, we tested whether any set of management efforts could reverse the genetic constitution of the Hawaiian duck×feral mallard hybrids found across Hawaiian Islands. The history and constant monitoring of Hawaiian duck provides high-quality ecological and genetic information, including demographic and vital rate differences between native Hawaiian duck on Kauai and hybrids elsewhere, allowing us to optimize management strategies based on wetland-specific conditions (Table 1; Table S1). Note that given that we used the Hawaiian duck as a case example, ecological models were based on their life cycle traits (Table 1). All simulations were done with an initial population size (N) of 100, and a starting fraction of focal (i.e. Hawaiian duck) ancestry specific to the O'ahu wetlands Hamukua, Kawainui and Ki'i (Table 1 and Table S1; Wells et al., 2019, Lavretsky et al., 2019), with a target frequency of 0.99 for the focal ancestry to be achieved over 20 generations, zero probability of extra-pair copulation, and considering an additional death rate of females during breeding (Table 1). Note that we followed Robinson et al., 2017 for density dependence, setting a moderately steep b (−2), along with parameter sets as $p=1.0$, $S_{min}=0.5$, $S_{max}=0.9$ (see Figure 1b). Both static and adaptive optimization models were run 100 times for each wetland. Moreover, 30 generations were used as this reflects when Hawaiian duck were re-introduced from Kauai into the other Hawaiian Islands; and thus, hybridization with already established feral mallards would have started (Engilis Jr et al., 2004).

3 | RESULTS

3.1 | Genetic and mating models

Whether using the point ancestry or 'junctions' genetic methods, final outputs were statistically identical if inputting values across parameters or optimizing outputs in either the static or adaptive optimization models (Figure 3). Importantly, when using the point ancestry or the 'junctions' genetic models, simulations in which no management strategies were undertaken (i.e. no supplementation or removing individuals) resulted in no change in the average local ancestry over time, and the population remained at the starting ancestry proportions (Table S1). However, the desired population ancestry goal of 0.99 for the focal population was achieved by supplementing individuals (Table 2). Even though the average behaviour between the point ancestry and 'junctions' methods was identical, there was higher variance among replicates under the 'junctions' model, indicating that the point model tends to underestimate the observed standing genetic variation (Figure 3), as expected.

Next, we found no statistical differences when evaluating between mating models (i.e. strict pair bonding vs. random mating) whether in the absence of a management strategy or when optimizing the management approach (Figure S1). This absence of differentiation between mating models is further reflected in the outcomes of management strategies (i.e. number of supplemented individuals and population size), even when evaluating a spectrum of extra-pair copulation rates ranging from 0 to 1 (Figure S2).

3.2 | Static versus adaptive simulation model optimizations

All analyses were based on the junctions ancestry genetic model. First, optimization of removing only resulted in no change of focal ancestry (e.g. Table 2), even when exploring variations in the genetic ancestry of the removed individuals across different levels of focal species ancestry (Table S2). Conversely, optimizing supplementation only reaches the target frequency over the time by consistently adding a greater number of individuals per generation with the static as compared to the adaptive model. However, focal ancestry was always reached with fewer individuals per generation when optimizing both supplementation and removal (e.g. Table 2). Applying totals that were recovered in the static simulation into the adaptive simulation model further optimized strategies for each generation (e.g. Table 2).

3.3 | Ecological parameter sensitivity

Sensitivity analyses were based on changes in the optimized number of individuals added to the population, which was estimated by changing each ecological parameter (Figure 4) while maintaining the target genetic frequency. Overall, we found that the required individuals to supplement per generation strongly correlated with the obtained population size as permitted by the used parameters that included, (a) lenient parameters allowed for large populations also caused large estimates for the required individuals to supplement,
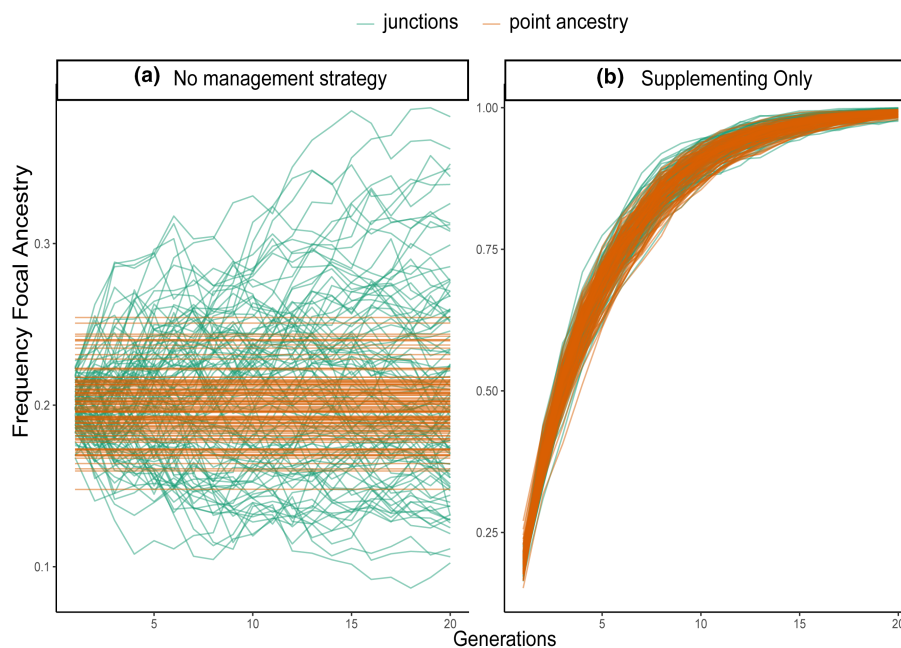

FIGURE 3 Comparing outputs for point ancestry (orange) and the junctions (green) genetic methods based on a (a) no management strategy versus (b) optimization of supplementation only, each run 100 times. As expected, no substantial change between the starting and final ancestries were attained with either genetic method if no management is done, whereas statistically similar (Wilcox-test p-value=0.95) results of substantial ancestry improvement was recovered with both genetic methods when optimizing supplementation.

