Received: 12 January 2024 | Revised: 25 July 2024 | Accepted: 30 September 2024

DOI: 10.1002/ecy.4495

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

# Demographic rescue falters when pathogens are present

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**Funding information**
Division of Environmental Biology, Grant/Award Number: DEB-1856710

**Handling Editor:** Kathryn L. Cottingham

## Abstract

As natural populations continue to decline globally, direct forms of intervention are increasingly necessary to prevent extinction. One type of intervention, known as demographic rescue, occurs when individuals are added directly to a population to increase abundance and ultimately prevent population extinction. However, the role of infectious disease in demographic rescue remains unknown. To examine the effects of pathogens on demographic rescue, we used a host–pathogen system with the aquatic crustacean *Daphnia dentifera* as the host and the fungus *Metschnikowia bicuspidata* as the pathogen. We constructed a randomized 3 × 2 factorial experiment with three rescue treatments (none, low, high) and two pathogen treatments (unexposed, exposed), where the pathogen was introduced via infected individuals during rescue events. We found that adding more individuals to demographically depressed populations increased abundance over the short term; highly supplemented populations initially had 62% more individuals than populations that had no introduced individuals. However, by the end of the experiment, populations that did not have any individuals introduced averaged 640% higher abundance than populations where infected individuals had been added. Thus, the introduction of infected individuals can result in worse demographic outcomes for populations than if no rescue is attempted.

**KEYWORDS**
augmentation, demographic rescue, disease, evolutionary rescue, genetic rescue, parasite, pathogen, population

## INTRODUCTION

When populations are rapidly declining to the point of greatly increased extinction risk, there are three general modes of rescue that can, at least theoretically, prevent extinction from occurring: demographic, genetic, and evolutionary (Hufbauer et al., 2015). Demographic rescue is the process of adding individuals to a population, either from captively bred or wild sources, to overcome intrinsic vital rates that are obstacles to recovery (e.g., Allee effects, density independence; Brown & Kodricbrown, 1977; Hutchings, 2021). Genetic rescue is the process of adding individuals from a different population to mitigate the effects of inbreeding load and

genomic erosion (Fitzpatrick et al., 2016; Whiteley et al., 2015). Finally, evolutionary rescue occurs when a population avoids extinction by responding to the agent(s) of selection via intrinsic standing genetic variation present within the population (Bell & Gonzalez, 2009; Carlson et al., 2014). Thus, evolutionary rescue does not require the addition of individuals but does require an adaptive, evolutionary response; genetic rescue requires successful introgression from outbred populations to mitigate various genomic issues; demographic rescue largely ignores genetics and evolution but focuses instead on reversing population declines through demographic processes.

It has been proposed that all three forms of rescue can be hampered by disease (Christie & Searle, 2018). Within a metapopulation framework, increased population connectivity (e.g., habitat corridors; Christie & Knowles, 2015) can be thought of as a type of demographic rescue and previous studies have highlighted trade-offs between migration and disease (e.g., Altizer et al., 2011; Jousimo et al., 2014). Demographic rescue is also often proposed as a primary motivation for supplementing wild populations with captive born or translocated individuals (Frankham et al., 2002; Willoughby & Christie, 2019), but many unanticipated challenges can occur.

There can be substantial risks associated with demographic rescue efforts, including a lack of any noticeable demographic effects (e.g., wasted resources; Chilcote et al., 2011; Jaeger & Scheuerell, 2023), negative genetic effects (Christie et al., 2012; Fisch et al., 2015), and accidental introduction or proliferation of pathogens (Diuk-Wasser et al., 2021; McCallum & Dobson, 2002). The likelihood that the simple addition of individuals is successful in rescuing a population (measured as a lower probability of extinction) is likely to be reduced if individuals added to the population are infected with a pathogen. If the pathogen reduces survival or fecundity, yet has moderate to high rates of transmission, then the addition of infected individuals into the population could cause lower population abundance than the complete absence of any type of intervention. Thus, it is important to understand the risks and benefits associated with the purely demographic addition of individuals to a population. While there is evidence that the accidental introduction of pathogens during supplementation or translocation events has resulted in negative impacts on the target populations (reviewed in Warne & Chaber, 2023), this phenomenon has not yet been experimentally tested.

