Ornithological Applications, 2024, 126, 1–12
https://doi.org/10.1093/ornithapp/duae022
Advance access publication 7 June 2024
Research Article

Small translocations of endangered *Gallinula galeata sandvicensis* (Hawaiian Common Gallinule) may be sufficient to generate a viable reintroduced population

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ABSTRACT

Where stable source populations of at-risk species exist, translocation may be a reasonable strategy for re-establishing extirpated populations. However, the success rates of such efforts are mixed, necessitating thorough preliminary investigation. Stochastic population modeling can be a useful method of assessing the potential success of translocations. Here, we report on the results of modeling translocation success for the *Gallinula galeata sandvicensis* or ʻalae ʻula (Hawaiian Common Gallinule), an endangered waterbird endemic to the Hawaiian Islands. Using updated vital rates, we constructed a model simulating 3 existing extant (wild) source populations and a hypothetical recipient site on another island. We then projected the effects of 6 different translocation scenarios and sensitivity of the results to variation of three important demographic parameters on the probability of extinction (PE) of the reintroduced and donor populations. Larger translocations, of at least 30 birds, had low probability of extinction in the reintroduced population, but raised extinction risk of the smallest source population. Spacing out translocations in time (e.g., 10 birds translocated in total in 3 installments over 9 years), led to lower PE than translocating all individuals at once (i.e., bulk translocations) for both the source and reintroduced populations. Brood size and hatch-year juvenile survival had a disproportionate impact on reintroduced population viability. Importantly, the reported juvenile survival rate is very near the threshold for population failure. This suggests that post-introduction and subsequent management of wetlands, particularly predator control, could be critical to reintroduction success. We recommend that individuals should be translocated from multiple, genetically distinct subpopulations to reduce the possibility of inbreeding depression. Based on this analysis, the recipient wetland should be sufficiently large that it can support at least 25 pairs of gallinules. Based on recent estimates of population densities on Oʻahu, such a wetland would need to be between 3.75 and 74.6 ha.

Keywords: assisted migration, ʻalae ʻula, endangered species, *Gallinula galeata sandvicensis*, Hawaii, Hawaiian Common Gallinule, population viability analysis, PVA, wetland conservation, Vortex, translocation

How to Cite
van Rees, C. B., and J. M. Reed (2024). Small translocations of endangered *Gallinula galeata sandvicensis* (Hawaiian Common Gallinule) may be sufficient to generate a viable reintroduced population. Ornithological Applications 126:duae022.

LAY SUMMARY

- Managers are considering potentially re-introducing the endangered *Gallinula galeata sandvicensis* (Hawaiian Common Gallinule) to an island in its former range, from which it was extirpated in the 1900s.
- Reintroduction efforts have a checkered past, including many failures, so it is worth testing whether such a measure would be feasible.
- We used simulations of *G. g. galeata* populations using the best available information on their life cycle to test whether small reintroductions might succeed.
- We also used these simulations to investigate whether collecting individuals for reintroduction might negatively affect the populations from which they were taken.
- We found that larger reintroduction efforts that involved moving more birds had a greater chance of success but that they also might negatively affect smaller source populations.
- We also found that splitting reintroductions up into a gradual format, moving a few birds at a time, increased the probability of success for the reintroduced population and reduced risks to the source populations.
- We recommend that any reintroduction effort draws birds from multiple populations, moves at least 10 birds in total, and reintroduces these individuals into a wetland habitat capable of supporting at least 25 breeding pairs.

Submission Date: November 27, 2023. Editorial Acceptance Date: May 3, 2024

Pequeñas translocaciones de *Gallinula galeata sandvicensis*, en peligro de extinción, pueden ser suficientes para generar una población reintroducida viable

RESUMEN

Donde existen poblaciones fuente estables de especies en riesgo, la translocación puede ser una estrategia razonable para restablecer poblaciones extirpadas. Sin embargo, las tasas de éxito de tales esfuerzos son mixtas, lo que requiere una investigación preliminar exhaustiva. El modelado poblacional estocástico puede ser un método útil para evaluar el éxito potencial de las translocaciones. Aquí, presentamos los resultados del modelado del éxito de la translocación para *Gallinula galeata sandvicensis* o ʻalae ʻula, un ave acuática en peligro de extinción endémica de las Islas Hawaianas. Usando tasas vitales actualizadas, construimos un modelo que simula tres poblaciones fuente existentes (silvestres) y un sitio receptor hipotético en otra isla. Luego proyectamos los efectos de seis escenarios de translocación diferentes y la sensibilidad de los resultados a la variación de tres parámetros demográficos importantes sobre la probabilidad de extinción (PE) de las poblaciones reintroducidas y donantes. Las translocaciones más grandes, de al menos 30 aves, tenían una baja probabilidad de extinción en la población reintroducida, pero aumentaban el riesgo de extinción de la población fuente más pequeña. Espaciar las translocaciones en el tiempo (e.g., 10 aves translocadas en total en 3 entregas durante 9 años), condujo a una PE más baja que translocar a todos los individuos a la vez (i.e., translocaciones masivas) tanto para las poblaciones fuente como reintroducidas. El tamaño de la nidada y la supervivencia juvenil en el año de eclosión tuvieron un impacto desproporcionado en la viabilidad de la población reintroducida. Es importante destacar que la tasa de supervivencia juvenil reportada está muy cerca del umbral del fracaso poblacional. Esto sugiere que la gestión posterior a la introducción y la gestión subsiguiente de los humedales, particularmente el control de depredadores, podrían ser críticos para el éxito de la reintroducción. Recomendamos que los individuos sean translocados de múltiples subpoblaciones genéticamente distintas para reducir la posibilidad de depresión por endogamia. Según este análisis, el humedal receptor debe ser lo suficientemente grande como para soportar al menos 25 parejas de *Gallinula*. Basado en estimaciones recientes de densidades poblacionales en Oʻahu, dicho humedal debería tener entre 3.75 y 74.6 ha.