TABLE 2 Optimized management strategies for three wetlands on O'ahu of varying starting average Hawaiian duck ancestry (Table 1).

Model	Management strategy	Wetland (current avg. Hawaiian duck ancestry of population)		
		Hamukua (28%)	Kawainui (48%)	Kii (74%)
Static optimization	Supplement only	Supplement 93 Hawaiian ducks/gen×20 gens=1860 Hawaiian ducks Final ancestry=0.999=Achieved	Supplement 84 Hawaiian ducks/gen×20 gens=1680 Hawaiian ducks Final ancestry=0.999=Achieved	Supplement 75 Hawaiian ducks/gen×20 gens=1500 Hawaiian ducks Final ancestry=0.999=Achieved
	Removing only	Remove 13 Hybrids/gen×20 gens=260 Hybrids Final ancestry=0.282=Failed	Remove 19 Hybrids/gen×20 gens=380 Hybrids Final ancestry=0.506=Failed	Remove 21 Hybrids/gen×20 gens=420 Hybrids Final ancestry=0.791=Failed
	Supplement+Removing	Supplement 64 Hawaiian ducks/gen×20 gens=1280 Hawaiian ducks + Remove 23 Hawaiian ducks/gen×20 gens=460 Hybrids Final ancestry=0.999=Achieved	Supplement 76 Hawaiian ducks/gen×20 gens=1520 Hawaiian ducks + Remove 5 Hawaiian ducks/gen×20 gens=100 Hybrids Final ancestry=0.999=Achieved	Supplement 60 Hawaiian ducks/gen×20 gens=1200 Hawaiian ducks + Remove 3 Hawaiian ducks/gen×20 gens=60 Hybrids Final ancestry=0.999=Achieved
Adaptive Optimization	Supplement only	Supplement 748 total Hawaiian ducks Vary strategy for 19 generations Final ancestry=0.986=Nearing	Supplement 647 total Hawaiian ducks Vary strategy for 19 generations Final ancestry=0.986=Nearing	Supplement 517 total Hawaiian ducks Vary strategy for 19 generations Final ancestry=0.99=Achieved
	Removing only	Remove 104 total Hybrids Vary strategy for 9 generations Final ancestry=0.306=Failed	Remove 20 total Hybrids Vary strategy for 1 generation Final ancestry=0.503=Failed	Remove 10 total Hybrids Vary strategy for 2 generations Final ancestry=0.807=Failed
	Supplement+Removing	Supplement 110 total Hawaiian ducks + Remove 50 total hybrids Vary strategy for 12 generations Final ancestry=1.000=Achieved	Supplement 120 total Hawaiian ducks + Remove 20 total hybrids Vary strategy for 12 generations Final ancestry=0.999=Achieved	Supplement 97 total Hawaiian ducks + Remove 30 total hybrids Vary strategy for 5 generations Final ancestry=1.000=Achieved

Note: Static and adaptive optimizations were done under management strategies including supplementation only, removing only, or a combination of supplementation and removal. Success of each strategy was determined by the predicted final ancestry, with the objective set to reach 99% Hawaiian duck ancestry. Note that while static optimization simply allocates the same number of individuals across set generations (gen), adaptive optimization varies the strategy across generations.
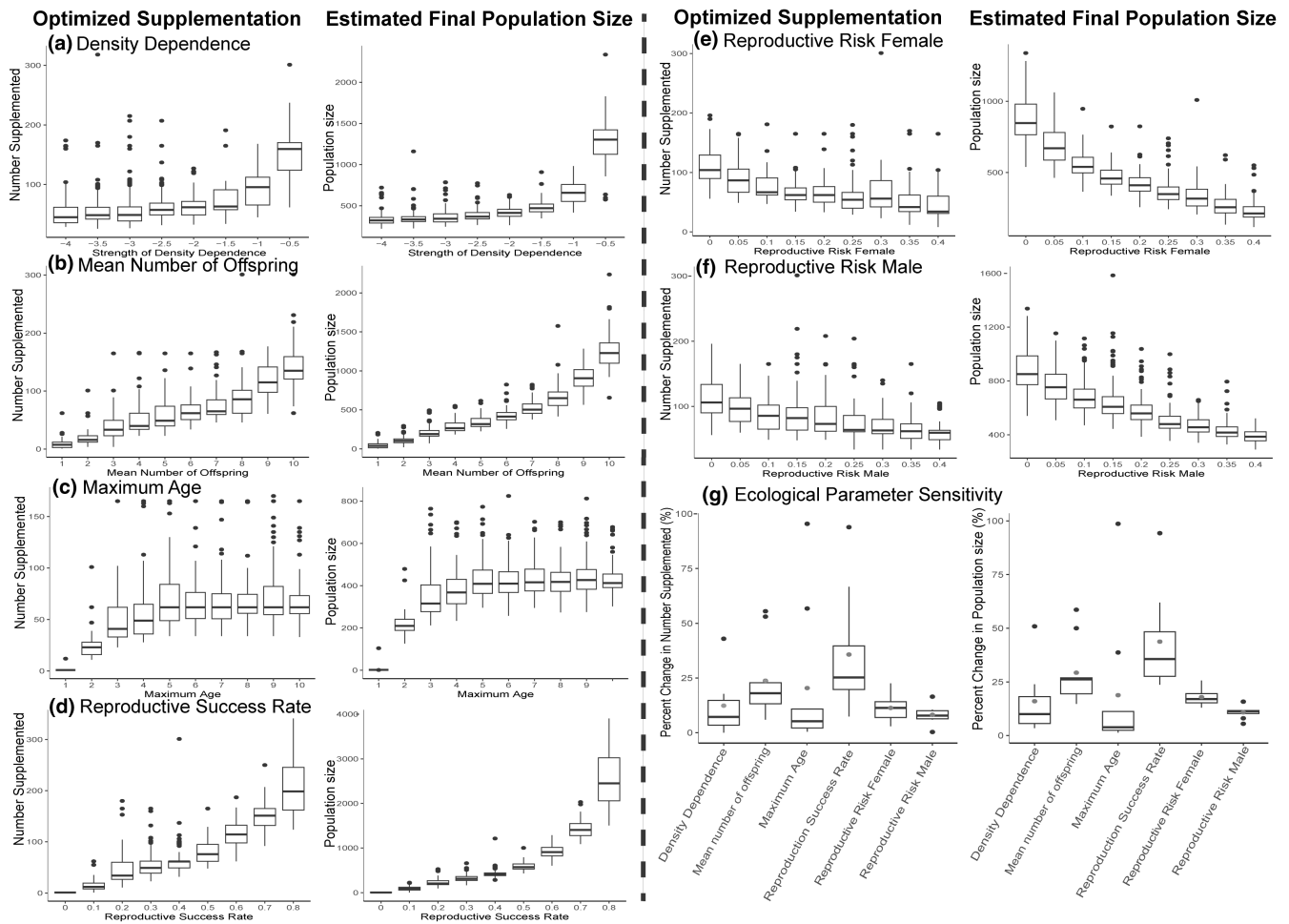
FIGURE 4 (a–f) Changes in optimized supplementation and final population sizes when varying ecological parameters present in the 'simRestore' R package. (g) Magnitude of change expressed as percentage when varying (a–f) ecological variables in estimating supplementation and population size and depicted as box plots with mean values denoted (grey circle).

