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Received: 21 December 2019 | Revised: 24 April 2020 | Accepted: 9 May 2020

DOI: 10.1111/ddi.13109

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Translocation with targeted vaccination is the most effective strategy to protect an island endemic bird threatened by West Nile virus

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Funding information
The Nature Conservancy; Smithsonian Institution; U.S. National Science Foundation, Grant/Award Number: 1754821

Abstract

Aim: Invasive pathogens are a growing conservation challenge and often occur in tandem with rapid environmental transformation, such as climate change, drought and habitat loss. Climate change appears to have facilitated the spread of West Nile virus (WNV), a cause of widespread avian mortality. WNV is considered the primary threat to island scrub-jays (*Aphelocoma insularis*), endemic to Santa Cruz Island, California. Two approaches have been proposed to safeguard island scrub-jays: (a) vaccination and (b) conservation translocation to re-establish a second population on neighbouring Santa Rosa Island, hypothesized to have a lower risk of WNV. These alternatives operate at regional scales but exemplify global concerns with strategic implications for conservation biogeography and climate adaptation.

Location: California Channel Islands, USA.

Methods: We compared the efficacy of vaccination and translocation strategies at minimizing 25-year quasi-extinction risk for island scrub-jays using a stochastic population model.

Results: Under current WNV-free conditions, the predicted quasi-extinction risk for island scrub-jays was low (~0%) but increased to ≥22% with simulated WNV outbreaks. Vaccinating ≥60 individuals reduced risk to <5%, but risk doubled if population size declined and further increased with more frequent droughts. Translocation performed best if Santa Rosa Island had a large starting population size and habitat extent, and, more importantly, a low risk of WNV establishment; if Santa Rosa Island was inhospitable to WNV, quasi-extinction risk dropped to near zero.

Main conclusions: Translocation with targeted vaccination during high-risk conditions was the most effective strategy to protect island scrub-jays from West Nile virus. Although vaccination often outperformed translocation, only scenarios that included a Santa Rosa population and vaccinations achieved acceptably low species-wide extinction risk across all potential future conditions. Our analysis informs strategies to improve the long-term viability of the most range-restricted bird species in the continental United States and provides a model for assessing conservation-translocation proposals for other species and threats.

KEYWORDS

Aphelocoma insularis, California Channel Islands, conservation translocation, invasive pathogens, population viability, vaccination, West Nile virus

1 | INTRODUCTION

Invasive pathogens threaten the viability of wildlife populations and represent a growing conservation challenge (Daszak, Cunningham, & Hyatt, 2000). Recent examples include the endangerment of island fox (*Urocyon littoralis*) from canine distemper (Timm et al., 2009), widespread declines in North American avifauna linked to West Nile virus (WNV, LaDeau, Kilpatrick, & Marra, 2007), and declines and extinctions of endemic Hawaiian honeycreepers caused by avian malaria (Liao, Atkinson, LaPointe, & Samuel, 2017). Epizootics often occur in tandem with rapid environmental change, such as habitat alteration, drought and climate change (Harvell et al., 2002; Liao et al., 2017). Management strategies must be designed to reduce threats from the interacting effects of disease and environmental transformation, particularly for small, isolated populations that cannot shift their ranges in response to changing conditions (Atkinson et al., 2014; Fortini, Vorsino, Amidon, Paxton, & Jacobi, 2015).

The island scrub-jay (*Aphelocoma insularis*), a single-island endemic passerine, presents a case study for designing management strategies to reduce the extinction risk of species confronted by invasive pathogens and environmental change. Restricted to the 250-km^2 Santa Cruz Island, California in Channel Islands National Park, recent surveys estimated its spring population size at just ~1,700 individuals (Sillett, Chandler, Royle, Kéry, & Morrison, 2012). Although the island scrub-jay is not currently listed as threatened or endangered by U.S. state or Federal agencies, the potential for novel threats linked to disease and climate change has sparked increased conservation concern (BirdLife International, 2012; Morrison et al., 2011). WNV is considered the principal near-term threat to the jay's viability (Boyce et al., 2011). Additionally, the recent extended drought in California appears to have caused widespread reproductive failures for island scrub-jays. Climate change is predicted to increase drought frequency and weather extremes in California (Diffenbaugh, Swain, & Touma, 2015; Swain, Langenbrunner, Neelin, & Hall, 2018), and direct climate stressors could interact with indirect climate-related disease threats.