Here, we used a model host–pathogen system (Ebert, 2022) with the aquatic crustacean *Daphnia dentifera* as the host species (hereafter "the host") and the fungus *Metschnikowia bicuspidata* as the pathogen species (hereafter "the pathogen"). The host is a freshwater grazer that is common in stratified lakes in the Midwestern United States (Hebert, 1995) and is facultatively parthenogenetic. The pathogen is an obligate killer that infects its host after consumption; spores of the pathogen puncture through the gut wall and proliferate in the hemolymph (Ebert et al., 2000). Infections are visible in live hosts as they turn the normally transparent host opaque (Duffy & Hall, 2008). In this study, we used a single genetic clone (isofemale line) of the host and single isolate of the pathogen. An advantage of this model system is that by using a single genetic clone, we can isolate the effects of demographic rescue from a potentially confounding background of evolutionary or genetic rescue because a population with no genetic variation cannot respond to selection (Barghi et al., 2020; Maruki et al., 2022). Another advantage is that we can add the same type of individual to the system (i.e., hold the genetic background constant across rescue regimes) as there is no genetic variation among individuals. We asked two questions: (1) Can the addition of individuals to a population reduce extinction risk and increase population size? (2) What is the overall demographic effect when a small percentage of individuals added to populations are infected with a pathogen?

# METHODS

## Experimental design and implementation

Both the host clone and the pathogen isolate used in our experiment were collected from a lake in Barry County, MI, USA, and propagated in the laboratory for over 10 years. At the start of the experiment, a total of 60 microcosms, representing 6 treatments with 10 replicates each, were initiated with five individuals in 300-mL well water placed within 400-mL beakers. The well water was sourced from a local well provided by the Purdue University animal facility; we used this water because it was unchlorinated. This low starting population size allowed for the possibility of extinction. We did not control the age of these initial hosts, but we allocated individuals across beakers based on size so that each population began with a similar size structure (Merrick & Searle, 2019; Searle et al., 2018). The experiment had a randomized 3 × 2 factorial design with three rescue treatments (none, low, high) and two pathogen treatments (unexposed, exposed; Figure 1). On day 0, beakers were randomized into treatments followed by immediate application of rescue and pathogen treatments. For the low- and high-rescue treatments, 5 or 10 individuals (1× or 2×