whereas (b) stringent parameter settings causing reduced population sizes and low estimates for the number of required individuals.

At the population level, we found that increasing the strength of density dependence (e.g. making the slope more negative) resulted in smaller populations and decreasing supplementation requirements (Figure 4a). Conversely, with the slope becoming closer to 0.0 and density dependence weakening, we found that population sizes became exponentially larger, and consequently the supplementation requirement per generation increased exponentially as well. Therefore, it seems better to underestimate the strength of density dependence as this results in overestimating the number to supplement; although, over-supplementation will still result in reaching the target genetic frequency. Next, we find that a shorter life expectancy reduces the required amount to be supplemented, plateauing for any maximum age extending past 6–7 years of age (Figure 4c) that is likely due to other mortality effects (density dependence, reproductive risk) acting before the focal individual reaches the maximum life expectancy.

At the mating stage, we find that the mean number of offspring is particularly important, with a 24% error in management strategy if the average number of offspring is inaccurate by even

±1 offspring (Figure 4b). As expected, population trends show an exponential increase with each increase in +1 offspring per breeding event. Next, miscalculating additional female or male mortality during reproduction causes deviations in the true supplement number with errors ranging from 3%–22% for females and 0%–16% in males (Figure 4e,f); as with density-dependence, overestimating reproductive risk results in reaching the desired focal ancestry albeit over-supplementation. As expected, we find that population trends are inversely associated with increases in mortality of either sex. Finally, both supplemental need and population growth follow an S curve as reproductive success rate increases, with an inflection point for reproductive success of ~50%, and plateauing once reproductive success is ≥80%. Generally, optimized supplementation was underestimated by ~25% for every 0.1% inaccuracy in estimated reproductive success (Figure 4d).

The ecological parameters showed different influences on the number of individuals to supplement and the population size in each generation (Figure 4g). At the population level, both parameters (i.e. density dependence and maximum age) showed a weak influence in the supplemental of individuals in a population, and therefore the population size. Specifically, the life expectancy parameter had the
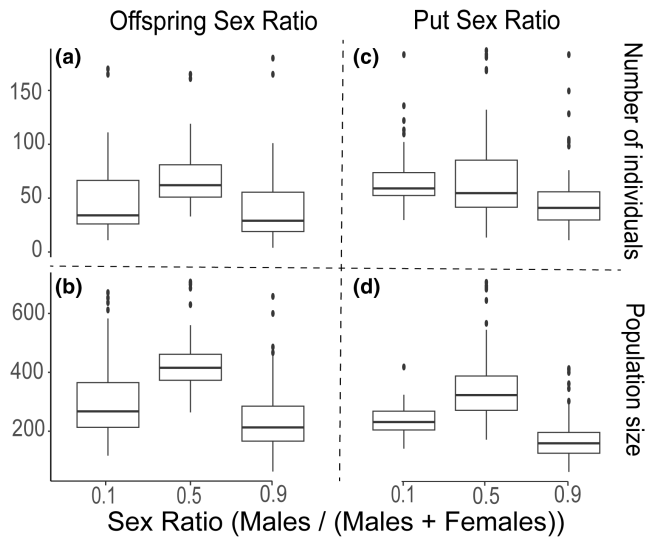
FIGURE 5 Changes in optimized supplementation (top row) and final population sizes (bottom row) when varying sex ratios of offspring (first column) or individuals added (second column) in the 'simRestore' R package. Sex ratio is expressed as males/(males+females), such that 0.5 indicates an even sex ratio, 0.9 indicates a male biased sex ratio and 0.1 indicates a female biased sex ratio.

lowest rank. At the mating stage, the number of offspring and reproductive success rate showed the strongest influence on the number of individuals needed to add to the population and therefore, the population size. However, the additional mortality rate of males during reproduction had the lowest rank among the parameters that influence the mating stage.