To reduce the extinction risk associated with WNV, managers initially vaccinated a subset of the island scrub-jay population proactively (Boyce et al., 2011), a strategy predicted to offer substantial protection from disease for other species (Doak, Bakker, & Vickers, 2013). However, for several reasons, this strategy may not be feasible for island scrub-jays in the long term. Jays are time-consuming to capture and challenging to recapture for boosters. The preferred vaccine, a DNA plasmid vaccine, is currently unavailable, while the second choice, a commercially available vaccine (Merial Recombitek® WNV equine vaccine), is manufactured with a canary pox adjuvant that may pose risks to island avifauna and challenge trials produced necrotic lesions at the site of injection in congeners (*A. californica*, California scrub-jay, Wheeler et al., 2011). Finally, vaccine efficacy based on trials in *A. californica* is assumed but not proven for island scrub-jay; species-specific challenge trials have not been conducted.

A second strategy proposed to reduce WNV-associated extinction risk is conservation translocation (Seddon, 2010) to re-establish a second population of island scrub-jays on 215-km^2 Santa Rosa Island, where jays once occurred (see below), located ~7 km west of Santa Cruz Island, a distance apparently too far for unaided dispersal (Morrison, 2014; Morrison et al., 2011). Safeguarding island scrub-jays by establishing a second population on Santa Rosa Island would require that the fates of each population not be perfectly correlated, such that one persists when a catastrophe or string of bad years afflicts the other. Indeed, spatial and temporal variation is hypothesized to be the key factor mitigating WNV effects on bird populations (Kilpatrick & Wheeler, 2019). Santa Rosa Island may also have a lower risk of WNV establishment because it is further from the mainland, has a somewhat cooler climate due to a different marine setting (Morrison et al., 2011) and appears to have less standing water and lower mosquito diversity (Spadoni, Miles, & Hayes, 1973). The conservation translocation strategy follows recommendations from scientists and managers to proactively combat climate-related threats by expanding the current geographic ranges of vulnerable endemics (Corlett, 2016; Hoegh-Guldberg et al., 2008). However, few quantitative analyses of concrete proposals exist to predict the extinction risk reduction associated with translocations compared to alternative approaches (Taylor et al., 2017).

We used a population viability management approach (Bakker & Doak, 2009) to develop a stochastic population model for island scrub-jays and estimated extinction risk for a range of scenarios involving vaccination and translocation. First, we built a demographic description for the island scrub-jay population on Santa Cruz Island and for a hypothetical population on Santa Rosa Island. Next, we used this two-population model to evaluate the viability implications of an avian epizootic such as WNV. Finally, we assessed the predicted extinction risk for alternative disease management strategies under different scenarios of disease dynamics, drought and habitat change.

2 | METHODS

2.1 | Study system and disease threat

Island scrub-jay pairs are territorial with a socially monogamous breeding system (Curry & Delaney, 2002). Approximately half of the adult population is non-breeding "floaters" (Sillett et al., 2012) that have overlapping home ranges and are generally tolerated by territorial pairs outside the breeding season. Jays mature reproductively in their second year, but typically take 3–7 years to recruit into the breeding population (Curry & Delaney, 2002; Desrosiers, 2013). The oldest known island scrub-jay was >16 years old (unpublished results).

Island scrub-jays have been isolated on the northern Channel Islands for ≥500,000 years (McCormack, Heled, Delaney, Peterson, & Knowles, 2011), which includes a lengthy period when sea levels were lower and the northern Channel Island archipelago formed a contiguous land mass. Multiple lines of evidence suggest jays may have been extirpated from Santa Rosa in the late 1800s due to habitat loss and other direct and indirect impacts of intensive sheep ranching (Collins, Guthrie, Whistlers, Vellanoweth, & Erlandson, 2018; Morrison, 2014). Introduced ungulates were eradicated on Santa Rosa Island by 2012. On Santa Cruz Island, island scrub-jays depend on oak, chaparral and pine habitats (Figure 1, see Caldwell et al., 2013; Langin et al., 2015). Seed-caching by island scrub-jays has accelerated recovery of these habitats on Santa Cruz Island and would on Santa Rosa Island as well (Pesendorfer et al., 2018).