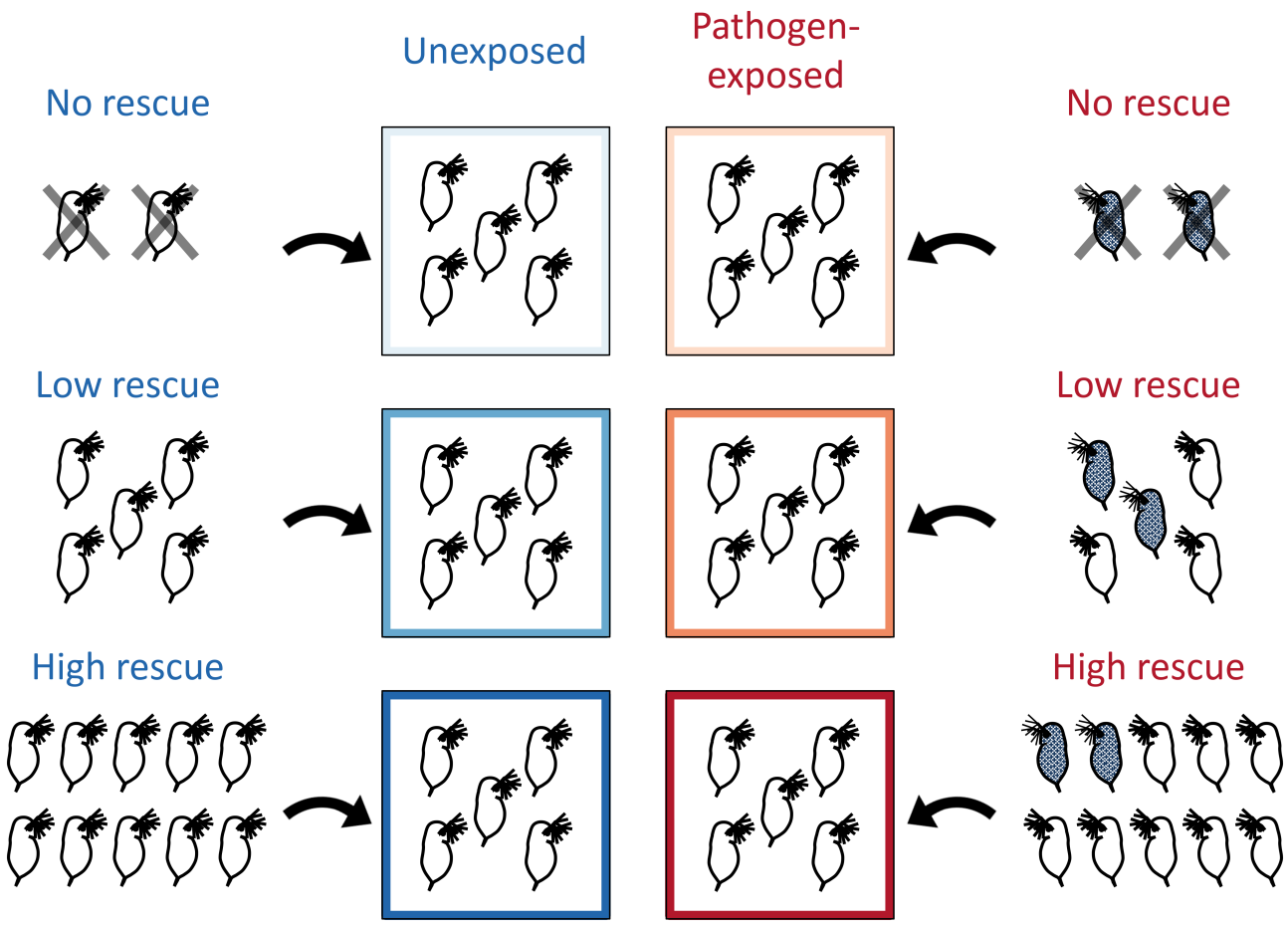


**FIGURE 1** Schematic of the 3 × 2 factorial experimental design. There were three rescue treatments (no-rescue treatment: two deceased, homogenized individuals added, where "X" indicates dead individuals; low-rescue treatment: five individuals added at each rescue event; and high-rescue treatment: 10 individuals added at each rescue event) and 2 pathogen treatments (pathogen-exposed or unexposed). The pathogen treatments were applied during rescue events by adding two deceased, homogenized infected individuals (no-rescue treatment) or two live infected individuals (low- and high-rescue treatments; shown as gray/solid individuals). Each treatment was replicated 10 times for 60 total experimental populations.

the original population size, respectively) were added at each introduction event. There were two introduction events for the rescue treatments: one on day 0 and one on day 7. Multiple introductions can increase introduction success (e.g., Dlugosch & Parker, 2008; Koontz et al., 2018), and one week is close to a generation of the host in these conditions (Searle et al., 2018). Pathogen treatments were also applied during each rescue event; for the pathogen-exposed treatments, two of the added individuals were infected with the pathogen for treatments that received additional individuals (i.e., the low and high-rescue treatments). For the no-rescue, pathogen-exposed treatment, we inoculated populations with the pathogen by homogenizing two infected hosts and adding the solution directly into the water. For the no-rescue, pathogen-unexposed treatments, we added two uninfected homogenized hosts to each population to control for any effects of the host fragments (Figure 1; see Appendix S1: Section S1 for more details on pathogen exposures and treatments). We visually identified infected individuals using a stereomicroscope before addition to the beakers or homogenization. To facilitate counting of large numbers of individuals on sampling days, we split the experiment into two blocks with half of the replicates from each treatment in each block. The timeline for each block was identical, but block 2 was initiated one day after block 1. Each day, we fed each population approximately $4.0 \times 10^6$ cells of the alga, *Ankistrodesmus falcatus*. We chose to add the same amount of food to all treatments to mimic a natural system with fixed resources; higher abundance likely caused higher competition for food, which reflects what would occur in natural systems in the absence of food supplementation.