Palabras clave: ʻalae ʻula, análisis de viabilidad poblacional, AVP, conservación de humedales, especies en peligro de extinción, *Gallinula galeata sandvicensis*, Hawái, migración asistida, translocación, Vortex

INTRODUCTION

Translocation is a common management strategy for harvested and at-risk species to increase gene flow, supplement extant populations, reintroduce, and to create new populations outside a native range (Berger-Tal et al. 2020, Sutherland et al. 2021, Gaywood et al. 2022). For birds, the most common translocations are introductions or reintroductions of game birds, ornamental species, and threatened species (Veltman et al. 1996, Wolf et al. 1996, Lever 2005, Dickens et al. 2009). Endangered species that are restricted to islands are common targets for translocation. In this situation, translocating birds might provide a reprieve while a threat, such as an introduced predator, can be removed or controlled. Translocation is also used as a tool to create population redundancy, which reduces the risk of extinction. High-profile examples include management of *Petroica traversi* (Black Robin) (Butler and Merton 1992), *Strigops habroptilus* (Kakapo) (Powlesland et al. 1992), and *Acrocephalus sechellensis* (Seychelles Warbler) (Wright et al. 2014).

Translocations of birds, including introductions and reintroductions, have had a highly variable success record, with a high failure rate, particularly for non-game species (e.g., Long 1981, Griffith et al. 1989, Duncan et al. 2003). For endangered species under certain circumstances (e.g., declining population, new threat), however, the potential cost of not translocating them could be extinction. Before translocations, particularly when the source population for the reintroduction is still small, it is worthwhile to conduct preliminary analyses of potential success. One important part of planning can be creating and projecting demographic models to assess alternative reintroduction strategies, and even to determine whether reintroduction or captive breeding might be a management strategy with a net expected benefit or harm to overall population persistence (Armstrong and Reynolds 2012, Knight 2012, Converse et al. 2013, Hunter-Ayad et al. 2020, Mitchell et al. 2022). The same types of trade-offs have been modeled for taking individuals out of the wild to create captive populations to further conservation goals (e.g., Beissinger 2014). For species with very small total populations, there is a potential conflict between maintaining established populations and reducing their numbers to seed a new population that could eventually increase overall security for the species (Easton et al. 2020).

We modeled a proposed translocation of wild-caught *Gallinula galeata sandvicensis* (Common Gallinules; also known by its Hawaiian name, ʻalae "ula, and formerly known as the Hawaiian Moorhen) to a currently unoccupied site on an island within the species" former range, and the potential consequences to population size and persistence to the source population(s). This is a federally endangered, endemic subspecies of waterbird persisting only on the islands of Oʻahu and Kauaʻi, though it formerly inhabited wetlands on all of the main Hawaiian Islands (Shallenberger 1977, Banko 1987). As with the other endangered Hawaiian waterbirds, *G. c. sandvicensis* is conservation reliant, and is threatened by habitat loss, sea level rise, and introduced, invasive predators and wetland plants (Reed et al. 2012, Underwood et al. 2013, van Rees and Reed 2018). The distribution of gallinules on the remaining occupied islands is naturally fragmented by the subspecies' ecological specialization on limited coastal freshwater wetlands, with greater isolation caused by wetland loss from anthropogenic landscape change (Van Rees and Reed 2014, van Rees et al. 2018b). Local subpopulations on both islands are generally small, most supporting fewer than 50 individuals, although there are a few larger populations that could be suitable source populations for translocation. One priority of the recovery plan for the species (USFWS 2011) includes creating at least one self-sustaining population on a currently unoccupied island via translocation. Translocations of wild birds have been prescribed and employed for other endangered Hawaiian birds (e.g., Freifield et al. 2016, VanderWerf et al. 2019). During the 1950s and 1960s, there were multiple releases of small numbers of translocated *G. c. sandvicensis* (where reported, ≤11 individuals per release) to multiple wetlands on Maui, Molokaʻi, Oʻahu, and the island of Hawaiʻi from captively bred birds; none of

the reintroductions met with more than short-term success (reviewed by Dibben-Young 2009). These empirical results are supported by a population viability analysis that found isolated populations of <15 *G. c. sandvicensis* very unlikely to persist (van Rees and Reed 2018).

So, what translocation strategies might work for establishing a new population of *G. c. sandvicensis*? Here, we used an updated version of a previously published individual-based stochastic simulation model of population viability for the *G. c. sandvicensis* (van Rees and Reed 2018), incorporating refined vital rate estimates (van Rees et al. 2024), to assess alternative translocation strategies for reintroducing birds from extant wild populations. Specifically, our goals were to (1) investigate the effects of removing individuals from source populations on their extirpation risk, (2) estimate the relative viability of introduced populations under a suite of translocation alternatives, and (3) rank the relative importance of key demographic parameters in the introduced population for minimizing extinction risk of the reintroduced population. The potential recipient site(s) for the translocation have not yet been identified and are not part of this assessment. We refer readers to van Rees and Reed (2018)'s sensitivity analysis of carrying capacity of *G. c. sandvicensis* subpopulations for an investigation of the minimum population size allowing a near-zero probability of extirpation. Rather than repeat that analysis, we assume here that an appropriate recipient site should support at least 50 individuals based on their findings. The present study goes beyond that previous analysis by using updated vital rates, including the first empirical estimates of juvenile survival in this subspecies, considering an additional subpopulation on Kaua'i, and simulating translocation dynamics between potential extant source sites and a recipient site.