The island scrub-jay is expected to be both highly susceptible to WNV, like other corvids (Foss et al., 2015), and immunologically naïve because of its isolation and small population size (Boyce et al., 2011), implying extreme vulnerability to WNV and other invasive arboviruses. Surveillance indicates that WNV has not yet established on

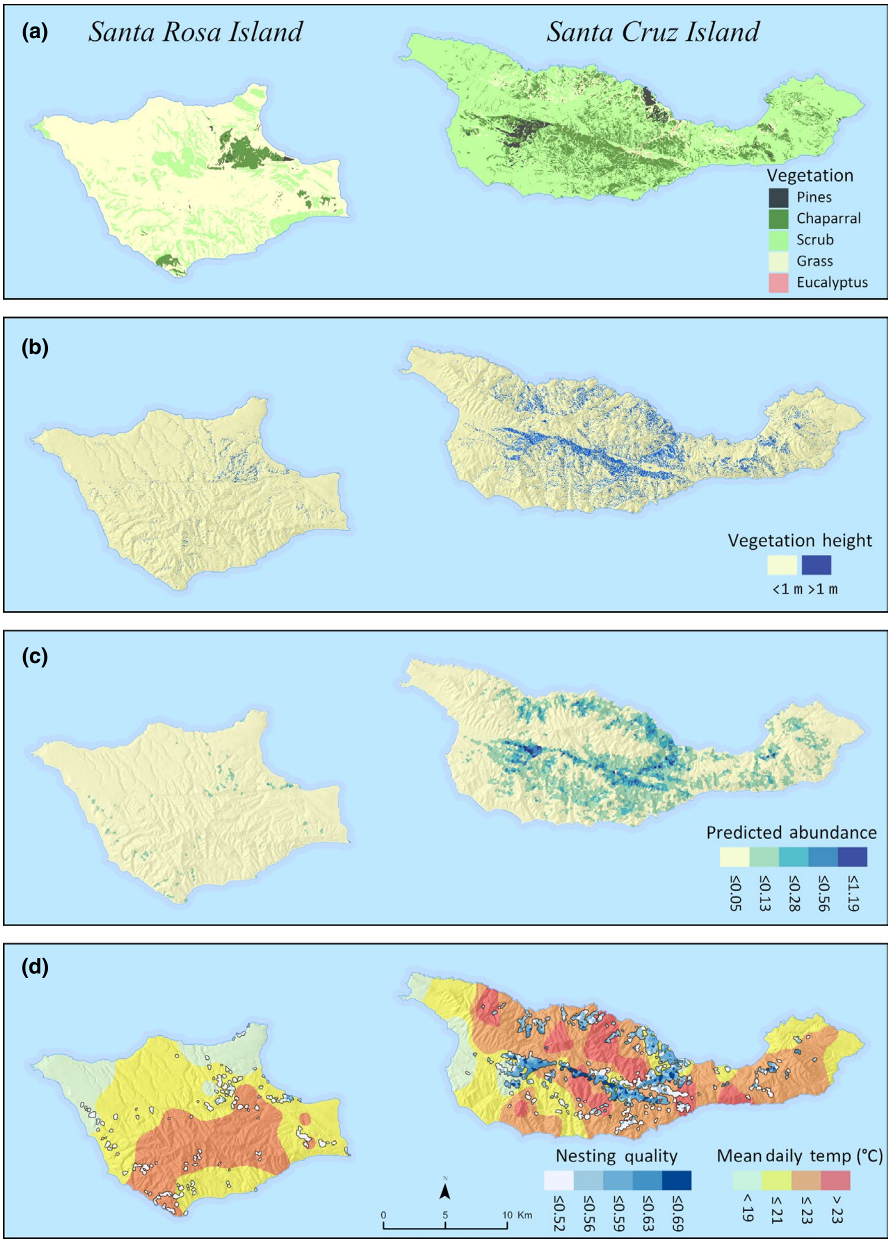

FIGURE 1 Santa Rosa and Santa Cruz islands, located ~30 km off the coast of southern California, USA. Shown are (a) vegetation types, (b) vegetation height, (c) predicted abundance of island scrub-jays in simulated territories (individuals/ha) and (d) nesting quality in simulated breeding territories (displayed as nest success for nests initiated at the start of the breeding season) with temperature zones used to simulated West Nile virus exposure (see Figure 2)

