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Warning sign of an accelerating decline in critically endangered killer whales (*Orcinus orca*)

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Wildlife species and populations are being driven toward extinction by a combination of historic and emerging stressors (e.g., overexploitation, habitat loss, contaminants, climate change), suggesting that we are in the midst of the planet's sixth mass extinction. The invisible loss of biodiversity before species have been identified and described in scientific literature has been termed, memorably, dark extinction. The critically endangered Southern Resident killer whale (*Orcinus orca*) population illustrates its contrast, which we term bright extinction; namely the noticeable and documented precipitous decline of a data-rich population toward extinction. Here we use a population viability analysis to test the sensitivity of this killer whale population to variability in age structure, survival rates, and prey-demography functional relationships. Preventing extinction is still possible but will require greater sacrifices on regional ocean use, urban development, and land use practices, than would have been the case had threats been mitigated even a decade earlier.

Challenges in conservation biology are generally assigned into small population or declining population paradigms[1]. Resource management typically distinguishes between decisions to protect the welfare of individuals and those to promote recovery of populations[2]. Below a critical threshold, populations become sufficiently small that demographic stochasticity (i.e., random fluctuations in birth and death rates) can result in extinction, even when the average population growth rate is positive[3]. Many of these extinction events are taking place undocumented, before a species has even been described scientifically, in a process termed memorably as dark extinction[4]. The concept of dark extinction could lead some to conclude falsely that extinction is largely an information deficit problem. In other words, if only we knew that a population or species were declining toward extinction, we would step in to mitigate anthropogenic stressors and reverse declines. In our experience, many populations and species are declining toward extinction in plain sight. We call this latter process a bright extinction, with thanks to Boehm and colleagues for inspiring the term.

Small populations can persist despite large variability in environmental conditions around some long-term stationary state, whereas a deteriorating trend in environmental conditions increases extinction risk in small populations[5]. Drake and Griffen hypothesize that "environmental degradation may cause a tipping point in population dynamics, corresponding to a bifurcation in the underlying population growth equations, beyond which decline to extinction is almost certain"[5]. In practice, demographic parameters of wild populations are rarely estimated with sufficient precision to detect these early warning signs (a bifurcation in population rates of change) until a decline may be irreversible[6,7]. Evidence-based conservation requires knowledge of demographic rates, as well as natural and anthropogenic influences on those rates, to guide timely and effective interventions[5,8,9]. While improved tools for data analyses to assess

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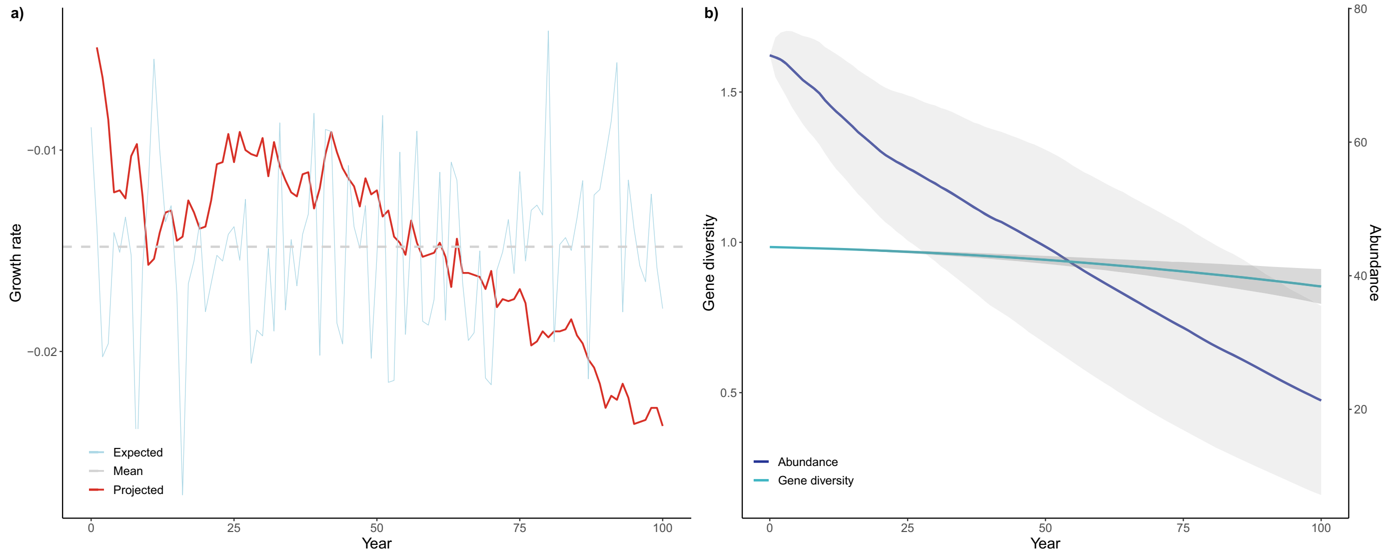

Fig. 1 | Southern Resident killer whale population growth, gene diversity and abundance over time. Population growth rate (r) (Fig. 1**a**) and number of whales and proportion of current gene diversity projected (Fig. 1**b**) over 100 years and averaged across 1000 iterations of the Baseline model of the SRKW population. The expected growth rate is in blue, the projected decline is in red, and the horizontal dashed line represents the mean rate. Note the bifurcation around 50 years (two killer whale generations) indicative of an accelerating decline, even without accounting for increasing threats[5]. Shading represents the 95% confidence intervals around SRKW abundance (dark blue line) and gene diversity (light blue line).

conservation status and extinction risks are needed urgently to protect data-poor species and populations[10,11], not all extinctions can be attributed to an information deficit alone[12,13]. To complicate matters further, the threats that lead to a legal listing recognizing a population's endangered status may not represent the same drivers likely to lead to population recovery. Instead, wildlife population dynamics and risk of extinction can be the net result of multiple concurrent, persistent, interacting, and evolving drivers that include both natural ecological and anthropogenic factors[14,15].