By default, the sex ratio of offspring is equal (e.g. offspring has a 50% probability to be of the male sex). Deviations from this even sex ratio significantly influenced outcomes if populations are strongly sex biased (e.g. 0.9 indicates a male biased sex ratio and 0.1 indicates a female biased sex ratio; Figure 5b,d). Similarly, the number of individuals required to supplement also deviated if the sex ratio of the supplementation population was not even (Figure 5a,c). In short, male biased supplementation resulted in overall population size declines, whereas female biased input resulted in population growth. Furthermore, female biased supplementation caused an increase in the number of individuals required to be put to reach the target genetic frequency, whereas male biased supplementation reduced this. Thus, the sex composition of the supplementing population can be skewed towards male or female if managers are attempting to simply change the genetic ancestry or also increase their population size respectively.

3.4 | Simulating potential Hawaiian duck conservation strategies

We simulated optimized management strategies to reverse the population's genetic ancestry for several wetlands on Oʻahu, Hawaii

with varying starting average Hawaiian duck ancestry (Table 2). First, however, all simulations clearly show that the removal of individuals does not substantially change the focal ancestry (Table 2). More importantly, whereas management strategies employing supplementation only eventually reach ancestry goals, these require substantially more individuals than what would be required if strategies included a mix of supplementation and removal efforts (Table 2). Finally, by varying the management strategy generationally, the adaptive model generally decreases the number of generations to reach ancestry goal as compared to the static model (Table 2). For example, static simulations suggest that the ancestry can be moved from 74% to 99% Hawaiian duck on Oʻahu's Kiʻi wetland complex by adding 60 Hawaiian ducks and removing 3 hybrids per generation for 20 generations. Conversely, applying the adaptive simulation model reaches 99% Hawaiian duck ancestry in five generations by varying the supplementation and removal strategies across generations (Table 2).

4 | DISCUSSION

Our software package simRestore uses a forward simulator platform that optimizes available management strategies to meet set conservation goal(s). We provide functionality to the program through a user-friendly GUI interface where anyone can change ecological parameters and genetic ancestry information to forward simulate actionable management strategies. Importantly, simRestore was developed to permit for management strategy optimization at any geographical (i.e. wetland, Island) and temporal (i.e. number of generations) scale, as well as under any project limitations (i.e. number of individuals available for input, time for project completions). Finally, assessing offspring ancestry allows for a direct test of the implemented strategy; and thus, permitting researchers to determine ecological or other factors that were not accurately accounted for in situations where simulated values are unaligned to empirical ones. In short, assessing simulation accuracy can be done annually by comparing genetic ancestry of offspring in the simulation with genetic ancestry assessed empirically. If genetic integrity is reversed but set ancestry goals are not attained following the required number of generations of stocking, then the newly established genetic information can be fed back into models to help guide the following year's strategies. In the end, the simRestore program provides a means for the adaptive management planning for species' conservation.

4.1 | Model considerations

Although the point and junctions genetic models resulted in identical average behaviour in resulting ancestry, there was a higher degree of variation when using the junctions model (Figure 3). We conclude that whereas the point model is a strong oversimplification of the underlying genetics, its fast computation and high similarity in outcome provides a great benefit over the more complex and demanding

junctions model. We suggest the use of the point model in management strategy optimization followed by an assessment in outcome variability and robustness with the junctions model. More importantly, for organisms for which more detailed genomic information remains lacking (i.e. chromosome size, recombination rate, etc.), and thus the use of the junctions genetic model is perhaps inappropriate, the point genetic model will still provide robust inferences. Similarly, varying both the mating models (strict and pair-bonded) and the EPC variable produced comparable changes in ancestry and management strategies, as they are not inherently tied to a particular ancestry type (e.g. males of native ancestry show a greater likelihood of involvement in EPC). However, we strongly recommend setting up the mating system of the studied organism to the best of our knowledge to ensure inference reliability.

Next, assessing the utility of the three management strategies, we conclude that removing only is similar to a no management strategy as the local ancestry is unaffected (Table 2; Table S2). This is not unsurprising, as removing individuals of a hybrid swarm still results in remaining breeding individuals being hybrid; confirming that a parental gene pool is required to reverse the genetic ancestry of a hybrid pool (Wells et al., 2019). Whereas supplementing only can reverse the genetic signature towards the focal species, the total number required to be supplemented is consistently higher and requiring more generations than when combining supplementation and removal efforts (Table 2; Table S2). Thus, the optimum management strategy is combining supplementation and removal when possible.

In addition to starting genetic ancestry, researchers will also need to know a suite of ecological parameters for their population(s) of interest. Life-history traits can influence how much maternal versus paternal genetic variation contributes to each generation (Table 1). Life-history traits therefore need to be correctly incorporated to ensure accurate model predictions. In short, we find that each of the ecological parameters within our model affects simulations differently, and with some being largely insensitive, while others are highly sensitive and require accurate estimates (Figures 4 and 5). Among parameters, researchers need to take particular care to have accurate estimates of the number of offspring (i.e. annual fecundity) and reproductive success rate in particular, as these have a disproportionate effect on population size, which in turn dictates management strategies. Moreover, researchers working in a female biased population and/or r-selected species will require substantial increases in supplemental efforts (Figure 5). More generally, however, we find that miscalculating most ecological parameters may not impact management outcomes, since doing so still typically results in the achievement of management goals, albeit on slightly different time frames and/or supplementation efforts. Specifically, unless known, we recommend that it is better to underestimate density dependency, overestimate reproductive risk, and assume a 50:50 number of offspring as all of these will result in optimum management strategies that can still achieve ancestry goals (Figures 4 and 5); though

at the expense of additional resources that would otherwise not be required.