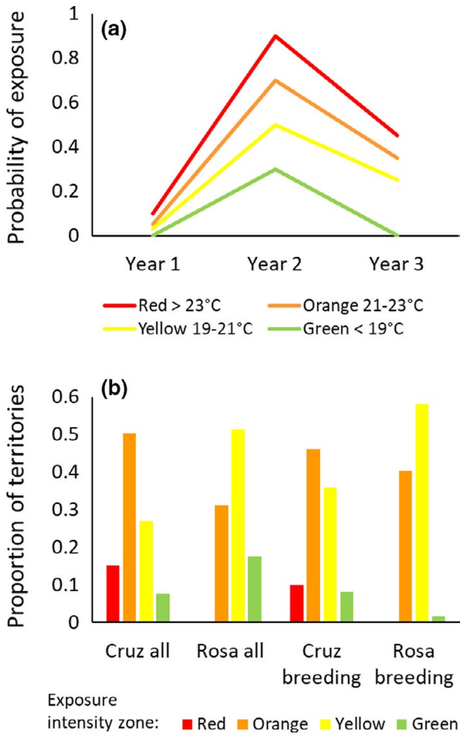

FIGURE 2 Temperature-based simulation of West Nile virus exposure on Santa Cruz and Santa Rosa islands. (a) Probability of West Nile virus exposure during three-year outbreaks for different temperature-defined exposure zones, and (b) proportions of all territories and breeding territories occurring in each temperature zone. See Figure 1 for map of territories and temperature zones

Santa Cruz Island, despite several resident mosquito species competent to host the virus (Boyce et al., 2011; Spadoni et al., 1973). WNV is present on the California mainland (Reisen et al., 2004), ~30 km away and avian hosts such as migratory passerines and seabirds regularly fly from the mainland to the Channel Islands.

Warmer temperatures appear to facilitate the spread and maintenance of WNV (Paz, 2015). North American outbreaks are more common when mean August air temperatures are ≥23°C (Wheeler et al., 2009), and the virus replicates most efficiently at >22°C (Reisen, Fang, & Martinez, 2006). Island-wide data suggest that during the warmest summers, temperatures reach this threshold on Santa Cruz Island and approach it on Santa Rosa Island (Figure 1d). Climate warming is expected to make coastal southern California increasingly hospitable to arthropod vectors of disease, including those of WNV (Paz, 2015).

2.2 | Temperature and habitat mapping

Temperature data collected at 95 data loggers across Santa Cruz and Santa Rosa islands from April 2009 to September 2010 were used to map isoclines of average temperatures for August and September to guide scenarios of virus transmission (Tercek, 2012). We quantified habitat using GIS layers and a canopy height model (Khosravipour, Skidmore, Isenburg, Wang, & Hussin, 2014) derived from raw March 2010 LiDAR returns (https://coast.noaa.gov/htdata/lidar1_z/geoid12a/data/1398/) using LAStools (Isenburg, 2014).

2.3 | Habitat and abundance

We developed a statistical model of habitat-specific abundance during the breeding season from hierarchical distance sampling at 307 random points on Santa Cruz Island in April 2009 (Sillett et al., 2012) and used it to estimate island scrub-jay distribution and abundance on Santa Rosa Island based on its current habitat. The best abundance model on Santa Cruz Island from Sillett et al., (2012) included chaparral and elevation but that study was not designed to evaluate canopy height. We added canopy height to the island scrub-jay abundance model for Santa Cruz Island (Supplement 1) to ensure greater applicability to Santa Rosa Island, which contains substantial areas of windswept low-stature (<1 m) scrub chaparral assumed to be suboptimal island scrub-jay habitat.

2.4 | Demographic analyses

Reproductive rates were derived from 2,740 observations of 453 nests on 107 territories during the 2008–2012 breeding seasons. We used generalized linear mixed models to assess whether habitat, weather and seasonal timing predicted three components of the reproductive rate: daily nest survival, egg-to-fledge survival and renesting probability. We also considered both territory and year as random effects in these models (Supplement 1). We used the proportion of occupied territories that fledged young to quantify the effects of the 2012–2014 drought on productivity (Supplement 1).