We sampled populations every seven days starting on day 7, when sampling occurred immediately before the

second and final rescue treatment. At each sampling event, we stirred the beakers to homogenize the population and then removed a 55-mL sample (~18% of the volume). We used a stereomicroscope to count each individual in every sample to estimate population abundance and classified each individual by infection status (infected or uninfected), sex (male or female), and age class (juvenile or adult). Males were distinguished from females by a lack of a brood chamber and the presence of elongated first antennae (Ebert, 2005), while juveniles were distinguished from adults by their small size and a narrow brood chamber. Immediately after counting, the hosts were placed back into their respective beakers. During this sampling process, we also conducted a full water change. The experiment concluded after eight weeks (56 days) for a total of eight sampling events, which is approximately seven host generations under these conditions (Searle et al., 2018).

## Statistical analyses

All analyses were conducted using R version 4.3.1 (R Core Team, 2023). Due to overdispersion, our main model for population abundance was a negative binomial mixed-effects model with pathogen treatment, rescue treatment, the pathogen × rescue interaction, week, and block as fixed effects and beaker as a random effect (function "glmer.nb" in the package "lme4"; Bates et al., 2015). We then performed model selection using Akaike information criterion and retained pathogen treatment, rescue treatment, and week as fixed effects, with beaker as a random effect. We report effect sizes as untransformed beta coefficients from this model. We also analyzed population abundance at each sampling date separately using a Poisson generalized linear model (GLM) with pathogen treatment and rescue treatment as predictors. Two replicates in the unexposed, no-rescue treatment were inadvertently exposed to the pathogen and were removed from all analyses.

To compare infection prevalence across treatments, we constructed a binomial generalized linear mixed-effects model (GLMM) with rescue treatment, week, the rescue treatment × week interaction, and block as fixed effects and beaker as a random effect using only data from the pathogen-exposed treatments. To compare the abundance of infected individuals across treatments, we used a mixed-effects Poisson GLM (function "glmer" in the package "lme4"; Bates et al., 2015) with rescue treatment, week, and block as fixed effects and beaker as a random effect.

We also calculated the proportion of the population that consisted of juveniles or males for each replicate on each sampling day and compared these values across treatments using the same predictor variables as we used for population abundance. For the proportion of juveniles, we used a binomial GLMM and for the proportion of males, we used a zero-inflated negative binomial GLMM (function "glmmTMB" in the package "glmmTMB"; Brooks et al., 2017) due to a large number of zero values in the proportion of males in our data.

# RESULTS

In our model for population abundance, exposure to the pathogen had a large negative effect on abundance ($\chi^2(1) = 129.13$, $p < 0.001$, $\widehat{\beta} = -1.17$) while rescue treatment had a very small positive effect on abundance ($\chi^2(1) = 5.13$, $p = 0.024$, $\widehat{\beta} = 0.09$; Figure 2; Appendix S1: Figure S1, Table S1). Time was also a significant predictor of abundance in this model ($\chi^2(1) = 22.86$, $p < 0.001$, $\widehat{\beta} = -0.08$). In sampling week 1, only the rescue treatment affected overall abundance, while for weeks 2–4, both pathogen treatment and rescue treatment affected abundance (Appendix S1: Table S2). In week 5, only pathogen treatment was a significant predictor of abundance, for weeks 6–7, both pathogen and rescue treatments affected abundance, but only pathogen treatment had an effect by week 8 (Appendix S1: Table S2). At week 8, populations in the unexposed, no-rescue treatment had an average 641% higher abundance than the treatments where infected individuals had been added. Thus, there was a general trend for the rescue treatments to have a stronger effect on abundance earlier in the experiment, whereas the pathogen treatment had a stronger effect on abundance later in the experiment (Figure 2).