METHODS

Study System

Gallinula c. sandvicensis are habitat specialists of freshwater wetlands with mixed emergent vegetation and open water areas along the coastal plains of the Hawaiian Islands (Griffin et al. 1989, Engilis and Pratt 1993). They are widespread on the island of Kaua'i, where such wetlands abound, and where other moist mesohabitats and artificial freshwater wetlands like taro lo"i (*Colocasia esculenta* or taro grown in standing water) and garden ponds are numerous (USFWS 2011). The subspecies" largest population stronghold is Hanalei National Wildlife Refuge (Kaua'i), a federally protected area managed by the U.S. Fish and Wildlife Service which likely supports over approximately 250–300 individuals (Hawai'i Biannual Waterbird Survey). *Gallinula c. sandvicensis* populations on O'ahu are smaller and more fragmented, consisting of 3–4 genetically distinct subgroups primarily in protected and actively managed wetland areas on the island (van Rees et al. 2018a, 2018b). The most populous habitats are James Campbell National Wildlife Refuge and Hamakua Marsh, managed by the U.S. Fish and Wildlife Service and Hawai'i Division of Natural Resources, respectively. We used a carrying capacity value of 50 individuals for Hamakua based on biannual waterbird count data, playback surveys, and extensive trapping data from 2014 to 2017 (M.A. Muñoz, C.B. van Rees, and J.M. Reed, personal observation). We set the carrying capacity of James Campbell National Wildlife Refuge at 80 based on recent counts. appear to be reluctant dispersers, with infrequent long distance movements between subpopulations on O'ahu (van Rees et al. 2018a, b, Paxton et al. 2023) and very little evidence for inter-island movements (Banko 1987; Sonsthagen et al. 2018). However, individual *G. c. sandvicensis* appear to move more frequently and readily across landscapes with greater coverage of natural and artificial wetlands, including linear features line streams, rivers, and canals (van Rees et al. 2018c).

Gallinula c. sandvicensis are aggressively territorial, monogamous breeders capable of nesting year-round (Byrd and Zeillemaker 1981, DesRochers et al. 2009). Precocial young reach near-mature size within 1 month of fledging, and mature offspring will remain in their natal territory and help raise subsequent broods when breeding opportunities are unavailable (Webber 2022). Rapid maturation, the capability for multiple broods, and suitable breeding conditions year-round drive a high potential reproductive rate (simulated stochastic growth rate $r = 0.25$; van Rees and Reed 2018), and juvenile (hatch-year) and adult mortality consequently have a disproportionately high impact on population growth rate and viability (van Rees and Reed 2018).

Population Simulations

Baseline population model

We used Vortex 10.6.0 (Lacy and Pollak 2023), a stochastic, individual-based population modeling software to simulate *G. c. sandvicensis* populations and conduct scenario and sensitivity analyses. We followed van Rees and Reed (2018) for baseline model settings, but updated key vital rates where new information was available (Table 1). We used updated distributions and summary statistics (mean and standard deviation) for nest success, brood size, and juvenile survival from van Rees et al. (2024). We used juvenile survival estimates from O'ahu due to the greater length of time series available for analysis, and because values from Kaua'i paradoxically predicted rapid population declines on that island under present conditions, which are not being observed in the study area. For an in-depth discussion of caveats and potential sources of uncertainty in these data, see van Rees et al. (2024). We modeled the subspecies as long-term monogamous, lacking any genetic or behavioral evidence of the occasional polygyny exhibited in related (sub)species (Bannor et al. 2002), despite years of close observation of banded mated pairs and the genotyping of >150 individuals including numerous banded offspring-parent groupings (van Rees et al. 2018a, b). Based on genetic sexing information from the same sample of trapped individuals caught between 2013 and 2017, we also assumed a 50:50 sex ratio in the population. We separated individuals into 2 age-classes, juvenile (hatch-year) and adult (after-hatch-year), and parameterized class-specific mortality rates using annual means and variances derived from van Rees et al. (2018a) and van Rees et al. (2024).

We defined extirpation (i.e., subpopulation extinction) as only 1 sex remaining, and modeled this probability over an 80-year time span (~20 generations). Our primary metric of population viability for source and translocated subpopulations was probability of extirpation (PE) over an 80-year time horizon. For our baseline model, we ran 1,000 iterations of each scenario to obtain parameter distributions.

TABLE 1. Parameters used in population viability scenarios in Vortex, including sampled values for sensitivity analysis, and references for data used. EV stands for environmental variation. HY stands for "hatch year," birds that are < 1 year old. AHY stands for "after-hatch-year," birds older than age 1. "Males in breeding pool" refers to the percentage of sexually mature males in the simulated population available to pair with females.

Parameter	Baseline value	Source	Perturbation	Log. regression
Reproduction				
Breeding system	Long-term monogamy	Bannor and Kiviat (2002)	N/A	N/A
Min–Max age of reproduction (yr)	2–10	Clapp et al. (1982), van Rees et al. (2018a)	N/A	N/A
Distribution of broods per year	0 to 4 by binomial distribution	Nagata (1983), Gibbons (1986), Greij (1994)	N/A	N/A
Mean brood size	Kaua'i: 3.37 (SD: 1.35) O'ahu: 4.39 (SD: 1.75)	van Rees et al. (2024)	0–10, by 1	1–8
Sex ratio at birth	1:1	Assumed	N/A	N/A
Percent females breeding ± EV	90 ± 10	van Rees and Reed (2018)	N/A	N/A
Males in breeding pool	100%	Assumed	N/A	N/A
Annual mortality rates				
Juvenile (HY) mortality (%) ± EV	75 (SD: 15)	van Rees et al. (2018a), van Rees et al. (2024)	0–100, by 5	15–100
Adult mortality (%) ± EV	27 (SD: 3.3)	van Rees et al. 2018a	N/A	N/A
Population parameters				
Carrying capacity ± EV	JCNWR: 80 Hanalei: 250 Hamakua: 50 Translocation site: 50	Hawai'i Biannual Waterbird Survey data, 2015–2022	N/A	N/A
Translocation parameters				
Harvest (Individuals)	10, 20, or 30 (split evenly among three source populations) Even sex ratio AHY birds	van Rees et al. (2018b)	N/A	N/A
Supplementation (individuals)	10, 20, or 30 Even sex ratio AHY birds	van Rees et al. (2018b)	N/A	N/A
Survival of translocated individuals (%)	85%	See text for justification	0–100, by 5	10–100

We modeled 3 source sites (James Campbell National Wildlife Refuge and Hamakua Marsh on O'ahu, and Hanalei National Wildlife Refuge on Kaua'i) as separate subpopulations with no dispersal, using the latest available abundance estimates for each site, and island-specific vital rates with the exception of hatch-year juvenile survival (see above). These sites were selected for having among the highest observed abundances and densities of *G. c. sandvicensis* in the state, suggesting the lowest probability of negative population effects from losing translocated individuals. Each site was assumed to be at or around carrying capacity based on relatively stable population observations in the last 5–8 years (Hawai'i Division of Forestry and Wildlife, personal communication), high densities, and a high incidence of observed pairs with helpers (Webber 2022). We assumed a stable age distribution for all source populations.