4.2 | Conservation implications

The incorporation of genetic data has become a fundamental source of information for species conservation (Walters & Schwartz, 2020). Genomic data have been used to shed light into species' effective population size, inbreeding demographic history and population structure that not only aid in management efforts (Hohenlohe et al., 2021), but are critical in efforts of biodiversity monitoring, resolving taxonomic uncertainty, wildlife forensics and designation of conservation units (Funk et al., 2012; Hohenlohe et al., 2021). However, there has been a severe lag and lack in the implementation of genomic data into management decisions (Walters & Schwartz, 2020); in part due to the lack of user-friendly methods (Hohenlohe et al., 2021). From the perspective of wildlife management, understanding the population genomics of wild populations can aid multiple traditional wildlife activities such as translocations, reintroductions, population augmentation and the identification of units of conservation concern (Funk et al., 2012; Hohenlohe et al., 2021; Tallmon et al., 2004; Walters & Schwartz, 2020; Whiteley et al., 2015). Among conservation efforts, understanding rates of hybridization and its implication to wildlife populations is now at the forefront of conservation science (Cooper & Shaffer, 2021; Hohenlohe et al., 2021; Searcy et al., 2016). Towards these efforts, our developed simRestore program provides a tool where managers can couple genetic and ecological data to optimize management strategies that directly feed into decision making when attempting to resolve hybridization issues. Once again, the ability to feed empirical data (i.e. genetic assignment probabilities of a population) back into models provides a powerful tool for management to be adaptive and specific to the species' needs.

We apply developed methods to understand the potential in artificially reversing genetic ancestry through directed management efforts for the endangered Hawaiian duck. Given the proximate threat to the Hawaiian duck is genetic extinction through ongoing anthropogenic hybridization with feral mallards (USFWS, 2012; Wells et al., 2019), we demonstrate that the reversal to a genetic native status of these hybrid swarms is theoretically possible (Table 2). Importantly, both molecular data (Lavretsky et al., 2019; Wells et al., 2019) and telemetry movement data (Malachowski, 2013; Malachowski et al., 2019, 2020; Malachowski & Dugger, 2018) suggest that movement is not only limited between Islands, but also among wetlands within Islands. Consequently, each wetland on Islands can be effectively considered a closed system, providing an important means to closely monitor how optimized management strategies impact the genetic integrity of that wetland's population (Table 2). We conclude that the developed models can help guide future Hawaiian duck conservation efforts, with work the

implementation of optimized strategies in a pilot program to determine real-world feasibility of the simulations.

5 | CONCLUSIONS

Conceptually, hybrid individuals are simply conduits of genes stemming from divergent lineages (Allendorf et al., 2001); and as a result, hybrids still possess the genetic diversity of the species of interest. Though hybrids pose a conservation concern due to the maladaptive potential when divergent genomes are admixed (i.e. outbreeding; Templeton, 1986), the genetic diversity of the focal species remains present. Given that species of conservation concern often suffer in population size and standing genetic diversity, continued losses in both are often detrimental. Here, we demonstrate that directed manipulation of hybrid populations can potentially reconstitute a hybrid population towards the focal population without additional loss of individuals and the genetic diversity they carry. However, what wildlife biologists are able to do to mitigate or reverse the continued loss of individuals to hybridization can be further limited by human dimensions (i.e. social rejection of particular management strategies; Cinque et al., 2012). Thus, the functionality of the simRestore program provides biologists and managers attempting to mitigate or reverse such trends, a decision-making tool for management optimization specific to the species or population of concern in an adaptive framework. By doing so, biologists not only have the means to evaluate possible conservation scenarios but critical information to explain and with which to engage their constituents.

DATA AVAILABILITY STATEMENT

The R package simRestore is available on CRAN via https://CRAN.R-project.org/package=simRestore, through Github at github.thijs janzen/simRestore, or via the Shiny app on https://thijsjanzen.shiny apps.io/simRestoreApp/.

SIMULATION CODE AND DATA ACCESSIBILITY

The simulation code described in this manuscript is available as an R package, accessible via CRAN, via github (www.github.com/thijs janzen/simRestore), or via the Shiny app on https://thijsjanzen.shiny apps.io/simRestoreApp/. All simulations performed in this manuscript were performed using genetic ancestry data presented in Table S1.

ORCID

Flor Hernández https://orcid.org/0000-0002-6709-4764
Thijs Janzen https://orcid.org/0000-0002-4162-1140
Philip Lavretsky https://orcid.org/0000-0002-5904-8821

REFERENCES

Abbott, R., Albach, D., Ansell, S., Arntzen, J. W., Baird, S. J., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C. A., Buggs, R., Butlin, R. K., Dieckmann, U., Eroukhmanoff, F., Grill, A., Cahan, S. H., Hermansen, J. S., Hewitt, G., Hudson, A. G., Jiggins, C., … Zinner, D. (2013). Hybridization and speciation. *Journal of Evolutionary Biology*, 26(2), 229–246. https://doi.org/10.1111/j.1420-9101.2012.02599.x

Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids: Setting conservation guidelines. *Trends in Ecology & Evolution*, 16(11), 613–622. https://doi.org/10.1016/S0169-5347(01)02290-X

Anderson, E. C., & Thompson, E. A. (2002). A model-based method for identifying species hybrids using multilocus genetic data. *Genetics*, 160(3), 1217–1229.