The number of infected individuals was higher in the high-rescue treatment than in the no-rescue and low-rescue treatments ($\chi^2(1) = 7.14$, $p = 0.007$, $\widehat{\beta} = 0.13$); both week and block were also significant predictors of the number of infected individuals (week: $\chi^2(1) = 8.64$, $p = 0.003$, $\widehat{\beta} = -0.04$; block: $\chi^2(1) = 6.70$, $p = 0.009$, $\widehat{\beta} = 0.21$; Appendix S1: Figure S2A, Table S3). Infection prevalence varied across weeks ($\chi^2(1) = 8.06$, $p = 0.005$, $\widehat{\beta} = 0.32$), but there was no effect of rescue treatment, the rescue treatment × week interaction, or block on infection prevalence ($p > 0.50$ for both predictors; Appendix S1: Figure S2B, Table S4).

The proportion of the population consisting of juveniles varied across weeks ($\chi^2(1) = 75.23$, $p < 0.001$, $\widehat{\beta} = -0.52$) and was higher in the unexposed treatments than in the pathogen-exposed treatments ($\chi^2(1) = 34.37$, $p < 0.001$, $\widehat{\beta} = -2.61$), but not different across rescue treatments ($\chi^2(1) = 2.15$, $p = 0.143$; Appendix S1: Figure S3A, Table S5). There was no difference in the