We modeled the translocated population as a single, isolated site with a carrying capacity of 50 individuals, which we judged to be a safe minimum size based on simulations from van Rees and Reed (2018). That previous study implied that small, isolated subpopulations with carrying capacities larger than 25–30 individuals had relatively trivial probabilities of extinction within 80 years. We used vital rates from O"ahu, the more developed and impacted of the 2 islands in the subspecies" range, for the translocation site. These data also come primarily from managed wetlands, which is likely representative of any future translocation site, which will by necessity be managed.

We modeled density dependence as in van Rees and Reed (2018), using a value of 0 for the Allee parameter (*A*, in Vortex), lacking evidence for strong Allee effects in this subspecies, and a value of 20 for the steepness parameter *B*. We assumed no inbreeding depression for default scenarios, lacking evidence of the phenomenon in this system, and with an increased likelihood of purged deleterious alleles because of a lengthy and severe historical bottleneck (Sonsthagen et al. 2017, van Rees et al. 2018b).

Translocation scenarios

For all translocation scenarios, we allowed only after-hatch-year (age > 1 year) birds to be translocated, and required approximately equal (or near-equal) proportions of translocated birds to be translocated from each wild-source population. We specifically chose this age class because they can

be readily distinguished from first-year juveniles, and have the highest probability of quickly establishing territories and breeding. Since it is difficult to distinguish second-year (i.e., sexually mature) birds from after-hatch-year birds by morphology, it would be difficult for managers to specifically select breeding-age birds for translocation. Within each simulation, an assigned number of AHY birds were withdrawn from each source population for each year of scheduled population supplementation, and those individuals were translocated to the recipient population after applying the probability of translocation survival. We tested 3 translocation sizes (10, 20, and 30 individuals) across 2 translocation schemes (bulk, or all individuals translocated in year 1, and gradual, 3 smaller translocations, once every 3 years, over a 9-year period) to investigate the effects of translocation size and rate. We reviewed the literature in search of optimal translocation strategies to look for assessments of bulk vs. gradual translocation within a year, but we found no examples of experimental or modeling assessments of that specific topic. We found many of both types of study relating to the number of animals released (more is better), and for allocation between multiple translocation sites (fill one site first), but none that investigated the allocation of individuals across time. We assumed an equal (1:1) sex ratio among translocated birds, as evidenced by the sex ratio of > 150 captured and genetically sexed individuals from O'ahu. Notably, field sexing of *G. c. sandvicensis* is not practical, and genetic methods necessitate greatly prolonging captivity, so any actual translocation is likely to be conducted as a random sample of source populations and without control over the actual sex ratio of translocated individuals. The same number of birds of each sex were taken from each source population each year, favoring females and Hanalei NWR whenever an odd-numbered bird was required (e.g., the fifth of five birds translocated).

We used a value of 85% survival (15% mortality) during the translocation. This is consistent with recommendations from Grevstad (1999), Armstrong and Reynolds (2012), and Easton et al. (2020) which suggest including negative demographic effects on translocated individuals. For example, Easton et al. (2020) including an initial mortality at release of ≤ 20%. Although actual mortality rates will likely, and hopefully, be much lower, this extra "penalty" functions in our modeling exercise to capture some of the potential depression in vital rates that might occur in reintroduced populations.

Sensitivity analyses

We also conducted 2 forms of sensitivity analysis on 3 demographic parameters that could be affected by management: mortality rate during translocation, juvenile (hatch-year) mortality (as mean annual mortality), and brood size at the translocation site. We conducted sensitivity analysis using the logistic regression approach to examine the relationship between parameter values and probability of extinction using randomized simulations within realistic bounds (McCarthy et al. 1995, Cross and Beissinger 2001), and the perturbation approach (Mortensen and Reed 2016) to identify parameter thresholds that indicate substantial shifts or thresholds between states with a very high or very low probability of extinction.

We performed perturbation analyses on translocation mortality, juvenile mortality, and brood size in the translocated subpopulation. For perturbation analysis, we ran models across all possible values (0 to observed maximum) to examine the full range of population behavior even to extreme events (Mortensen and Reed 2016, van Rees and Reed 2018, van Rees et al. 2022). We varied translocation mortality, juvenile mortality, and mean nest success from 0 to 1 by intervals of 0.1. As in van Rees and Reed (2018) and van Rees et al. (2022), we represented nest success implicitly in the distribution of broods per year in the translocation site, employing a mean nest success value, binomial equation, and a maximum of 4 breeding attempts per year to simulate a distribution of successful breeding attempts.

We followed van Rees and Reed (2018) for logistic regression analysis, using Latin Hypercube sampling in Vortex to randomly generate parameter sets selected from uniform distributions that we determined using observed and feasible values for *G. c. sandvicensis*. We ran 10 iterations for each parameter set, resulting in 10,000 total simulations. We ran 10 iterations for each parameter set, resulting in 10,000 total simulations for regression analysis. We then performed logistic regression using the *car* package (Fox and Weisberg 2011) in R 4.3.1 (R Core Team 2023), treating extirpation (or persistence) at 80 years as the dependent variable. We sampled each parameter from a uniform distribution, bounded by the same values listed above for perturbation analysis. We combined these parameters as predictor variables in a single generalized linear model with probability of extirpation (PE) as the response variable. We compared the explanatory value of different parameters using their standardized regression coefficients, calculated by dividing the regression coefficient by its standard error. All sensitivity analyses were run on the bulk translocation scenario with 30 individuals.

RESULTS

Probability of extinction (PE) for the reintroduced population ranged from 0.00 to 0.06 (Table 2). Both larger reintroductions and those spread across multiple events had lower PE, with the lowest values for translocations of 20 or 30 individuals over 3 installments (gradual translocation). Mean stochastic growth rate r was potentially slightly higher in gradual translocations (0.17 for all gradual translocations, 0.15–0.16 for bulk scenarios). Ending population sizes were not affected by the translocation scenario. Translocations of 10 total individuals resulted in a mean extinction probability of 0.00 for all 3 source populations (Table 3). However, larger translocations (20 and 30 individuals) showed some small increases in PE for the smallest source population, Hamakua marsh, at its modeled carrying capacity. Gradual translocations yielded lower PE at Hamakua than bulk translocations in these larger-translocation scenarios. PE at the larger source populations, JCNWR and Hanalei, was 0.00 for all translocation scenarios.