Population assessment of Southern Resident killer whales (SRKW, *Orcinus orca*) is extremely data-rich compared with those of many other wild mammals. These whales represent the smallest (75 individuals[16]) of four separate, non-interbreeding, behaviorally, and culturally distinct, fish-eating ecotypes of killer whales in the eastern North Pacific Ocean. Every individual in the population has been censused annually by the Center for Whale Research and colleagues since the 1970s[17]. Depleted in the 1960s and 1970s by an unsustainable live-capture fishery for aquaria displays, the population has failed to recover due to a combination of sublethal and lethal stressors, including reduced availability and quality of Chinook salmon (*Oncorhynchus tshawytscha*), its preferred prey; noise, which further reduces foraging efficiency[18]; contaminant exposure, which is associated with decreased fecundity, increased calf mortality, and other adverse effects[19,20]; and vessel strikes[21]. The whales' preferred prey, Chinook salmon, are themselves heavily depleted, and the ability of Chinook salmon stocks to support survival, let alone recovery of SRKW has been in question for over two decades[22,23]. Years with low Chinook salmon abundance are temporally associated with low SRKW reproduction and survival[22,23]. Ensuring recovery of SRKW and the salmon on which they depend hinges on explicit recognition of the costs and conflicts associated with recovery of predator and prey alike[24].

Results and discussion

Given observed demographic rates over the last 40 years, the baseline population dynamics model predicts a mean annual population decline of roughly 1% (Fig. 1a, b). This average decline is characterized by gradual reduction for roughly two generations (~40 years), followed by a stereotypical period of accelerating decline that presages extinction (Fig. 1). This baseline model is optimistic, because all evidence suggests that natural and anthropogenic drivers of population status are dynamic, transient, and multifactorial, and many threats are expected to worsen in future.

By using more recent data, the aforementioned relationships between interannual variability in Chinook salmon and SRKW survival and fecundity[25] are changing enough that we predict that prey-mediated changes in SRKW survival and reproduction (Fig. 2a, b) are likely to lead to even more dramatic declines in the coming decades than the prior baseline model suggests (Fig. 3). Our analyses reveal that the population shows lower recovery potential than previously estimated, due to reduced leverage of prey availability on SRKW demography, adverse stochastic effects (e.g., few female offspring in recent years, mortality from vessel strikes), and potentially amplifying effects of inbreeding[20,26,27]. Ultimately, overexploitation caused the initial decline, but proximate effects of habitat degradation and loss (and possibly destruction) are inhibiting SRKW recovery[19]. The whales are also obligate prey specialists on the largest, fattiest Chinook salmon, which limits their ability to adapt to a changing environment. Accordingly, SRKW epitomize the naturally rare, wide-ranging or broadly distributed species that may be hardest to protect.

Immediate, multidisciplinary approaches, including supporting Chinook salmon recovery and appropriate veterinary interventions when indicated, will be necessary to stabilize the population (Fig. 4). Although no single scenario can help SRKWs reach one stated recovery objective of 2.3% sustained growth over 28 years, concerted efforts can reverse the decline and possibly reach 1% annual recovery. Slowing or halting the population decline might provide opportunities to develop and implement new strategies to mitigate and facilitate recovery of SRKW that are not yet feasible. In a population of 75 individuals, a single birth or death represents an annual population growth or decline of 1.4%, underscoring the value of each individual in preventing the disappearance of a population.

Recovery considerations

Treating individual wild animals to promote population recovery only benefits conservation when individual animals are known and populations are small enough for individual survival to make a considerable difference[28], such as in the recovery of habituated mountain gorillas[29], Ethiopian wolves[30], and Hawaiian monk seals[31]. For SRKWs to attain a 1% population growth, non-invasive diagnostic investigations, informed clinical

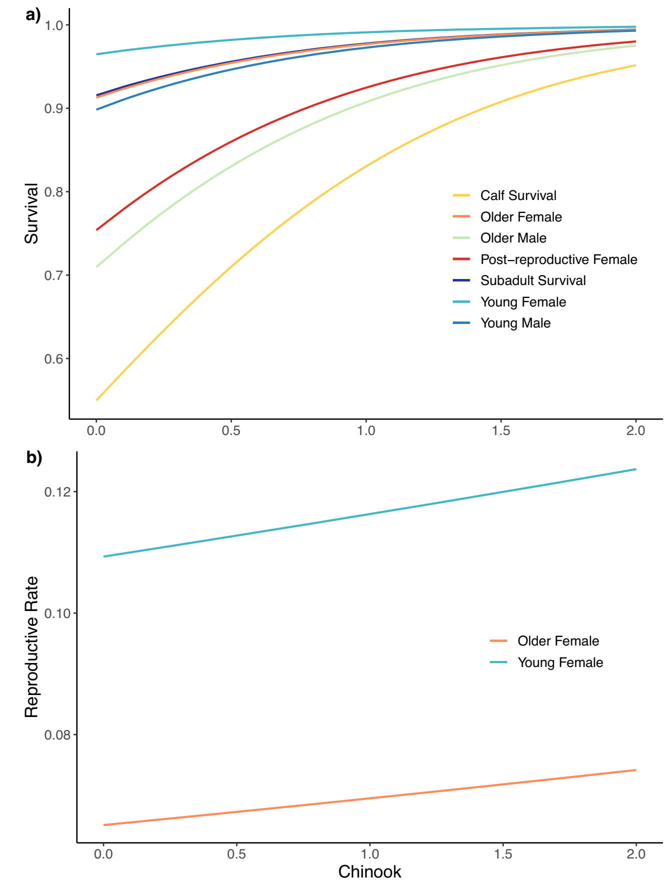

Fig. 2 | Relationship of survival and reproductive rates and Chinook Index. Annual survival rates (Fig. 2**a**) and reproductive rates (the proportion of breeding age females producing a calf) (Fig. 2**b**) for SRKW of different age-sex classes (Table 1) predicted from logistic regressions against the Chinook salmon prey abundance. Calf survival is in yellow, post-reproductive female is in red, older male is in green, older female is in orange, subadult survival is in dark blue, young female is in light blue, and young male is in blue.