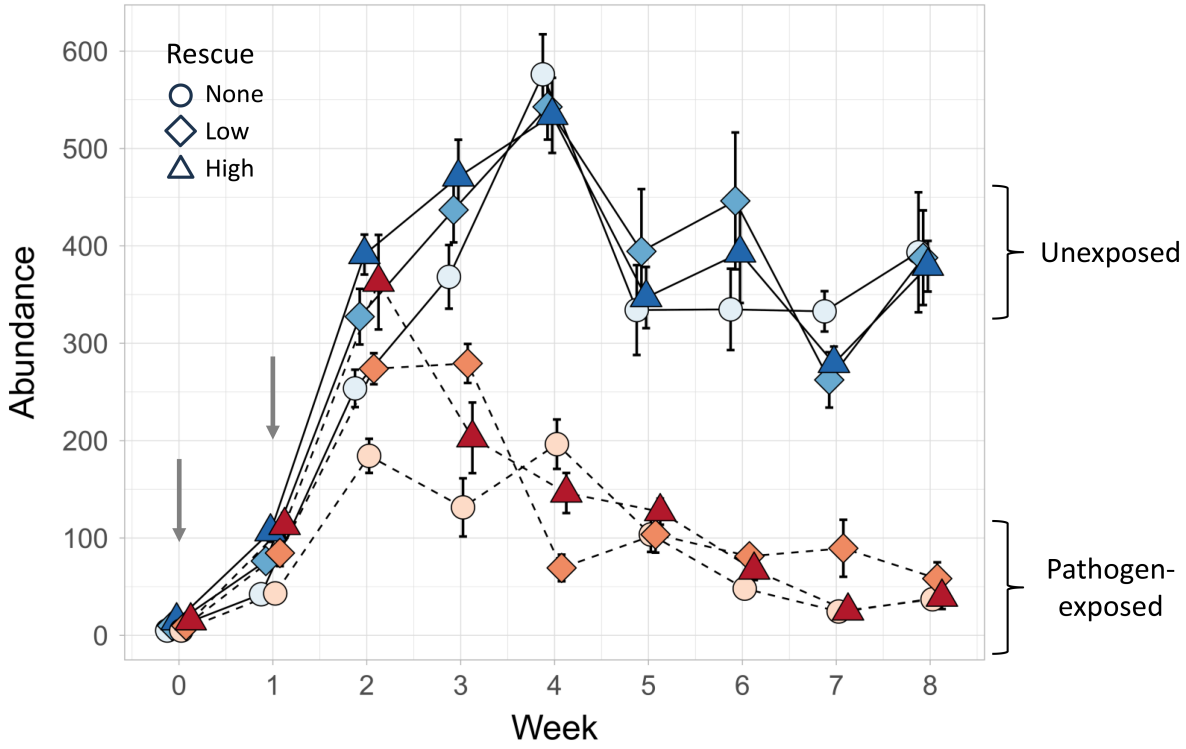


**FIGURE 2** Population abundance through time. Pathogen treatments are shown as blue (pathogen absence) or red/orange (pathogen presence). Rescue treatments are shown as light circles (no-rescue treatment), diamonds (low-rescue treatment), or dark triangles (high-rescue treatment). Points are average values in each treatment (±SE). Arrows indicate days when rescue treatments were applied. Abundance was estimated by sampling ~18% of the population on each sampling day.

proportion of the population consisting of males across treatments or through time ($p > 0.10$ for all predictors; Appendix S1: Figure S3B, Table S6).

## DISCUSSION

We found that adding more individuals to a demographically depressed population can increase abundance over the short term (a result that has been previously found in some populations, e.g., Hess et al., 2012; Hufbauer et al., 2015). One week after the second rescue event (week 2), the highly supplemented populations had an average of 62% more individuals than the populations in the no-rescue treatments. As the experiment progressed, we saw that the demographic gain associated with introducing individuals was erased, with the no-rescue, unexposed populations having the highest average population abundance in weeks 4 and 7, and all three unexposed treatments having nearly identical abundances in week 8 (Figure 2). Thus, it appears that introducing uninfected individuals can provide a short-term demographic increase to small populations and may facilitate demographic rescue when there are no other constraints on the population.

There were no substantial differences between pathogen-exposed and -unexposed treatments in our first sampling week (Figure 2). By the second week, we began to see negative effects of the pathogen treatments on abundance, but the high-rescue treatment with the pathogen still had a higher average abundance than both no-rescue treatments. However, by week 3, all pathogen-exposed populations had lower average abundances than the unexposed populations, a trend that continued until the end of the experiment (Figure 2). In fact, by the end of the experiment (week 8), there were no detectable effects of rescue treatment, and the only predictor of abundance was whether the population had been exposed to the pathogen (Figure 2; Appendix S1: Table S2). Pathogen-exposed treatments were also unable to compensate for the negative effects of the pathogen through reproduction; populations exposed to the pathogen had a lower proportion of juveniles than the unexposed populations (Appendix S1: Figure S3A). Thus, the introduction of infected individuals can result in a worse demographic outcome than if no individuals had been added to the population. Jointly, these results illustrate the inherent trade-offs associated with any demographic rescue efforts: If the release of infected individuals can be prevented, the additional individuals

can provide a short-term demographic increase to the supplemented population, but if infected individuals are accidentally released, the demographic outcomes can be worse than if no intervention effort was initiated.

In practice, demographic rescue efforts would not intentionally release infected individuals into a population, but depending on the pathogen, the presence or absence of infection can be very difficult to detect (Ryser-Degiorgis, 2013; Warne & Chaber, 2023). Pathogens can live on or within hosts at very low abundance and often increase rapidly when environmental factors, including stress, change host tolerance or resistance (Brown et al., 2012; Vicente-Santos et al., 2023). Releasing individuals into a new environment, as occurs during demographic rescue, can be very stressful (Batson et al., 2017; Jenni et al., 2015) such that individuals intended for reintroduction may appear healthy but still harbor low levels of infection that proliferate after introduction into the novel environment (Jacobson, 1993). Understanding the life cycle and ecology of a host's pathogens can be useful for prioritizing which pathogens to monitor. For example, monitoring for pathogens that are more likely to have negative effects on host populations, such as those with high virulence, should take priority. Nevertheless, given the outcomes presented here, careful monitoring for even low levels of infection, via eDNA (Huver et al., 2015; Miaud et al., 2019) or other sensitive assays, could help ensure that demographic rescue attempts are successful.