Logistic regression sensitivity analysis revealed that mean annual juvenile mortality (standardized coefficient value = 40.6), followed by mean brood size (24.3), had great impacts on PE for the translocated population. This is in line with the results of van Rees and Reed (2018). Although translocation survival, a modifier of the number of birds introduced in each translocation instance, showed a clear impact on model outcome (7.8), it was comparably minor.

TABLE 2. Probability of extirpation in 80 years, mean stochastic growth rate (r), and mean and standard deviation (SD) ending population size for a simulated, small, introduced population consisting of individuals translocated from Hamakua marsh, Hanalei NWR, and James Campbell NWR. Simulations were carried out over an 80-year time horizon. Numbers under the scenario column represent the total number of introduced individuals. Bulk translocation scenarios involve a single translocation event at year 2 of the simulation, while gradual scenarios consist of 5 smaller introductions at 2-year intervals over 10 years.

Scenario	$P(E)$	Mean r (SD)	Mean ending population size (SD)
10 (Bulk)	0.06	0.16 (0.49)	41.6 (11.4)
20 (Bulk)	0.024	0.15 (0.49)	41.5 (12.2)
30 (Bulk)	0.014	0.15 (0.49)	41.5 (11.4)
10 (Gradual)	0.059	0.17 (0.49)	41.7 (11.6)
20 (Gradual)	0.009	0.17 (0.50)	41.8 (11.5)
30 (Gradual)	0.014	0.17 (0.49)	41.8 (11.8)

TABLE 3. Estimated probabilities of extinction (PE) and mean ending population sizes at 80 years (N80) of simulated source populations of *G. c. sandvicensis* under different translocation scenarios and averaged over 1,000 model runs. N80 values represent only the mean size of populations extant at 80 years. In each case, the "burden" of translocated individuals was split as evenly as possible between all three source populations. JCNWR = James Campbell National Wildlife Refuge. K = simulated carrying capacity.

Translocation scenario	Hanalei ($K = 250$)	JCNWR ($K = 80$)	Hamakua ($K = 50$)
10 (Bulk)	PE = 0.00	PE = 0.00	PE = 0.00
	N80 = 217.7	N80 = 69.19	N80 = 43.32
20 (Bulk)	PE = 0.0	PE = 0.0	PE = 0.03
	N80 = 218.07	N80 = 69.27	N80 = 40.96
30 (Bulk)	PE = 0.00	PE = 0.00	PE = 0.09
	N80 = 217.36	N80 = 69.86	N80 = 41.73
10 (Gradual)	PE = 0.00	PE = 0.00	PE = 0.02
	N80 = 216.14	N80 = 68.80	N80 = 41.08
20 (Gradual)	PE = 0.00	PE = 0.00	PE = 0.04
	N80 = 218.17	N80 = 69.58	N80 = 42.84
30 (Gradual)	PE = 0.00	PE = 0.00	PE = 0.05
	N80 = 216.17	N80 = 69.41	N80 = 43.02

Sensitivity testing via perturbation analysis showed that mean brood sizes below 3 individuals resulted in sharply elevated PE, reaching 1.0 at brood sizes less than ~1.25 (Figure 1). Annual juvenile mortality rates above 80% resulted in a high PE, reaching 1.0 at 90% (Figure 2). Translocation survival rates above 25% showed a low or near-zero PE, with moderate values from 10 to 25% survival of translocated individuals (Figure 3).

DISCUSSION

We assessed a variety of translocation scenarios involving the *G. c. sandvicensis* from 3 extant, wild source sites to a hypothetical single recipient site on a different island, and examined the resulting population viability at that site and to the source populations. Based on a population viability analysis (PVA) and associated sensitivity analyses of a similar model by van Rees and Reed (2018), the recipient site should have a carrying capacity above 30 individuals to minimize the PE. Our simulated carrying capacity of 50 individuals showed low overall PE (Table 2), and we believe this larger number provides a sufficient precautionary margin of error. Comparisons among alternative scenarios showed that gradual translocations, compared to bulk (all-at-once) translocations, reduced PE of the reintroduced population by as much as half, although even the highest observed PEs for any translocation scenario with a recipient carrying capacity of 50 were < 0.1. Importantly, the acceptable threshold of PE is a social question that is culturally constructed, and not one that can be determined quantitatively based on biological rules (Reed et al. 2006). Thus, whether the differences in PE between the modeled approaches are trivial will depend on the degree of risk that resource managers and conservationists are willing to accept.

Due to the relative ease of capture at the modeled source population sites, the quantity of introduced individuals should be manageable, and gradual translocations spread over multiple years should be possible. Given that for all modeled scenarios, PEs were low, another important metric of comparison like monetary cost or minimization of stress or mortality risk for individual birds, might be prudent to consider. Specifically, where multiple capture and transport actions are needed to translocate birds across time, equipment and personnel costs increase dramatically, presenting a significant logistical concern for gradual translocations. This warrants thorough consideration as planning efforts for potential reintroductions progress.

Individual "harvest"—removal from relatively large extant source populations—had trivial effects on PE for larger source populations in all scenarios. However, using an estimated carrying capacity of 50 individuals for Hamakua marsh, we

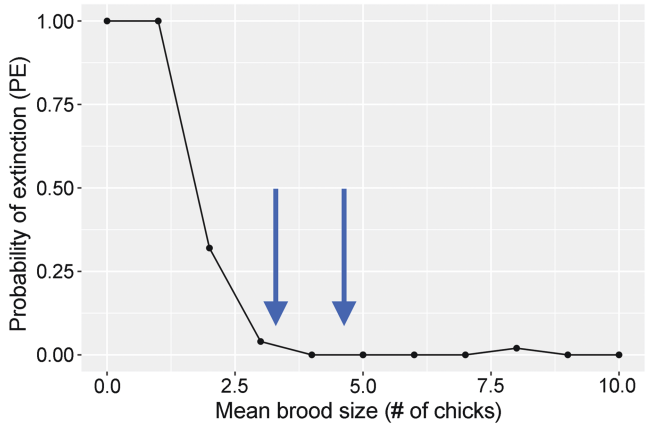

FIGURE 1. Results of perturbation sensitivity analysis of mean brood size versus probability of extinction for a small, introduced population. Arrows indicate values used in the baseline model (O'ahu right arrow, Kauai left, value in Table 1; the O'ahu value was used for the introduced population; see text for explanation). Probability of extinction declines sharply at mean brood sizes of 1 and above, reaching a minimum at a mean brood size > 3.