intervention, and ongoing post treatment monitoring of animals that present with serious morbidity or clinical disease is warranted. This extreme conservation measure enables humans to reduce mortality in high value animals, such as reproductively active females. When feasible, *post mortem* examination of stranded SRKWs is critical to inform future clinical decisions and management options. Interventions should be rank ordered and those injuries attributed to human activities, such as vessel strike or net, line or hook entanglement, or potential oil exposure are priorities that may warrant immediate intervention[21]. Other future interventions may include remote administration of antiparasitic drugs and other treatments[32] for treating disease[33]. It may be time to discuss more drastic measures, including pre-emptive vaccination to protect individuals against pathogens with known high morbidity and mortality rates among cetaceans (e.g., cetacean morbillivirus, *Brucella cetorum*, *Toxoplasma gondii*)[34]. We encourage transboundary and inter- agency discussions to coordinate emergency plans for veterinary intervention, including permits and decision trees, before a high-profile crisis necessitates implementation. Emergency veterinary intervention plans could be modeled on similar bilateral, multi-agency plans to respond to an oil spill in these transboundary waters[35]. With timely and effective management actions (such as mandated reduced vessel speeds near whales to minimize vessel strike) to reduce human-caused mortality[36], we estimate that up to 28% of natural mortality could be deferred each year (Fig. 4, Supplementary Notes). Given the delay between medical interventions and demographic changes (e.g., survival, growth, fecundity, abundance) regular evaluation of short-term health benchmarks (e.g., body

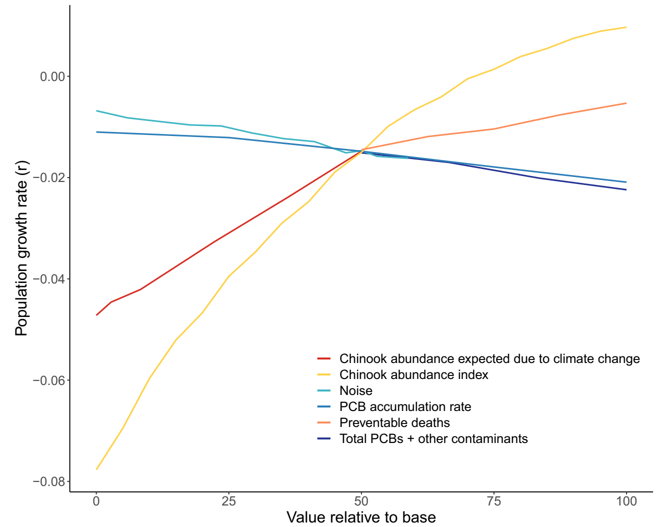

Fig. 3 | Five influential factors affecting Southern Resident killer whale population growth. Spider plot showing relative impacts of the 5 most influential factors affecting SRKW population growth. The x-axis is scaled for each factor so that the Baseline value is set to 50, and the range scaled from 0 to 100. (See Table 2 for definitions of factors and ranges tested.) Chinook abundance expected due to climate change is in red, the Chinook abundance index is in yellow, noise is in light blue, the PCB accumulation rate is in blue, preventable deaths is in orange, and total PCBs plus other contaminants is in dark blue. Other factors listed in Table 2 had lesser impacts on SRKW population growth, and their relative impacts are provided in Supplementary Notes and Supplementary Fig. S20.

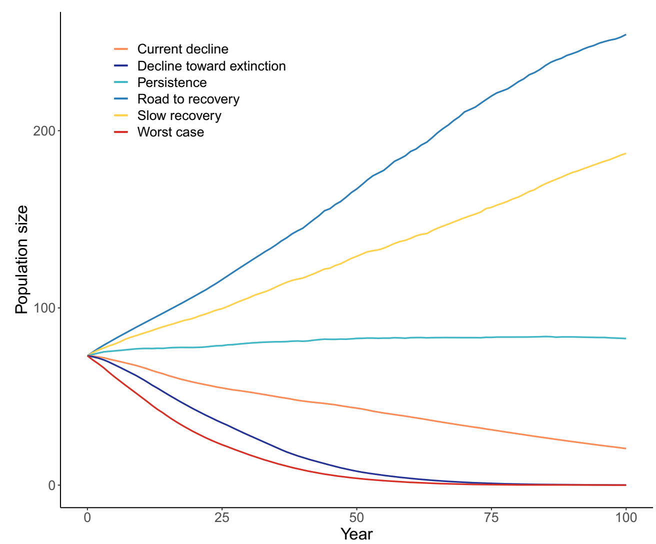

Fig. 4 | Southern Resident killer whale population size projected 100 years in the future. Projections of SRKW population size, averaged across 1000 iterations for six scenarios that range from optimal to pessimistic: "Road to recovery" (in blue) assumes direct and indirect human impacts on the whales and their habitats re removed (1.5× Chinook, no climate change effects, no noise, human-caused mortalities prevented, no PCBs or other contaminants); "Slow recovery" (in yellow) assumes lesser but still considerable improvements to threats (1.3× Chinook, no climate change, no noise, no human-caused mortalities, environmental PCBs reduced with 25-year half-life); "Persistence" (in light blue) assumes each threat reduced to half as much as in "Slow recovery"; "Current decline" (in orange) is the Baseline; "Decline toward extinction" (in dark blue) adds further threats (8% reduction in prey size, climate change decimating Chinook salmon stocks, total contaminants 1.67× PCB, a low probability of oil catastrophic spills); "Worst case" (in red) adds further plausible increases in threats (0.7× Chinook, noise disturbance 100% of time, oil spills at higher frequency).

condition, reproductive potential of existing population, behavior, pregnancies, etc.) is critical to strike a balance between risk and reward of any particular intervention.

Southern Resident killer whales are known to be among the most contaminated marine mammals in the world, with polychlorinated biphenyl (PCB) concentrations readily exceeding established thresholds for health effects, including growth and development, immune function, and reproductive performance[37]. However, PCBs are an important, but not exclusive, contaminant class found in SRKW. Despite their phase-out under the terms of the international Stockholm Convention on Persistent Organic Pollutants (POPs), the persistence of PCBs in the marine environment and resistance to metabolic elimination means that it will take decades before this population is considered to be 'safe' from PCB and other legacy contaminant-related health effects[38]. This lag between mitigation and benefits to wildlife, together with the co-occurrence of many other contaminants, suggest that threats attributable to POPs will decline, but the population consequences will linger. This lag time was accounted for using the predicted PCB level trends in this killer whale population[38] and a 1.75× factor was applied to our previously modeled population impact attributed to PCBs to capture the contribution and associated risk of other POPs, including legacy organochlorine pesticides (OCPs). This 1.75× factor was derived from a endocrine disruption risk-based quotient for local harbor seals (*Phoca vitulina*)[27], a species that has been used previously as a surrogate to characterize Resident killer whale contaminant levels and risk in the North Pacific[39]. Contaminant mitigation alone will be insufficient to promote population growth, but should be considered as one pillar of a comprehensive, 'action'-oriented plan to protect at-risk coastal cetaceans[40,41].