We estimated survival rates for adults and fall hatch-year birds from monthly resighting data collected from 2008 to 2013. We used Cormack-Jolly-Seber models in program MARK (version 7.1), considering age, sex, breeder status, year, season and capture month as predictors (Supplement 1). We did not consider weather or habitat as predictors of survival because we did not have habitat data for all marked individuals, our resighting data only spanned the early part of the drought, and as a long-lived, resource-hoarding bird, the jay's natural history suggests resilience to such factors over the relatively short span of our data. Because nestlings were not marked, we used surrogate data from congeneric Florida scrub-jays (*A. coerulescens*) to estimate a single time- and habitat-constant survival of the four-month neonatal period from fledging to first fall (Woolfenden & Fitzpatrick, 1991).

We estimated uncertainty in all rates and incorporated it into simulation models. We included parameter uncertainty in covariate models by drawing random parameter sets for each simulated population trajectory from appropriate distributions and adding unexplained stochastic annual variance (Bakker et al., 2009). Although we used habitat-specific reproductive rates derived from Santa Cruz Island to simulate island-wide spatial variance in reproduction on both Santa Cruz and Santa Rosa islands, we were unable to quantify inter-island or within-island site-specific variation in demographic rates due to other effects. Our predictions for Santa Rosa Island do not account for these potentially important sources of uncertainty.

2.5 | Overview of conservation management scenarios

We sought to characterize local and global extinction risk of island scrub-jays under interacting scenarios of disease, habitat and climatic conditions, coupled with proactive and reactive management interventions. We examined the baseline scenario of no management and estimated island scrub-jay viability on Santa Cruz Island with and without WNV under a range of starting population sizes and with and without increased drought frequency. We then examined the effect of a second island scrub-jay population on Santa Rosa Island across a range of initial sizes, with and without WNV, drought and active management of the created metapopulation (i.e. translocating individuals among islands to rescue a population in decline, Supplement 2, Figure S2.2). Finally, we examined two vaccination strategies: proactive vaccination of a population subset, and reactive vaccination in response to an observed disease outbreak. We explored a range of starting population sizes for both islands to assess the robustness of one versus two island systems in a variety of potential future conditions, including high-risk conditions in which the Santa Cruz Island jay population declines due to drought or other factors. We did not cap the total population at the current size of the source population when initializing two-island simulations, but instead assumed that the two-island system might well be established prior to WNV introduction and thus population sizes on each island could range from low to high, depending on the timing of translocations and WNV introductions as well as droughts, other threats and stochastic variance. However, we did explore scenarios simulating metapopulation management of established two-island systems in which one island population is a source to rescue the other, and these scenarios do account for the effect of removals on the source population size. We did not account for potential added mortality for translocated individuals because suitable data are not available to estimate this. The severity of WNV outbreaks appears to moderate over time (Reed et al., 2009), so our principal concern was ensuring island scrub-jays persist over a relatively short time-frame; thus we examined viability over 25 years. We set a quasi-extinction threshold of 30 birds and summarized extinction risk and population sizes for 1,000 replicate trajectories for each scenario. We also evaluated the relationship between population sizes and vaccination levels and risk of extinction using logistic regression (see Supplement 3 for methods).

2.6 | Population structure, simulation methods and scenario details

Survival varied by age and breeder status as well as year and season. To reflect these differences, we based simulations on a female-only, stage-based stochastic demographic matrix model, ages 0 to 16, with demographic rates constant for individuals ≥16 (Supplement 2). Although we had inadequate data to detect senescence in our survival analyses, we assumed an annual decline in survival of 2% starting at age 10, based on rates reported for Florida scrub-jays (McDonald, Fitzpatrick, & Woolfenden, 1996). The proportion of the observed population ≥10 was 0.9% (Supplement 1), and thus, we did not adjust mean survival to account for discounting of older survival. Other state variables included breeding status (breeder/nonbreeder) and WNV susceptibility (susceptible/immune). Age-specific recruitment rates were estimated from Corey (1994).

To take advantage of substantial data on the effects of habitat on reproduction, the first row of the matrix (i.e. reproduction) was replaced with the output of simulations of habitat-driven reproduction (Supplement 2). The procedure we used assumes that jays will generally, but imperfectly, choose territories with higher past occupancy and higher habitat quality. For each simulation, we used one of three sets of random territories drawn across both islands using Delaunay triangles sized to match the mean observed size of breeding territories (Figure 1, Caldwell et al., 2013). For each set of territory definitions, we restricted the pool of potential territories to the 20% on Santa Cruz Island and the 10% on Santa Rosa Island (~1,400 of 7,200 and ~600 of 6,000 territories, respectively, Figure 1) for which habitat-based models predicted the highest abundances of island scrub-jay during the breeding season. Breeding pairs were then assigned randomly to one of these possible territories, the habitat characteristics of which influenced reproductive parameters.