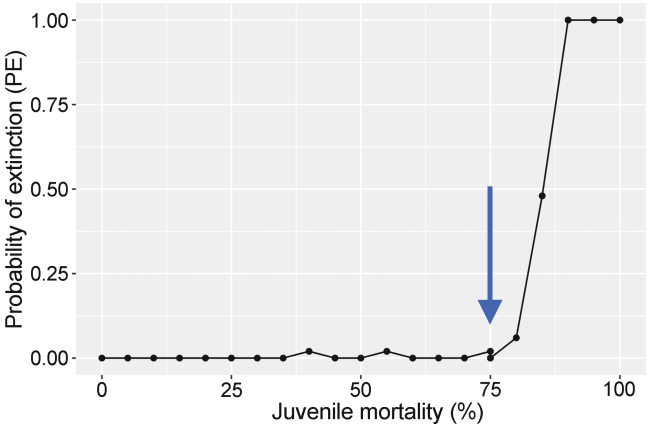

FIGURE 2. Results of perturbation sensitivity analysis of mean juvenile mortality versus probability of extinction for a small, introduced population. Arrow indicates value used in the baseline model (see Table 1), derived from brood survival data on O'ahu. Probability of extinction approaches 1 when juvenile mortality exceeds 80%.

observed significant increases in PE for that subpopulation, at translocation sizes of 20 to 30 individuals (implying the removal of 6–7 or 10 total individuals). In each of these cases, gradual translocations nearly halved this elevated risk (e.g., from 0.09 to 0.05 for the largest translocation size), presumably by giving the subpopulation some chance to recover. These findings align with van Rees and Reed's (2018) aforementioned analyses of carrying capacity, because such large removals of individuals bring the population to a size close to where nontrivial PE was observed in that study. Accordingly, source populations with more than 50 individuals should be prioritized, or else captures for translocation should be kept small enough to maintain any source population confidently above 35-40 individuals.

Importantly, there is substantial uncertainty around the carrying capacity of wetland habitats for *G. c. sandvicensis* on O'ahu and their present population sizes. While the biannual waterbird survey provides important long-term trends in relative population sizes (van Rees et al. 2022), detection, especially of *G. c. sandvicensis*, has large and presently unquantified impacts on population estimates, implying a negative bias. Using the playback method from DesRochers et al. (2008) and conducting extensive trapping, M.A. Muñoz, C.B. van Rees, and J.M. Reed (personal observation) estimated a population at Hamakua in excess of 80 individuals, although visual surveys suggested a much lower abundance. Furthermore, source sites like James Campbell National Wildlife Refuge and Hamakua Marsh Wildlife Sanctuary have the additional advantage of being embedded in a "wetland complex" with many adjacent refugia with which they share dispersal connectivity (van Rees et al. 2018b, c). Although some wetlands are particularly isolated from dispersal, these two populations show genetic signals of close connectivity to one or more nearby subpopulations. Consequently, we expect these source populations to be minimally affected by removal of translocated individuals, which might be rapidly compensated for by nonbreeding individuals entering the breeding pool, or dispersal from nearby wetlands.

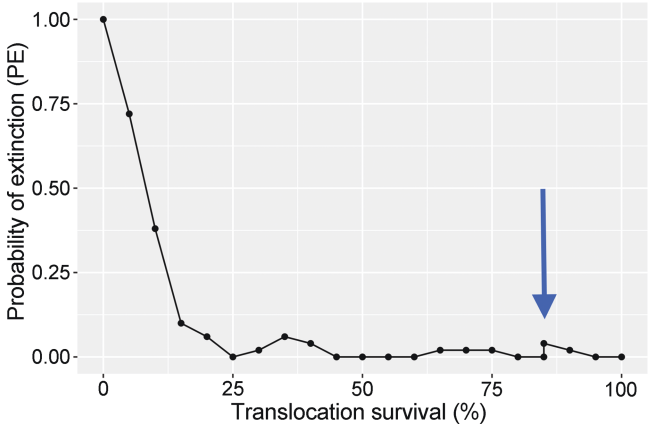

FIGURE 3. Results of perturbation sensitivity analysis of translocation survival versus probability of extinction (PE) for a small introduced population. Arrow indicates value used in the baseline model (see Table 1). Probability of extinction is low for translocation survival rates above 25–50% in a scenario where 10 individuals per year are introduced at 3-year intervals for 3 year (for a total of 30 translocated individuals).

We note that translocations as high as 20–30 total individuals, the largest values simulated in this study, may not be logistically feasible or even necessary. These values help sample the behavior of the modeled system across a range of potential management actions. By simulating these large values, we are not necessarily advocating that those massive translocations be undertaken, but examining the impacts that might occur if they did. The high projected success rate of even relatively small translocations in our simulation suggests that more modest translocations (on the order of 10–15 individuals) might have a high chance of success without risking impacts on source populations.

Importantly, some smaller sites on O'ahu (e.g., Keawāwa wetland or the Klipper golf links at Marine Corps Base Hawai'i) support genetically distinct demes of this subspecies, potentially enriching the translocated population (van Rees et al. 2018a), but would also be more sensitive to the loss of translocated individuals. The larger of these at Klipper may have as many as 20 individuals, while Keawāwa's population may now be below 10.