Biological resilience is partially determined by genetic diversity. Due to the decline in the SRKW population from the 1960s, the population is currently so small that there are relatively few breeders (especially males) and, that we anticipate inbreeding will exacerbate this process and population decline (Fig. 1). In this way, the continued loss of genetic diversity will likely hamper the population's ability to adapt to an ever-evolving threatscape. Kardos et al. found that the SRKW population is already partly inbred and that reduced survival further jeopardizes its recovery potential[26]. Recovery is currently more difficult than if effective measures had been initiated a few decades ago, although other small marine mammal

Table 1 | Annual mortality and reproductive rates for each age-sex class

	Annual mortality		Reproduction	
Age class	Mean	EV	Mean (SD)	EV
Calf	0.1694	0.2160		
Subadult	0.0225	0.0182		
Females:				
Young (10–30 y)	0.0090	0	0.1163	0.0354
Older (30–45 y)	0.0232	0	0.0697	0.0415
Post-reproductive (>45 y)	0.0752	0.0502	0	
Males:				
Young (10–21 y)	0.0274	0.0271	(see Table 2)	
Older (>21 y)	0.0925	0.0799	(see Table 2)	

Classes are defined as calf (up to 1 year), subadults (1–10 years, pre-reproductive), young adult females (10–30 years), older adult females (30–45 years), post-reproductive females (>45 years), young adult males (10–21 years), older adult males (>21 years). Males are assumed to begin reproductive lifespan between 12 years and 18 years; and to cease breeding after 60 years.

Table 2 | Summary of the baseline estimates for parameters describing threats to Southern Resident killer whales, and the ranges considered in sensitivity testing

Input parameter	Baseline (current)	Range tested	
Prey impacts		Low	High
Prey abundance (index relative to long-term mean)	1.0	0.5	1.5
Modeling demographic consequences of anthropogenic threats			
Climate change: percent decline in Chinook abundance over 40 years	No climate change impacts on prey	No decline in prey	90% decline over 40 years
Changes in Chinook size years to 8% decline	No decline	20 y	60 y
Noise (percent of feeding time with disturbance)	85%	0%	100%
Contaminants			
Accumulation rate	2 ppm/y	0 ppm/y	4 ppm/y
Impact on calf survival (logistic slope)	−0.02	−0.01	−0.03
Half-life of PCBs in environment	No decline	25 y	75 y
Total equivalents of PCBs plus other contaminants	**1.0**	**1.0**	**2.0**
Other threats			
Direct human-caused mortality (potentially preventable)	28.3% of deaths (included within annual mortality)	No reduction	All 28.3% of natural mortality prevented each year
Inbreeding impact (lethal equivalents/diploid)	6.29 LE	0 LE	12 LE
Variance in male breeding success (sampled from beta distribution with mean=0.4)	SD = 0.4	SD = 0.3	SD = 0.5
Fishery reductions, closures, or relocations	No increase in percentage of Chinook available to SRKW	3% increase	25% increase amplified by another 40% improvement in size over 50 years
Oil spill	None	Small: 1.08% frequency; 12.5% mortality Large: 0.21% frequency; 52% mortality	Small: 2.16% frequency Large: 0.42% frequency

Note that parameter ranges drawn from the literature are noted as such in the text; otherwise, ranges were provided by coauthors with subject-matter expertise as a first-order approximation of plausible values.

populations with low genetic diversity have continued to reproduce effectively[42].

The time scales needed to detect demographic effects of threats and benefits of mitigation might be too long in this species to be the primary metrics by which we gauge success (Fig. 4). Short-term benchmarks (e.g., body condition, growth rate, pregnancy, behavior, etc.) for measuring the success of mitigation measures are critical given the long lifespan, low reproductive rate, and small sample size in this population. In fact, Canada's Species At Risk Act outlines a recovery goal to: "ensure the long-term viability of Resident Killer Whale populations by achieving and maintaining demographic conditions that preserve their reproductive potential, genetic variation, and cultural continuity[43]." Environmental degradation may manifest in social network fragmentation and loss of cultural traditions (e.g., resting lines and greeting ceremonies) long before demographic effects become detectable against background fluctuations.

Marine species are no more or no less vulnerable than terrestrial counterparts to extinction[44]. Although indiscriminate exploitation and unintentional bycatch tend to be the dominant factors in decline and extinction of marine taxa, habitat loss is a close second[44]. Predicting when and how a species is likely to go extinct is extremely challenging, but it is a fundamental task of conservation science[45]. Without rich demographic data on wildlife populations, extinction risk due to habitat loss can be modeled in a species-area relationship framework. Species-area approaches can overestimate the proportion of habitat loss that would result in the removal of the last individual from a population. An inverse relationship has been found between species diversity and density, so protecting part of a species' range, without considering density, habitat use, or sampling effort, can lead to a false sense of confidence about population-level protection[46]. One study found a 53-year average lag between the time of the last sighting of a species and its reported extinction[44]. None of these statistical issues are at play for SRKW, in which clinically ill and lost animals are recognized through ongoing surveys and a census that is conducted annually.

Although wildlife censuses are rare in conservation biology, many seemingly irreversible and overt population declines are being witnessed in plain sight, even when the causes of these declines are well known. We use the term bright extinction to refer to data-rich cases where a decline toward extinction has been identified early, the driver(s) of the decline have been well quantified, but the population has declined to a precarious state nonetheless despite interventions. The loss of the baiji (Yangtze River dolphin, *Lipotes vexillifer*) illustrates the bright extinction concept well[7]. The species was extirpated from part of its range by the 1950s, and a precipitous decline in its core habitat was well documented between the 1980s and 1990s. In this case, the cause was attributed to fisheries-related mortality. By 2006, the population was declared functionally extinct. Proposals to create an ex situ or semi-natural reserve were made and ignored since the 1980s; perhaps policy-makers thought we had more time than we did[47]. A similar bright-extinction process appears to be underway for vaquita (*Phocoena sinus*) in the northern Gulf of California, Mexico[48]. The species has been declining since the 1990s due to unsustainable bycatch levels in fish and shrimp gillnet fisheries. Although the decline is well documented and the cause well understood, management actions have proven insufficient[49]. By 2018, only nine individuals were thought to be left[50]. Numbering in the low hundreds, North Atlantic right whales (*Eubalaena glacialis*) are also facing unsustainable levels of human-caused mortality due to vessel strikes and entanglement in fishing gear[51].