All individuals had the potential to recruit into the breeding population, but opportunities were limited by available breeding habitat. We assumed breeding habitat on Santa Cruz Island was saturated at the time of the most recent survey (Sillett et al., 2012) and set carrying capacity for breeders as the number of breeders expected at the stable age distribution for the estimated population size at that time. Likewise, on Santa Rosa Island, we set the capacity of breeding habitat based on the estimated total number of individuals the habitat could sustain and the proportion that would be breeders. We included annual variance in the habitat capacity for breeders assuming a coefficient of variation drawn from a uniform distribution (0–0.1). Overall carrying capacity on both islands was set at 1.5 times these population sizes. To assess the effects of habitat restoration on Santa Rosa Island, we considered scenarios in which the number of breeding territories on that island doubles.

For each annual cycle, we simulated reproduction by re-assigning breeders to simulated territories randomly and iterated daily reproductive rates based on the habitat in territories, with demographic stochasticity in adult survival, daily nest survival, egg-to-fledge survival and renesting probability. Stochastic variance was incorporated by simulating annual process variance in survival and random spatial and temporal effects in reproductive rates, as well as catastrophic drought effects on nest success; due to data limitations, we were unable to estimate or include temporal correlations in survival and reproductive variations. Drought effects were simulated based on random annual rainfall across the region and increased drought was simulated by modest changes in the mean (−10%) and variance (+20%) of annual rainfall (Supplement 1).

2.7 | Disease and vaccination models

We simulated the temporal dynamics of WNV outbreaks on the Channel Islands based on WNV dynamics observed in southern California (Kwan, Kluh, Madon, & Reisen, 2010, see also Supplement 4). We introduced WNV at an annual probability of 0.3, approximately half the apparent frequency of recurrence on the mainland. Epizootics were modelled to last 3 years followed by 2 years in which WNV could not recur. The predicted temperature in simulated territories determined the probability of breeder exposure, with non-breeders distributed across temperature zones proportional to breeders (Figures 1d and 2, Supplements 2 and 4). The probability of WNV introductions on Santa Rosa Island was equal to that of Santa Cruz Island (P_{epi} = 0.3), or half that (P_{epi} = 0.15), or zero (P_{epi} = 0), with two inter-island correlations in introductions: zero and 100%. Because we sought to simulate reasonably anticipated worst-case scenarios over the next 25 years, we based our spatial pattern of WNV exposure on the warmer of the two monitored summers (i.e. 2009, Tercek, 2012).

As immunologically naïve corvids, exposed individuals were assumed to have a very high probability of mortality (>60%–83% mortality for experimentally infected western scrub-jays, Wheeler et al., 2009; Wheeler et al., 2011). We assumed 100% mortality for most scenarios but ran a subset in which the lethality of WNV diminished (Reed et al., 2009), dropping to 70% mortality after the second outbreak, with exposed survivors acquiring future immunity. Mortality occurred in fall after reproduction and was constant across age classes.

To manage WNV, we simulated vaccination of 30, 60 or 90 birds. For reactive vaccination, we simulated lags of 1 or 2 years after outbreak initiation, assuming WNV would not be reliably detected on the island in its first year when exposure is low (≤0.1 in high exposure zones, 0 in low exposure zones). We assumed vaccine efficacy was 87.5% based on California scrub-jay challenge trials (Wheeler et al., 2011). We simulated random vaccination with respect to age and location. To reflect potential difficulty detecting and capturing the required number of individuals to vaccinate, we simulated two island-wide surveys with a detection probability of 0.37 per survey (Sillett et al., 2012) and a capture probability of 0.95 (unpublished results).

3 | RESULTS

3.1 | Temperature, habitat and abundance

Population estimates and thermal regimes differed between islands. The estimated spring island scrub-jay population size on Santa Cruz Island with canopy height included into the hierarchical abundance model was 1803 (Supplement 1). Based on this estimate and our demographic model, habitat capacity for breeders was set at 515 pairs. On Santa Rosa Island, we estimated the available habitat could sustain 453 individuals and 129 breeding pairs. Mean temperatures (Figure 1d) exceeded 23°C in the warmest parts of Santa Cruz Island in August and September in both monitored years (Tercek, 2012). Santa Rosa Island was somewhat cooler, with none of the island exceeding 23°C.