Unsurprisingly, perturbation sensitivity analyses of vital rates on PE showed similarly high sensitivity to annual juvenile mortality as found in van Rees and Reed (2018). The current empirical estimates of juvenile mortality from protected areas on O'ahu (~75%) and Kaua'i (~91%) are very close to the values at which PE approached 1.0 (80–90%) in our perturbation sensitivity analysis. Accordingly, management to increase juvenile survival should be a major priority for any reintroduction to minimize the probability of extirpation in that smaller, incipient subpopulation. Our perturbation analysis of mean brood size showed that a higher mean brood size was necessary to achieve near-zero PE than found in van Rees and Reed (2018). While the latter study observed near-zero PE above brood sizes of 1.5, our analyses using improved vital rate estimates suggest that brood sizes in excess of 3 chicks would be necessary to maximize population viability. It is important to recall that the vital rate data used in our PVA come almost exclusively from managed populations (i.e., habitat manipulation and predator control), so that the expectation from unmanaged populations is higher PE for any given population size.

The proximity of estimated juvenile mortality rates to the threshold resulting in a population crash requires further discussion. Available data on juvenile mortality on Kaua'i come from Webber (2022) and van Rees et al. (2024), and the value is much lower than the O'ahu value used in our models—75% mortality in the models vs. 91% mortality on Kaua'i. Using the latter value in our model scenarios universally predicts extinction of the population, regardless of population size. We see two potential explanations: (1) The data from Webber (2022) come from research not specifically designed to study post-hatch survival, so perhaps this value is an underestimate of survival rate. We suggest this because if it reflected the true survival rate of juveniles at Hanalei, the population would be steeply declining, which it is not at present. (2) It is possible that the large and dense subpopulation at Hanalei, where Webber's study took place, is at carrying capacity. If so, we expect strong density-dependent feedback because *G. c. sandvicensis* are aggressively territorial (van Rees et al. 2021), and this could reduce population growth through increasing first-year mortality. Such mortality could be caused by a variety of factors, such as predation, which could be a greater risk in an unfamiliar environment, injuries from fights, or relegation due to territorial behaviors to low-quality habitat with higher mortality risk. For example, at Keawāwa, one nonbreeding female tracked by radio transmitter was forced repeatedly into a country club parking lot by a dominant, breeding female in the nearby wetland. The latter's aggressive territoriality kept this nonbreeder in this riskier habitat, where she was eventually struck by a vehicle and killed. Consequently, when population size is near carrying capacity, realized population growth rate is stochastically near 0, and the population would have the appearance of a pseudo-sink (Watkinson and Sutherland 1995). If density-dependence in this species manifests through reducing juvenile survival, then as population carrying capacity is approached for the newly created population, resource managers should expect greatly reduced hatch-year survival and recruitment. And that this would be a sign of a healthy population, rather than an indicator of a sudden problem with the population. Note that a co-associated sudden decline in population size would be a different matter, indicating a severe population problem.

Our perturbation analyses of different degrees of translocation mortality indicated that, where 50 individuals were translocated across 5 intervals of 10 individuals each (gradual translocation), survival as low as 20% of transported individuals (i.e., ~2 surviving individuals per reintroduction event) might still be sufficient to initiate a viable population. Importantly, perturbation analysis in this context is a numerical exercise meant to demonstrate the range of behaviors of a system including potential threshold values of management interest, and not to explore specific management recommendations. Accordingly, while 20% survival rates of translocated individuals would be unacceptable in implementation, it is useful to identify a lower bound for feasibility in simulated populations. However, other vital rates might also be depressed simultaneously after introduction, so it will be preferable to err on the side of caution. We thus suggest that values above 30% are likely necessary.

The threshold values for vital rates reported here, and by van Rees and Reed (2018), beyond which PE greatly increases, should be considered overly conservative limits for resource managers. That is, our perturbation-style sensitivity analysis considers each parameter in isolation. Consequently, more moderate values of these vital rates may still entail considerable risk when combined with other pressures on the population. Departing from a purely numerical exercise and considering the reality of implementation, if survival rates of translocated birds fell much below 70–80% in practice, the ethical and legal consequences of such "take" on a listed species could become a substantial concern. We do not mean to suggest that survival rates below this are acceptable, only that they may still permit the establishment of viable introduced subpopulations. Although translocation methods are poorly studied in this taxon, effective measures to minimize translocation mortality in similar species will be critical to planned efforts. For example, captive rearing of individuals intended for translocation might decrease stress associated with handling by humans (Beauchamp et al. 2009). Importantly, however, captive-bred releases have lower documented success rates than wild-caught individuals (Griffith et al. 1989). For wild-caught individuals, minimizing travel and holding times are also characteristic of successful efforts (Woinarski et al. 2016).

Our analysis did not consider the potential impacts of sea level rise. However, as noted in several studies (Kane et al. 2015, Htun et al. 2016, van Rees and Reed 2018, Harmon et al. 2021), sea level rise is likely to shrink most of this species' major subpopulation strongholds, including the 3 source subpopulations simulated in this study over the next 80 years. Any proposed site for reintroduction in Hawai'i should be selected with attention to these predicted sea level scenarios, bearing in mind that salinization from salt spray and/or groundwater influences may still degrade habitat quality even if freshwater wetlands are not inundated (Kane et al. 2015). Our findings demonstrate that even rather substantial translocations of birds from extant wild populations are predicted to have trivial impacts on large source populations, particularly when spread among 3 major subpopulations of *G. c. sandvicensis*, and if these are undertaken within 10–20 years of this study, well before the major anticipated impacts of sea level rise, these impacts on source populations should be trivial.

In our model we assumed no effect of inbreeding depression because we currently lack information for *G. c.*

sandvicensis. Inbreeding depression can affect vital rates in a variety of direct and indirect ways (Keller and Waller 2002, Marr et al. 2006), and it has been documented in translocated populations, even for island-endemic bird species (Jamieson et al. 2007, Taylor et a. 2017). Although past genetic bottlenecks of *G. c. sandvicensis* may suggest that inbreeding depression may have limited relevance in this subspecies due to the purging of deleterious alleles (Sonsthagen et al. 2017), purging does not always occur (Kennedy et al. 2014). In addition, nontrivial impacts of inbreeding depression have been documented in other rallids (Nusser et al. 1996, Brook et al. 1997, Jamieson and Ryan 2000, Grueber et al. 2010). Our modeled translocation strategy of evenly sampling individuals from 3 genetically distinct subpopulations (as documented by Sonsthagen et al. 2018, van Rees et al. 2018b) should minimize this potential risk. However, resource managers should monitor vital rates of the introduced population as a matter of course.