Importantly, these select examples represent cases where declines in small and highly vulnerable populations have been detected. The loss of each animal reduces the power to detect decreases in population abundance[52]. If we are unable to implement timely interventions of these high-profile species, what hope do we have for meeting our current and future biodiversity conservation objectives at large?

Preventing bright extinctions: from knowledge to action

Preventing extirpation of small populations may require extraordinary measures, but several populations of terrestrial and marine wildlife recovered from the brink of extinction offer a useful roadmap to ensure survival and recovery of SRKW.

The California condor (*Gymnogyps californianus*) was decimated to 27 individuals by 1987, from a combination of poaching, cyanide and lead poisoning, and habitat degradation. Captive breeding saved the population from extinction. Although infectious disease did not cause the initial decline, the US Fish and Wildlife Service has begun testing avian influenza vaccines in captive condors and considers capture and vaccination of wild condors in face of the ongoing multi-year epizootic[53]. Owing to declines in prairie dog (*Cynomys* sp.) (prey species) and their habitat, the black-footed ferret (*Mustela nigripes*) was once thought to be extinct; however, after the species was rediscovered in Wyoming in 1981, captive breeding and reintroductions, habitat protection, vaccination against canine distemper and cloning helped restore this species to over 300 free-ranging animals. Like SKRW, black-footed ferrets were largely dependent on a single prey species, prairie dogs. All of those conservation efforts for the black-footed ferret could be undone by a single outbreak of plague in their prey, necessitating management vigilance to prevent a disease outbreak[54]. By the time the whooping crane was listed as endangered in 1967, only 50 birds remained. Whooping cranes (*Grus americana*) remain one of North America's most threatened birds, but their recovery to an estimated 600 birds today is a testament to the progress that is made possible by acting decisively[55]. Mountain gorillas (*Gorilla beringei beringei*) were thought to be extinct by the end of the 20th century, but a large population now resides in protected forest in Uganda, Rwanda, and the Democratic Republic of the Congo[29]. Extreme vigilance in the form of veterinary monitoring and intervention is now needed to prevent backsliding and gorilla mortality[56]. Other populations brought back from the brink include black robin (*Petroica traversi*)[57] and the Eastern barred bandicoot (*Perameles gunnii*)[57]. In both cases, low levels of genetic diversity did not prevent recovery. Brazil's golden lion tamarin (*Leontopithecus rosalia*) was recovered from a few hundred individuals in the 1970s to about 3700 individuals in 2014 after actions were taken to restore habitat, re-establish connectivity via wildlife corridors, and release captive animals and conduct translocations among wild tamarins[58]. A yellow-fever epidemic in 2017–2018 reduced the population to about 2600 individuals, a decline that would have doomed the species had their habitat and population numbers not been previously recovered[58].

Meanwhile, as Caughley warned[1], many previously wide-ranging species have declined in plain sight. Boreal woodland caribou *(Rangifer tarandus caribou)* have been extirpated from vast sections of their range due to habitat loss and hunting, with few signs of success following recovery efforts[59]. Having failed to address those root causes, predation on calves now appears to be inhibiting population growth[60]. Karner blue butterfly (*Plebejus samuelis*) are dependent on the native sundial lupine, which has been eliminated from much of its range due to habitat loss and replacement in the northeast by *Lupinus polyphyllus*, a western species that has been introduced in the east. Conservation of Karner blue butterfly cannot be assured without aggressive measures to reduce ultimate population stressors and protect the microsites on which large fractions of the population depend[61]. Decades of warnings failed to prevent the functional extinction of northern white rhino (*Ceratotherium simum cottoni*) due to hunting and poaching, while conservation organizations and governments debated if, when, how, and who should act[62]. There is an ongoing debate whether radical proposals to clone the northern white rhino may come at the cost of urgently needed measures to prevent the extinction of southern white rhinos[63].

While many species have been brought back from the brink through interventions such as captive breeding programs, SRKW recovery will require aggressive actions to protect and restore their habitat, which includes mitigating effects to both SRKWs and their primary prey, Chinook salmon. Our analysis showed that the threat with the greatest impact to SRKW population growth is the availability of Chinook salmon (Fig. 3, Supplementary Fig. S20). Salmon recovery is a crucial component of achieving SRKW recovery. Although no salmon recovery scenario alone resulted in a fully recovered SRKW population, all of the successful multi-threat mitigation scenarios included some ambitious salmon recovery scenario.

Vessel noise can reduce the amount of time SRKWs spend foraging[18], but it can also have a direct impact on the behavior of prey species[64], limiting the number of salmon available to SRKWs. Efforts to mitigate impacts from vessel noise include a suite of approaches ranging from building quieter ships to designating slowdown areas[65]. Voluntary efforts to slow ships in important feeding areas for SRKWs has been shown to reduce noise levels by nearly half[66], which in turn results in increased foraging activity by killer whales[18]. While efforts are underway to reduce noise from existing ships, a number of development applications are underway that would increase shipping traffic in the region[67]. It may be necessary to consider ocean noise budgets, caps, or limits that allow killer whales to hunt scarce prey efficiently.

Protecting SRKWs appears to be impossible without restoring diminished populations of Chinook salmon, which in turn requires effective implementation of conservation and precautionary resource management measures. Implementation will require acknowledgement of the potential trade-offs involved between conservation and resource management, including harvest, and open dialog between involved agencies and stakeholders[24]. Both Canada and the USA have produced recovery plans and strategies for SRKW[43,68]. Those plans have recognized the need to ensure adequate prey sources for survival and recovery of SRKW since at least 2008. In a declining population, the longer the lag time between knowledge and mitigation, the more draconian the recovery actions can become, with a larger social cost, and a higher risk that harm reduction actions may not work[69,70]. Unfortunately, a legal species listing alone is insufficient to ensure survival and recovery of threatened taxa[63]. In the face of bright extinction, targeted threat reduction measures and community involvement, in addition to monitoring, are needed to reverse declines[71]. Yet the capacity to determine what we can do often outstrips our ability to decide what we will do; a dilemma that leads to delays in threat reduction measures and perpetuates extinction debt, especially in long-lived species[72].