Baird, S. J. E. (1995). A simulation study of multilocus clines. *Evolution*, 49(6), 1038–1045. https://doi.org/10.1111/j.1558-5646.1995.tb04431.x

Barton, N. H. (2013). Does hybridization influence speciation? *Journal of Evolutionary Biology*, 26(2), 267–269. https://doi.org/10.1111/jeb.12015

Bortolotti, L. E., Harriman, V. B., Clark, R. G., & Dawson, R. D. (2011). Can changes in provisioning by parent birds account for seasonally declining patterns of offspring recruitment? *Canadian Journal of Zoology*, 89(10), 921–928. https://doi.org/10.1139/z11-068

Brennan, A., Woodward, G., Seehausen, O., Muñoz-Fuentes, V., Moritz, C., Guelmami, A., Abbott, R. J., & Edelaar, P. (2014). Hybridization due to changing species distributions: Adding problems or solutions to conservation of biodiversity during global change? *Evolutionary Ecology Research*, 16, 475–491.

Brouwer, L., & Griffith, S. C. (2019). Extra-pair paternity in birds. *Molecular Ecology*, 28(22), 4864–4882.

Browne, R. A., Griffin, C. R., Chang, P. R., Hubley, M., & Martin, A. E. (1993). Genetic divergence among populations of the Hawaiian duck, Laysan duck, and mallard. *The Auk*, 110(1), 49–56. https://doi.org/10.1093/auk/110.1.49

Chang, W., Cheng, J., Allaire, J., Xie, Y., & McPherson, J. (2022). Shiny: Web application framework for R. R package version 1.7.3. URL https://cran.r-project.org/package=shiny.

Christie, M. R., Marine, M. L., French, R. A., & Blouin, M. S. (2012). Genetic adaptation to captivity can occur in a single generation. *Proceedings of the National Academy of Sciences*, 109(1), 238–242. https://doi.org/10.1073/pnas.1111073109

Cinque, S., Johansson, M., & Morf, A. (2012). In D. J. Decker, S. J. Riley, & W. F. Siemer (Eds.), *Human Dimensions of Wildlife Management*. The John Hopkins University Press Retrieved from https://www.press.jhu.edu/books/title/10090/human-dimensions-wildlife-management

Cooper, R. D., & Shaffer, H. B. (2021). Allele-specific expression and gene regulation help explain transgressive thermal tolerance in non-native hybrids of the endangered California tiger salamander (*Ambystoma californiense*). *Molecular Ecology*, 30(4), 987–1004. https://doi.org/10.1111/mec.15779

Crispo, E., Moore, J.-S., 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(7), 508–518. https://doi.org/10.1002/bies.201000154

Engilis, A., & Pratt, T. (1993). Status and population trends of Hawaii's native Waterbirds, 1977-1987. *The Wilson Bulletin*, 105, 142–158.

Engilis, A., Jr., Pyle, R., & David, R. (2004). Status and occurrence of migratory birds in the Hawaiian islands: Part 1 – Anseriformes: Anatidae (waterfowl). *Bishop Museum Occasional Papers*, 81, 1–28.

Engilis, A., Jr., Uyehara, K. J., & Giffin, J. G. (2020). Hawaiian duck (*Anas wyvilliana*), version 1.0. In A. F. Poole, & F. B. Gill (Eds.), *Birds of the World*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.hawduc.01

Fisher, R. A. (1954). A fuller theory of "junctions" in inbreeding. *Heredity*, 8(2), 187–197. https://doi.org/10.1038/hdy.1954.17

Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., & Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evolutionary Applications*, 11(7), 1035–1052. https://doi.org/10.1111/eva.12569

Frankham, R. (2015). Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology*, 24(11), 2610–2618. https://doi.org/10.1111/mec.13139

Funk, W. C., McKay, J. K., Hohenlohe, P. A., & Allendorf, F. W. (2012). Harnessing genomics for delineating conservation units. *Trends in Ecology & Evolution*, 27(9), 489–496. https://doi.org/10.1016/j.tree.2012.05.012

Gaillard, J. M., Coulson, T., & Festa-Bianchet, M. (2008). Recruitment. In S. E. Jørgensen & B. D. Fath (Eds.), *Encyclopedia of ecology* (pp. 2982–2986). Academic Press. https://doi.org/10.1016/B978-008045405-4.00655-8

Grant, P. R., & Grant, B. R. (1992). Hybridization of bird species. *Science*, 256(5054), 193–197. https://doi.org/10.1126/science.256.5054.193

Gunnarsson, G., Elmberg, J., Pöysä, H., Nummi, P., Sjöberg, K., Dessborn, L., & Arzel, C. (2013). Density dependence in ducks: A review of the evidence. *European Journal of Wildlife Research*, 59(3), 305–321. https://doi.org/10.1007/s10344-013-0716-9

Hedrick, P. W., & Fredrickson, R. (2010). Genetic rescue guidelines with examples from Mexican wolves and Florida panthers. *Conservation Genetics*, 11(2), 615–626. https://doi.org/10.1007/s10592-009-9999-5

Hennessy, S. M., Wisinski, C. L., Ronan, N. A., Gregory, C. J., Swaisgood, R. R., & Nordstrom, L. A. (2022). Release strategies and ecological factors influence mitigation translocation outcomes for burrowing owls: A comparative evaluation. *Animal Conservation*, 25(5), 614–626. https://doi.org/10.1111/acv.12767

Hirashiki, C., Kareiva, P., & Marvier, M. (2021). Concern over hybridization risks should not preclude conservation interventions. *Conservation Science and Practice*, 3(4), e424. https://doi.org/10.1111/csp2.424

Hoban, S., Gaggiotti, O., Consortium, C., & Bertorelle, G. (2013). Sample planning optimization tool for conservation and population genetics (SPOTG): A software for choosing the appropriate number of markers and samples. *Methods in Ecology and Evolution*, 4(3), 299–303. https://doi.org/10.1111/2041-210x.12025

Hohenlohe, P. A., Funk, W. C., & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Molecular Ecology*, 30(1), 62–82. https://doi.org/10.1111/mec.15720

Hoover, J. P., & Reetz, M. J. (2006). Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. *Oecologia*, 149(1), 165–173.