Another logistical concern for gallinule reintroduction in Hawai'i is the sex ratio of translocated individuals. Population growth rate and PE can be strongly affected in small populations by the degree of bias in sex ratio (Brook et al. 2000, Lee et al. 2011, Levy and Reed 2023). Assuming relatively small, episodic reintroductions, it will be important to ensure that a roughly even number of male and female individuals are translocated. Unfortunately, sexing *G. c. sandvicensis* in the field is challenging, with substantial overlap in biometrics between males and females (DesRochers et al. 2009; van Rees et al. 2021). Consequently, there is no ready solution to ensuring a relatively even mix of males and females in the introduced population. Fortunately, van Rees et al. (2018a, b) detected no evidence of sex bias in the capture of >150 individuals on O'ahu, suggesting that if the same capture methods are used, relatively even sex ratios might be expected for translocation. Nonetheless, we recommend that blood samples be taken for subsequent genetic sexing, for post-reintroduction monitoring. Behavioral observations might contribute significantly to solving this issue. Several researchers have observed that mated pairs tend to visit traps together during bouts of foraging (A. Nadig, U.S. Fish and Wildlife Service, personal communication). Placing two traps side-by-side or end-to-end might enable capturing the male and female breeders of a given territory together, ensuring a more even sex ratio and potentially increasing their chances of readily breeding together in a new location.

Capture, translocation, and (re)introduction of birds can cause physiological stress (Dickens et al. 2010, Parker et al. 2012); however, the presence of nearby human disturbance and possible proximity to urbanization is not associated with elevated physiological stress in 'alae 'ula (Gormally et al. 2020), so this is encouraging for translocated birds in the case of peri-urban introductions. There is a generally low success rate of introductions, especially when the number of introduced individuals is low (Blackburn et al. 2011, citations in introduction). Empirical studies of species introduction and reintroduction have noted depressed survival (Tavecchia et al. 2009, Gross et al. 2024), and reproduction (Lloyd et al. 2009). Gross et al. (2024) found that translocated organisms have 70% decreased odds of out-performing their wild-resident counterparts. Consequently, Grevstad (1999), Armstrong and Reynolds (2012), and Easton et al. (2020) suggest anticipating short-term negative demographic effects on translocated individuals, and including that effect in viability assessments. The degree to which it needs to be included in a population model will require new data from post-release tracking. In our models, we included a cost of translocation as added mortality in one time step. However, the increased mortality, and effects on reproduction just mentioned, might persist for a year or more as animals habituate to a new setting and delineate territorial boundaries. The biggest concern, based on our sensitivity analyses, would be any temporary decrease in brood size or first-year survival of the translocated birds. Accordingly, these parameters should be high priorities for monitoring post-(re) introduction.

We also note that random capture of small numbers of birds can lead to translocation of birds with an unstable age distribution. This can cause deviations from our short-term (several years for this species) persistence projections because of transient population growth dynamics (Koons et al. 2005, Fefferman and Reed 2006). Depending on the age structure, PE could be moderately higher or lower. Because this species cannot be aged in the field, however, it is not something under the control of managers.

It is imperative that the new site where translocated individuals are introduced be sufficiently large to accommodate the new population. Estimating this area is straightforward if one knows the sustainable density for the target species; this is not known for *G. c. sandvicensis*. Therefore, we used observed population densities on O'ahu that were quantified from playback followed by extensive trapping and marking of birds. Gormally et al. (2020) and M.A. Muñoz, C.B. van Rees, and J.M. Reed (personal observation) reported densities of *G. c. sandvicensis* on wetlands on O'ahu ranging from 0.7 to more than 13 individuals per hectare. We excluded 2 sites they surveyed that had extremely high densities because they were inflated due to an artificially high food source (grass), and where most of the birds were nonbreeding. This leads to an estimate of a minimum of 3.75–74.6 ha required at the recipient site.

How might one minimize area requirements for a reintroduced subpopulation? Habitat structure should affect the required size range. Each of the endangered waterbird species uses a different microhabitat type (Griffin et al. 1989, USFWS 2011), so managing specifically for *G. c. sandvicensis* will increase densities. Because there is strong interspecific aggression between 'alae 'ula and *Fulica alai* (Hawaiian Coots, 'alae ke'oke'o; van Rees et al. 2021), habitat management to favor *G. c. sandvicensis* will disfavor *F. alai*, which will allow denser populations. To maintain higher densities, active vegetation management will be required to maintain the desired habitat structure, as well as predator control (Reed et al. 2012, Underwood et al. 2013). Line of sight may be an important determinant of territorial aggression. Therefore, the effects of population density of *G. c. sandvicensis* might interact with interspersion of small patches of tall emergent vegetation, open water, and groundcover vegetation for foraging. That is, increased interspersion may allow greater densities of individuals and nesting pairs within a confined reintroduction area (M.A. Muñoz, C.B. van Rees, and J.M. Reed, personal observation). We recommend erring on the size of more habitat than might be needed for 25 pairs rather than less because population sizes that are too small are unlikely to persist, including buffering against environmental stochasticity.

ACKNOWLEDGEMENTS

We thank Bob Lacy and Phil Miller for advice on implementing our model in VORTEX, and Bruce Dugger, Bryn Weber, and Mike Silbernagle for feedback early in the planning stages of this project. We thank 2 anonymous reviewers and Paul Doherty for valuable suggestions for an earlier draft of this manuscript.

Funding statement

Funding in support of this project came from the National Fish and Wildlife Foundation, and the Hawai'i Division of Forestry and Wildlife.

Ethics statement

No animals were used as part of this study.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

C.B.v.R. and J.M.R. conceived of, and wrote the manuscript, and obtained funding. C.B.v.R. conducted the simulations.

Data availability

Data and program code used to fit the models presented in this study are available at van Rees and Reed (2024).

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