Abundant examples, however, of successful rescues of plants, insects, and animals in aquatic, terrestrial, and aerial environments confirm that we can halt the loss of endangered wild species and that extraordinary measures can even recover critically imperiled ones. Unfortunately, these eleventh-hour rescues carry higher environmental and societal costs than earlier actions might have. Preventing extinctions of populations on the brink require a high degree of planning and coordination by scientists, managers, decision makers, stakeholders, and affected communities, and may require higher levels of threat reduction than would have been the case had actions been taken sooner. The benefits of species recovery may be difficult to define, both in terms of reversing global biodiversity loss and to the long-term resiliency and health of ecosystems. Rising to the challenge of biodiversity conservation requires robust data on species and threats, but also acting on those threats in a timely manner[73].

Methods

We used program Vortex 10.6.0 to parameterize a population viability analysis (PVA) model (software and manual available at scti.tools/vortex) for Southern Resident killer whales (SRKW)[20] with demographic rates observed over 1976 through 2022. We tested the sensitivity of population growth to variability and uncertainty in fecundity and survival rates (by age class), and prey-demography functional relationships[22,23]. Next, we constructed a PVA that explores population consequences of the three primary anthropogenic threats to SRKWs identified in Canadian and USA recovery plans, namely prey limitation (Chinook salmon), noise-mediated disruption of foraging, and effects of contaminants (e.g., PCBs).

We ran more speculative scenarios to consider the threat of not only PCBs, but also other POPs including legacy organochlorine pesticides (OCPs), pathways of effects of contaminants on calf survival[74,75], climate-mediated impacts of Chinook salmon on SRKW demography[22,23], climate- and fisheries-related declines in the size of Chinook salmon[76], and increased oil spill risk related to industrial development applications in the Salish Sea[67]. In addition to modeling population consequences of threats, efforts were made to model the likely population-level benefits of management measures intended to mitigate human-caused impacts to abundance and population structure from fisheries.

Addressing prey needs requires increasing the abundance of large, older Chinook. Increased abundance and quality of prey within SRKW critical habitat can be realized by changing fishing practices. Moving Pacific Salmon Treaty fisheries in Alaska and BC away from Chinook rearing grounds and migration routes into terminal river and estuarine locations results in an immediate increase of Chinook salmon in critical habitat of up to 25% (Supplementary Table S2). Secondly, transitioning marine fisheries to terminal (river-based) areas can recover a more archetypical Chinook age structure (early- mid 20th century). By not harvesting immature fish in marine fisheries, and then allowing large females to pass through terminal fisheries to spawning grounds, a size increase up to 40% can occur over a 50-year period. Scaling these scenarios to consider both improved value and abundance of mature Chinook salmon in critical habitat results in increases of 35%, 28%, 18%, and 9% at the end of 50 years, if scaled for effectiveness at 100%, 75%, 50%, and 25% (Supplementary Table S2). While not quantified, freshwater habitat restoration and protection would further support recovery of wild Chinook abundance.

The relative importance of each threat and mitigation opportunities were explored by projecting the population growth across the possible range of each threat. Finally, we used the PVA to explore the degree to which threats would have to be mitigated, alone or in combination, to stop the decline and achieve positive population growth toward recovery[68].

For the baseline model, parameters for fecundity and survival (for calves; subadults young, older, and post-reproductive adult females; young and older adult males) were estimated from 1976 to 2022 data (Table 1). Prey availability was drawn from the Chinook prey indexed to the mean from 1976 to 2022 (i.e., impacts scaled such that when Chinook = 1, demographic rates are the means over that time span). The prey-demography relationship of killer whale breeding rate and survival of each age class to the Chinook salmon index was drawn from a recent re-analysis[77]. Inputs for noise (disturbance) impacts and its effect on feeding were as in Lacy et al.[20]. We used the model from Hall et al.[74] for PCB accumulation and depuration parameters and the impact on calf survival was estimated through a comparison between a sympatric killer whale population, Northern Resident killer whales and SRKWs. A 1.75× factor was applied to our previously modeled population impact attributed to only PCBs to capture the contribution and associated risk of other POPs, including legacy OCPs. The factor was derived from a risk-based quotient for endocrine disruption for local harbor seals (*Phoca vitulina*)[27]. Inputs for variance in male breeding success were sampled from beta distribution (mean = SD = 0.40). Effects of inbreeding depression were set to 6.29 lethal equivalents per diploid, imposed via reduced calf survival.

Data availability

Please see additional technical details on methods and results in the Supplementary Notesfile. The data needed to replicate the model can be found on Zenodo at: Lacy, Robert C, & Williams, Rob. (2023). Vortex project file for PVA of Southern Resident Killer Whale — manuscript by Williams et al. (1.0) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.8099710.

Code availability

The Vortex code needed to replicate the model can also be found on Zenodo at: Lacy, Robert C, & Williams, Rob. (2023). Vortex project file for PVA of Southern Resident Killer Whale — manuscript by Williams et al. (1.0) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.8099710.