3.2 | Demographic rates

Reproductive parameters were conditional on habitat and temporal factors (Supplement 1). High daily nest survival and egg-to-fledge survival were best predicted by extensive tall canopy or chaparral cover, fewer days into the breeding season and fewer nest observations (Caldwell et al., 2013). High renesting probability was best predicted by a failed current attempt, with tall canopy important as the breeding season progressed. Mean days from first egg to fledging were 45.3 (±2.8 *SD*), and mean days between nest attempts were 10.5 (±6.3 *SD*). Clutch size averaged 3.6 (range 1–5). Egg sex ratio was assumed 0.5. Simulated island-wide nest success was ~15%–20% higher than the mean observed at three study sites in Caldwell et al. (2013) after correction for observer effects. Both 2013 and 2014 were considered drought years, and the number and success of nesting attempts declined sharply, with numbers of fledges per nest equalling 10% of non-drought years (Supplement 1).

Survival varied by breeder status, year, season, first month of observation (i.e. transient effect), and age (Supplement 1). Breeders and birds under age 3 experienced higher survival. In average years, survival of younger breeders and non-breeders was 0.967 (±0.019 *SE*) and 0.859 (±0.041 *SE*) respectively, whereas survival of older breeders and non-breeders was 0.908 (±0.031 *SE*) and 0.729 (±0.060 *SE*), which is consistent with the mean breeder survival of 0.935 (±0.04 *SE*) reported by Atwood, Elpers, and Collins (1990) for 651 colour-banded jays from 1975 to 1985. Because a telemetry study of 60 yearlings over 3 years found the six-month survival probability from first fall to subsequent spring was 0.9–0.95 (T. S. Sillett, pers comm.), consistent with our young breeder annual survival, we assumed that the hatch-year effect indicating lower survival in the first winter was due to emigration.

3.3 | Population simulations

Under current conditions, simulated island scrub-jay populations on Santa Cruz and Santa Rosa islands were safe from 25-year quasi-extinction risk at initial population sizes >200 (Figure 3a). Populations on Santa Rosa Island were predicted to grow rapidly (mean stochastic lambda for extant population trajectories = 1.09). The median trajectory for a starting population of 50 reached 200 in 13 years and 400 in 20 years (Supplement 3, Figure S3.1).

Increased drought frequency and the introduction of WNV elevated extinction risk (Figures 3 and S3.2). Annual probability of drought when simulating observed rainfall was 0.09; increasing variance and decreasing mean rainfall increased drought probability to 0.17, which reduced island scrub-jay viability, especially when starting population sizes were low (risk increased 3%–4%, Supplement 3). Extinction risk rose substantially with introductions of WNV. Assuming high disease introduction probabilities, 25-year quasi-extinction risk on Santa Cruz Island under other parameter combinations was always ≥35% at population sizes ≤600 and ~22% at population sizes of 1,200 (Figure 3a). WNV-associated extinction risk was lower on Santa Rosa than Santa Cruz island at population sizes <600, presumably due to cooler temperatures in simulated breeding territories. Because carrying capacity is ~450 on Santa Rosa Island, extinction risk rapidly plateaued (Figure 3a). An island scrub-jay population on Santa Rosa Island reduced species-wide extinction risk by up to 14% even with high and correlated WNV introduction probabilities (Figure 3a, up to 20% with uncorrelated WNV introductions, Figure S3.2d). Inter-island transfers reduced extinction risk on each island but did not decrease species-wide risk (Figure S3.2b). When WNV established in the system, extant populations stabilized at much lower sizes than in a disease-free system (Figure S3.3).