A few specifics of our study are worth discussing. First, we did not allow for a response to selection that could theoretically prevent extinction within several generations (sensu Hufbauer et al., 2015). This experimental design was intentional so that we could isolate demographic processes. In natural systems, however, populations may often experience a joint benefit of genetic and demographic rescue due to conservation interventions (e.g., Kronenberger et al., 2017). Second, in our experiment, the host and pathogen have overlapping species distributions and therefore have coevolved with one another (Duffy & Hall, 2008; Hebert, 1995). Thus, there has been some selection for host tolerance or resistance in our system (e.g., Duffy & Sivars-Becker, 2007). In systems where non-native or recently introduced pathogens occur, the lack of coevolutionary history could lead to worse demographic outcomes than those in systems where coevolution has occurred. Finally, we used a host with relatively high fecundity manipulated in a simplified environment, which could affect the applicability of our results to natural systems. Many at-risk populations and species have relatively low fecundity (i.e., "slow" life history; Purvis et al., 2000) which could lead to a stronger effect of demographic rescue than we found in our study. Additionally, complex species interactions that occur in nature could result in unanticipated effects of the surrounding ecological community on the host and pathogen. These complexities should be acknowledged when considering demographic rescue as a part of species-specific conservation or management plans.

Several variables can increase the chances of successful demographic rescue when a pathogen may be present. For example, "headstarting" individuals, whereby individuals from early life stages are maintained in captivity through periods of high mortality in the wild, may help reduce the chances of introducing pathogens if infection can be monitored and treated in the captive environment. Additionally, it would be useful to identify which species and populations are most likely to experience strong Allee effects and thus may benefit the most from demographic rescue (e.g., Deredec & Courchamp, 2007; Kanarek et al. 2015). Lastly, in the case of reintroduction events for previously extirpated populations, the potential risks of introducing a pathogen may be lower than those for an existing population because even though the reintroduction attempt may fail, the alternative action of no intervention is unlikely to restore an extirpated population unless colonization from neighboring populations is possible.

In conclusion, we found that adding infected individuals to a population can result in worse demographic outcomes than if no individuals had been added. This potential for a large negative effect of a rescue attempt means that conservation and management actions should carefully consider the pros and cons associated with demographic rescue. On the one hand, if there can be some modicum of assurance toward no infected individuals being released (e.g., via careful preventative measures), then the population may experience a short-term demographic benefit that could potentially lower the probability of extinction. On the other hand, if infected individuals are unintentionally released, then the negative demographic effects can be severe. These potential costs and benefits should be weighed in a formal risk–benefit framework (Harwood, 2000; Sanders et al., 2016) where the context of the ecosystem, life histories of the host and pathogens, and other contextual nuances can be rigorously assessed. Other potential costs such as time, effort, and limited financial resources should also be considered and weighed against other forms of mitigation (e.g., habitat restoration). That such stark differences in demographic outcomes can occur depending on the presence or absence of a pathogen suggests that a carefully considered and well-informed decision-making process must be implemented before any individuals are released in attempts at rescuing a population.

## AUTHOR CONTRIBUTIONS

Catherine L. Searle contributed to project design, data analysis, and writing. Stephanie O. Gutierrez led project implementation and data collection. Ilinca I. Ciubotariu contributed to project implementation and data collection. Alana López-Cruz contributed to project implementation and data collection. Mark R. Christie contributed to project design and writing. All authors provided feedback on the project implementation and manuscript.

## ACKNOWLEDGMENTS

We thank L. Papai and B. Berggren for their assistance with this project. Funding was provided by a National Science Foundation grant to Catherine L. Searle and Mark R. Christie (DEB-1856710).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Searle et al., 2024a) are available in Dryad at https://doi.org/10.5061/dryad.rjdfn2zn5. Code (Searle et al., 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.13904519.

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## SUPPORTING INFORMATION

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

**How to cite this article:** Searle, Catherine L., Stephanie O. Gutierrez, Ilinca I. Ciubotariu, Alana López-Cruz, and Mark R. Christie. 2025. "Demographic Rescue Falters When Pathogens are Present." *Ecology* 106(1): e4495. https://doi.org/10.1002/ecy.4495