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References

1. Caughley, G. Directions in conservation biology. *J. Animal Ecol.* **63**, 215–244 (1994).

2. Sekar, N. & Shiller, D. Engage with animal welfare in conservation. *Science* **369**, 629–630 (2020).
3. Mace, G. M. et al. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biol.* **22**, 1424–1442 (2008).
4. Boehm, M. M. A. & Cronk, Q. C. B. Dark extinction: the problem of unknown historical extinctions. *Biol. Lett.* **17**, 20210007 (2021).
5. Drake, J. M. & Griffen, B. D. Early warning signals of extinction in deteriorating environments. *Nature* **467**, 456–459 (2010).
6. Taylor, B. L., Martinez, M., Gerrodette, T., Barlow, J. & Hrovat, Y. N. Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Sci.* **23**, 157–175 (2007).
7. Turvey, S. L. et al. First Human Caused Extinction of a Cetacean Species? *Biol. Lett.* **3**, 537–540 (2007).
8. Conde, D. A. et al. Data gaps and opportunities for comparative and conservation biology. *Proc. Natl Acad. Sci.* **116**, 9658–9664 (2019).
9. Sutherland, W. J., Pullin, A. S., Dolman, P. M. & Knight, T. M. The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305–308 (2004).
10. Kindsvater, H. K. et al. Overcoming the data crisis in biodiversity conservation. *Trends Ecol. Evol.* **33**, 676–688 (2018).
11. Ashe, E. et al. Minding the data-gap trap: exploring dynamics of abundant dolphin populations under uncertainty. *Front. Marine Sci.* **8**, 606932 (2021).
12. Serrouya, R. et al. Saving endangered species using adaptive management. *Proc. Natl Acad. Sci.* **116**, 6181–6186 (2019).
13. Barnosky, A. D. et al. Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
14. Kimmel, K., Clark, M. & Tilman, D. Impact of multiple small and persistent threats on extinction risk. *Conserv. Biol.* **36**, e13901 (2022).
15. Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. Biodiversity: The ravages of guns, nets and bulldozers. *Nature* **536**, 143–145 (2016).
16. CWR. *Southern Resident Orca (SRKW) Population*, https://www.whaleresearch.com/orca-population (2023).
17. Balcomb, K. C. & Bigg, M. A. in *Behavioral Biology of Killer Whales Zoo Biology Monographs* (eds B. C. Kirkevold & J. S. Lockard) 85-95 (Alan R. Liss Inc., 1986).
18. Williams, R. et al. Reducing vessel noise increases foraging in endangered killer whales. *Marine Pollut. Bull.* **173**, 112976 (2021).
19. Williams, R. et al. Destroying and restoring critical habitats of endangered killer whales. *Bioscience* **71**, 1117–1120 (2021).
20. Lacy, R. C. et al. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. *Sci. Rep.* **7**, 1–12 (2017).
21. Raverty, S. et al. Pathology findings and correlation with body condition index in stranded killer whales (*Orcinus orca*) in the northeastern Pacific and Hawaii from 2004 to 2013. *PloS One* **15**, e0242505 (2020).
22. Ford, J. K. B., Ellis, G. M., Olesiuk, P. F. & Balcomb, K. C. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biol. Lett.* **6**, 139–142 (2010).
23. Ward, E. J., Holmes, E. E. & Balcomb, K. C. Quantifying the effects of prey abundance on killer whale reproduction. *J. Appl. Ecol.* **46**, 632–640 (2009).
24. Linnell, J. D. C. et al. Confronting the costs and conflicts associated with biodiversity. *Animal Conserv.* **13**, 429–431 (2010).
25. Nelson, B. W., Ward, E. J., Linden, D. W., Ashe, E. & Williams, R. Identifying drivers of demographic rates in an at-risk population of marine mammals using integrated population models. *Ecosphere* **15**, e4773 (2024).
26. Kardos, M. et al. Inbreeding depression explains killer whale population dynamics. *Nat. Ecol. Evol.* **7**, 675–686 (2023).
27. Melbourne, B. A. & Hastings, A. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**, 100–103 (2008).
28. Clay, A. S. & Visseren-Hamakers, I. J. Individuals Matter: Dilemmas and Solutions in Conservation and Animal Welfare Practices in Zoos. *Animals* **12** https://doi.org/10.3390/ani12030398 (2022).
29. Robbins, M. M. et al. Extreme conservation leads to recovery of the Virunga mountain gorillas. *PloS One* **6**, e19788 (2011).
30. Sillero-Zubiri, C. et al. Feasibility and efficacy of oral rabies vaccine SAG2 in endangered Ethiopian wolves. *Vaccine* **34**, 4792–4798 (2016).
31. Harting, A. L., Johanos, T. C. & Littnan, C. L. Benefits derived from opportunistic survival-enhancing interventions for the Hawaiian monk seal: the silver BB paradigm. *Endangered Species Res.* **25**, 89–96 (2014).
32. Gulland, F. M. D. The role of nematode parasites in Soay sheep (*Ovis aries L.*) mortality during a population crash. *Parasitology* **105**, 493–503 (1992).
33. Gobush, K., Baker, J. & Gulland, F. Effectiveness of an antihelminthic treatment in improving the body condition and survival of Hawaiian monk seals. *Endangered Species Res.* **15**, 29–37 (2011).
34. Viana, M. et al. Dynamics of a morbillivirus at the domestic–wildlife interface: Canine distemper virus in domestic dogs and lions. *Proc. Natl Acad. Sci.* **112**, 1464–1469 (2015).
35. Northwest Area Committee. Northwest Area contingency plan. https://www.rrt10nwac.com/NWACP/Default.aspx (2020).
36. McHugh, K. A. et al. Staying alive: long-term success of bottlenose dolphin interventions in southwest Florida. *Front. Mar. Sci.* **7**, 1254 (2021).
37. Ross, P. S., Ellis, G. M., Ikonomou, M. G., Barrett-Lennard, L. G. & Addison, R. F. High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: effects of age, sex and dietary preference. *Marine Pollut. Bull.* **40**, 504–515 (2000).
38. Hickie, B. E., Ross, P. S., Macdonald, R. W. & Ford, J. K. B. Killer whales (*Orcinus orca*) face protracted health risks associated with lifetime exposure to PCBs. *Environ.Science & Technology* **41**, 6613–6619 (2007).
39. Mos, L., Cameron, M., Jeffries, S. J., Koop, B. F. & Ross, P. S. Risk-based analysis of polychlorinated biphenyl toxicity in harbor seals. *Integrated Environ. Assess. Manag.* **6**, 631–640 (2010).
40. Ross, P. S. et al. Ten guiding principles for the delineation of priority habitat for endangered small cetaceans. *Marine Policy* **35**, 483–488 (2011).
41. Braulik, G. T. et al. Red-list status and extinction risk of the world's whales, dolphins, and porpoises. *Conserv. Biol.* 37(5), e14090 (2023).
42. Morin, P. A. et al. Reference genome and demographic history of the most endangered marine mammal, the vaquita. *Mol. Ecol. Resour.* **21**, 1008–1020 (2021).
43. Fisheries and Oceans Canada. *Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada.* Species at Risk Act Recovery Strategy Series (Fisheries and Oceans Canada, 2018).
44. Dulvy, N. K., Sadovy, Y. & Reynolds, J. D. Extinction vulnerability in marine populations. *Fish and fisheries* **4**, 25–64 (2003).
45. Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. Predicting extinction risk in declining species. *Proceedings of the royal society of London*. *Ser. B Biol. Sci.* **267**, 1947–1952 (2000).
46. Williams, R. et al. Prioritizing global marine mammal habitats using density maps in place of range maps. *Ecography* **37**, 212–220 (2014).
47. Chen, P. & Hua, Y. in *Biology and Conservation of the River Dolphins* (eds Perrin, W. F., Brownell, Jr. R. L., Kaiya, Z. & Jiankang, L.) 81–85 (IUCN, 1989).
48. Rojas-Bracho, L., Reeves, R. R. & Jaramillo-Legorreta, A. Conservation of the vaquita *Phocoena sinus*. *Mammal Rev.* **36**, 179–216 (2006).