Janzen, T., & Diaz, F. (2021). Individual-based simulations of genome evolution with ancestry: The GenomeAdmixR R package. *Methods in Ecology and Evolution*, 12(8), 1346–1357. https://doi.org/10.1111/2041-210X.13612

Janzen, T., & Miró Pina, V. (2022). Estimating the time since admixture from phased and unphased molecular data. *Molecular Ecology Resources*, 22(3), 908–926. https://doi.org/10.1111/1755-0998.13519

Janzen, T., Nolte, A. W., & Traulsen, A. (2018). The breakdown of genomic ancestry blocks in hybrid lineages given a finite number of recombination sites. *Evolution*, 72(4), 735–750. https://doi.org/10.1111/evo.13436

Kearns, A. M., Restani, M., Szabo, I., Schrøder-Nielsen, A., Kim, J. A., Richardson, H. M., Marzluff, J. M., Fleischer, R. C., Johnsen, A., & Omland, K. E. (2018). Genomic evidence of speciation reversal in ravens. *Nature Communications*, 9(1), 906. https://doi.org/10.1038/s41467-018-03294-w

Knights, A. M., Firth, L. B., & Walters, K. (2012). Interactions between multiple recruitment drivers: Post-settlement predation mortality and flow-mediated recruitment. *PLoS One*, 7(4), e35096. https://doi.org/10.1371/journal.pone.0035096

Lavretsky, P., Janzen, T., & McCracken, K. G. (2019). Identifying hybrids & the genomics of hybridization: Mallards & American black ducks of eastern North America. *Ecology and Evolution*, 9(6), 3470–3490. https://doi.org/10.1002/ece3.4981

Lavretsky, P., Mohl, J. E., Söderquist, P., Kraus, R. H. S., Schummer, M. L., & Brown, J. I. (2023). The meaning of wild: Genetic and adaptive consequences from large-scale releases of domestic mallards. *Communications Biology*, 6, 819. https://doi.org/10.1038/s42003-023-05170-w

Lavretsky, P., Peters, J. L., Winker, K., Bahn, V., Kulikova, I., Zhuravlev, Y. N., Wilson, R. E., Barger, C., Gurney, K., & McCracken, K. G. (2016). Becoming pure: Identifying generational classes of admixed individuals within lesser and greater scaup populations. *Molecular Ecology*, 25(3), 661–674. https://doi.org/10.1111/mec.13487

Leitwein, M., Gagnaire, P.-A., Desmarais, E., Berrebi, P., & Guinand, B. (2018). Genomic consequences of a recent three-way admixture in supplemented wild brown trout populations revealed by local ancestry tracts. *Molecular Ecology*, 27(17), 3466–3483. https://doi.org/10.1111/mec.14816

Lima, S. L. (2009). Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, 84(3), 485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

López-Caamal, A., & Tovar-Sánchez, E. (2014). Genetic, morphological, and chemical patterns of plant hybridization. *Revista Chilena de Historia Natural*, 87(1), 16. https://doi.org/10.1186/s40693-014-0016-0

Malachowski, C. P. (2013). *Hawaiian duck (Anas wyvilliana) behavior and response to wetland habitat management at Hanalei National Wildlife Refuge on Kaua'i.*

Malachowski, C. P., & Dugger, B. D. (2018). Hawaiian duck behavioral patterns in seasonal wetlands and cultivated Taro. *The Journal of Wildlife Management*, 82(4), 840–849.

Malachowski, C. P., Dugger, B. D., & Heard, D. J. (2020). Extrusion of Intracoelomic Radiotransmitters by Hawaiian ducks. *Wildlife Society Bulletin*, 44(4), 741–748. https://doi.org/10.1002/wsb.1134

Malachowski, C. P., Dugger, B. D., & Uyehara, K. J. (2019). Seasonality of life history events and behavior patterns in the Island endemic Hawaiian duck (*Anas wyvilliana*). *Waterbirds*, 42(1), 78–89. https://doi.org/10.1675/063.042.0109

Mallet, J. (2005). Hybridization as an invasion of the genome. *Trends in Ecology & Evolution*, 20(5), 229–237. https://doi.org/10.1016/j.tree.2005.02.010

Mallet, J. (2007). Hybrid speciation. *Nature*, 446(7133), 279–283. https://doi.org/10.1038/nature05706

McFarlane, S. E., & Pemberton, J. M. (2019). Detecting the true extent of introgression during anthropogenic hybridization. *Trends in Ecology & Evolution*, 34(4), 315–326. https://doi.org/10.1016/j.tree.2018.12.013

Miller, J. M., Poissant, J., Hogg, J. T., & Coltman, D. W. (2012). Genomic consequences of genetic rescue in an insular population of bighorn

sheep (*Ovis canadensis*). *Molecular Ecology*, 21(7), 1583–1596. https://doi.org/10.1111/j.1365-294X.2011.05427.x

Nolte, A. W., & Tautz, D. (2010). Understanding the onset of hybrid speciation. *Trends in Genetics*, 26(2), 54–58. https://doi.org/10.1016/j.tig.2009.12.001

Norrdahl, K., & Korpimäki, E. (1998). Does mobility or sex of voles afect risk of predation by mammalian predators? *Ecology*, 79(1), 226–232.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rhymer, J. M. (2006). S33-4 extinction by hybridization and introgression in anatine ducks. *Acta Zoologica Sinica*, 52, 583–585.