49. Rojas-Bracho, L. & Reeves, R. R. Vaquitas and gillnets: Mexico's ultimate cetacean conservation challenge. *Endangered Species Res.* **21**, 77–87 (2013).
50. Jaramillo-Legorreta, A. M. et al. Decline towards extinction of Mexico's vaquita porpoise (*Phocoena sinus*). *R. Soc. Open Sci.* **6**, 190598 (2019).
51. Pace, R. M., Corkeron, P. J. & Kraus, S. D. State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecol. Evol.* **7**, 8730–8741 (2017).
52. Taylor, B. L. & Gerrodette, T. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conserv. Biol.* **7**, 489–500 (1993).
53. Kozlov, M. US will vaccinate birds against avian flu for first time—what researchers think. *Nature* **618**, 220–221 (2023).
54. May, R. M. Species conservation: The cautionary tale of the black-footed ferret. *Nature* **320**, 13–14 (1986).
55. Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P. & Fagan, W. F. Social learning of migratory performance. *Science* **341**, 999–1002 (2013).
56. Zimmerman, D. M. et al. Projecting the impact of an ebola virus outbreak on endangered mountain gorillas. *Sci. Rep.* **13**, 5675 (2023).
57. Ardern, S. & Lambert, D. Is the black robin in genetic peril? *Mol. Ecol.* **6**, 21–28 (1997).
58. Ruiz-Miranda, C. R. et al. Estimating population sizes to evaluate progress in conservation of endangered golden lion tamarins (*Leontopithecus rosalia*). *Plos One* **14**, e0216664 (2019).
59. McLoughlin, P. D., Dzus, E., Wynes, B. O. B. & Boutin, S. Declines in populations of woodland caribou. *J. Wildlife Manag.* **67**, 755–761 (2003).
60. Levy, S. The new top dog. *Nature* **485**, 296 (2012).
61. Delach, A. et al. Agency plans are inadequate to conserve US endangered species under climate change. *Nat. Clim. Change* **9**, 999–1004 (2019).
62. Hillman-Smith, K., ma Oyisenzoo M., & Smith, F. A last chance to save the northern white rhino? *Oryx* **20**, 20–26 (1986).
63. Callaway, E. Geneticists aim to save rare rhino. *Nature* **533**, 20–21 (2016).
64. van der Knaap, I. et al. Behavioural responses of wild Pacific salmon and herring to boat noise. *Mar Pollut Bull* **174**, 113257 (2022).
65. Williams, R., Veirs, S., Veirs, V., Ashe, E. & Mastick, N. Approaches to reduce noise from ships operating in important killer whale habitats. *Marine Pollut. Bull.* **139**, 459–469 (2019).
66. Joy, R. et al. Potential benefits of vessel slowdowns on endangered southern resident killer whales. *Front. Marine Sci.* **6**, 344 (2019).
67. Gaydos, J. K., Thixton, S. & Donatuto, J. Evaluating Threats in Multinational Marine Ecosystems: A Coast Salish First Nations and Tribal Perspective. *PLoS One* **10**, e0144861 (2015).
68. National Marine Fisheries Service. Recovery Plan for Southern Resident Killer Whales (*Orcinus orca*). 251 (National Marine Fisheries Service, Northwest Region, Seattle, WA, USA, 2008).
69. Gerber, L. R. Conservation triage or injurious neglect in endangered species recovery. *Proc. Natl Acad. Sci.* **113**, 3563–3566 (2016).
70. Martin, T. G. et al. Acting fast helps avoid extinction. *Nature* **5**, 274–280 (2012).
71. Jaramillo-Legorreta, A. et al. Saving the Vaquita: Immediate Action, Not More Data. *Conserv. Biol.* **21**, 1653–1655 (2007).
72. Kuussaari, M. et al. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571 (2009).
73. Nature. Is a single target the best way to cut biodiversity loss? *Nature* **583**, 7 (2020).
74. Hall, A. J. et al. Individual-Based Model Framework to Assess Population Consequences of Polychlorinated Biphenyl Exposure in Bottlenose Dolphins. *Environ. Health Perspect.* **114**, 60–64 (2006).
75. Hall, A. J. et al. Predicting the effects of polychlorinated biphenyls on cetacean populations through impacts on immunity and calf survival. *Environ. Pollut.* **233**, 407–418 (2018).
76. Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L. & Zabel, R. W. Climate change threatens Chinook salmon throughout their life cycle. *Commun. Biol.* **4**, 222 (2021).
77. Nelson, B. W. Ecosphere-SRKW-modeling. github https://github.com/benjaminnelson/Ecosphere-SRKW-modeling (2023).

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Author contributions

R.W. conceived of the study, coordinated the project, and contributed to writing. R.C.L. conceived of the study, performed all statistical modeling with custom code, and contributed to writing and editing. E.A. conceived of the study and contributed to writing. L.B.L. contributed to writing. T.M.B. contributed to writing. J.K.G. contributed to writing and editing. F.G. contributed to writing. M.M. contributed to writing and editing. B.W.N. parameterized the prey-demography part of the model. K.A.N. generated figures and contributed to writing and editing. H.N. contributed to writing, particularly related to veterinary interventions. S.Raverty contributed to writing. S.Reiss assisted with project coordination. P.S.R. contributed to writing, particularly related to prey impacts. M.S.C. generated figures and contributed to writing and editing. R.S. contributed to writing. P.P. contributed to writing and editing.

Competing interests

The authors declare no competing interests.

Additional information

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