Rieseberg, L. H., & Gerber, D. (1995). Hybridization in the Catalina Island mountain mahogany (*Cercocarpus traskiae*): RAPD evidence. *Conservation Biology*, 9(1), 199–203.

Rigby, E. A. (2008). *Recruitment of mottled ducks (Anas fulvigula) on the upper Texas gulf coast*. (Thesis). Retrieved from https://ttu-ir.tdl.org/handle/2346/9189

Robinson, O. J., McGowan, C. P., & Devers, P. K. (2017). Disentangling density-dependent dynamics using full annual cycle models and Bayesian model weight updating. *Journal of Applied Ecology*, 54(2), 670–678. https://doi.org/10.1111/1365-2664.12761

Searcy, C. A., Rollins, H. B., & Shaffer, H. B. (2016). Ecological equivalency as a tool for endangered species management. *Ecological Applications*, 26(1), 94–103. https://doi.org/10.1890/14-1674

Seehausen, O., Takimoto, G., Roy, D., & Jokela, J. (2008). Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Molecular Ecology*, 17(1), 30–44. https://doi.org/10.1111/j.1365-294X.2007.03529.x

Simmons, L. W., & Kvarnemo, C. (2006). Cost of breeding and their effects on the directial of sexual selection. *Proceedings of the Royal Society B*, 273(1585), 465–470. https://doi.org/10.1098/rspb.2005.3309

Söderquist, P., Elmberg, J., Gunnarsson, G., Thulin, C.-G., Champagnon, J., Guillemain, M., Kreisinger, J., Prins, H. H., Crooijmans, R. P., & Kraus, R. H. S. (2017). Admixture between released and wild game birds: A changing genetic landscape in European mallards (*Anas platyrhynchos*). *European Journal of Wildlife Research*, 63(6), 98. https://doi.org/10.1007/s10344-017-1156-8

Soulsbury, C. D. (2010). Genetic patterns of paternity and test size in mammals. *PLoS One*, 5(3), e9581. https://doi.org/10.1371/journal.pone.0009581

Stronen, A. V., & Paquet, P. C. (2013). Perspectives on the conservation of wild hybrids. *Biological Conservation*, 167, 390–395. https://doi.org/10.1016/j.biocon.2013.09.004

Tallmon, D. A., Luikart, G., & Waples, R. S. (2004). The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, 19(9), 489–496. https://doi.org/10.1016/j.tree.2004.07.003

Templeton, A. R. (1986). *Coadaptation and outbreeding depression*. Sinauer Associates.

Todesco, M., Pascual, M. A., Owens, G. L., Ostevik, K. L., Moyers, B. T., Hübner, S., Heredia, S. M., Hahn, M. A., Caseys, C., Bock, D. G., & Rieseberg, L. H. (2016). Hybridization and extinction. *Evolutionary Applications*, 9(7), 892–908. https://doi.org/10.1111/eva.12367

Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068), 90–92. https://doi.org/10.1126/science.179.4068.90

Uller, T., & Olsson, M. (2008). Multiple paternity in reptiles: Patterns and processes. *Molecular Ecology*, 17(11), 2566–2580. https://doi.org/10.1111/j.1365-294X.2008.03772.x

USFWS. (2012). Recovery plan for Hawaiian Waterbirds, second revision | U.S. *Fish & Wildlife Service.*, 3–19. Retrieved November 7, 2022, from FWS.gov website: https://www.fws.gov/species-publication-action/recovery-plan-hawaiian-waterbirds-second-revision-2

van Wyk, A. M., Dalton, D. L., Hoban, S., Bruford, M. W., Russo, I.-R. M., Birss, C., Grobler, P., van Vuuren, B. J., & Kotzé, A. (2017). Quantitative evaluation of hybridization and the impact on biodiversity conservation. *Ecology and Evolution*, 7(1), 320–330. https://doi.org/10.1002/ece3.2595

Walters, A. D., & Schwartz, M. K. (2020). Population genomics for the management of wild vertebrate populations. In P. A. Hohenlohe & O. P. Rajora (Eds.), *Population genomics: Wildlife* (pp. 419–436). Springer.

Wells, C. P., Lavretsky, P., Sorenson, M. D., Peters, J. L., DaCosta, J. M., Turnbull, S., Uyehara, K. J., Malachowski, C. P., Dugger, B. D., Eadie, J. M., & Engilis, A., Jr. (2019). Persistence of an endangered native duck, feral mallards, and multiple hybrid swarms across the main Hawaiian islands. *Molecular Ecology*, 28(24), 5203–5216. https://doi.org/10.1111/mec.15286

Whiteley, A. R., Fitzpatrick, S. W., Funk, W. C., & Tallmon, D. A. (2015). Genetic rescue to the rescue. *Trends in Ecology & Evolution*, 30(1), 42–49. https://doi.org/10.1016/j.tree.2014.10.009

Wolf, D. E., Takebayashi, N., & Rieseberg, L. H. (2001). Predicting the risk of extinction through hybridization. *Conservation Biology*, 15(4), 1039–1053.

Zhang, X., Wu, R., Wang, Y., Yu, J., & Tang, H. (2020). Unzipping haplotypes in diploid and polyploid genomes. *Computational and Structural Biotechnology Journal*, 18, 66–72. https://doi.org/10.1016/j.csbj.2019.11.011

SUPPORTING INFORMATION

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