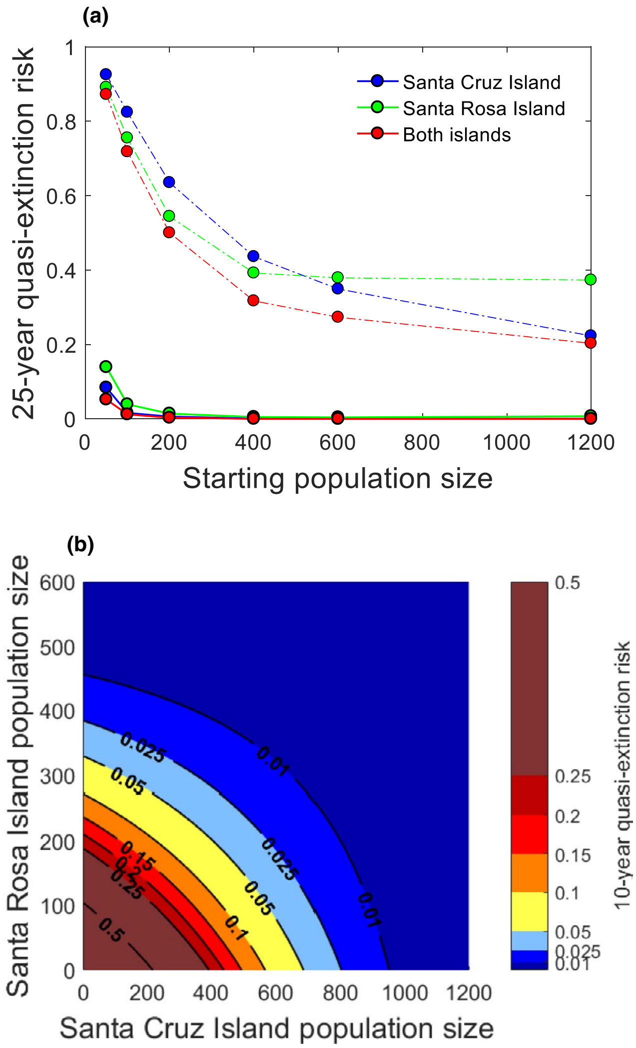

FIGURE 3 Extinction risk predictions for island scrub-jay on Santa Cruz Island, Santa Rosa Island and both islands for a range of population sizes. (a) Predicted 25-year quasi-extinction risk for a range of starting population sizes with (dotted) and without (solid) ongoing outbreaks of West Nile virus occurring at high probability (P_{epi} = 0.3) on both islands . (b) Predicted 10-year quasi-extinction risk for different observed population sizes when there is a high probability (P_{epi} = 0.3) of WNV outbreaks on both islands. Shown are scenarios in which outbreaks are perfectly correlated (*r* = 1) and droughts occur at the currently observed frequency. See Figure S3.2 for additional scenarios

Together, the sizes of both populations were robust predictors of short-term (10-year) species-wide quasi-extinction (Figure 3b, Table S3.1), indicating both contributed to ameliorating risk. For example, in the riskiest scenario—high probability, temporally correlated WNV introductions and increased drought—if the Santa Rosa population size was 200, 10-year quasi-extinction risk exceeded 1% when the Santa Cruz population was <800. However, if the Santa Rosa population was 400, risk exceeded 1% only when the Santa Cruz population was <350 (Figure 3b).

Vaccination on Santa Cruz Island alone substantially reduced the risk of species-wide extinction from WNV (Figure 4). Proactive vaccination and reactive vaccination with a one-year detection lag had similar effectiveness. Risk reduction increased with numbers vaccinated: when Santa Cruz populations were large, risk was cut from a baseline of 18% to 7%, 4% and 3% with 30, 60 and 90 birds vaccinated. Two-year lagged vaccination performed consistently poorly, with extinction risk always ≥12% with this approach. Although the relative effectiveness of proactive vaccination remained high when population sizes were small, absolute extinction risk increased (Figure 4b), especially if drought increased (Figure S3.4).

The ability of a Santa Rosa population to ameliorate WNV-associated extinction risk increased with starting population size and habitat area, and, most notably, with decreasing probability of WNV establishment on Santa Rosa Island (Figure 4). If the probability of WNV introduction was high on both islands and the Santa Cruz population was large, then a Santa Rosa population offered only modest risk reduction, but if the WNV introduction probability on Santa Rosa was half that of Santa Cruz Island, then Santa Rosa populations >200 decreased species-wide extinction risk by at least half. If the WNV introduction probability on Santa Rosa Island was zero, then the translocation strategy reduced extinction risk to at or near zero for all starting population sizes (≥200). Increasing the Santa Rosa population size enhanced the effectiveness of this strategy (Figure 4), especially if habitat increased (Figure S3).

The most effective strategies for minimizing island scrub-jay extinction risk were hybrid approaches that combined the establishment of a second population with vaccination of individuals on both islands. In high-risk conditions of low population sizes on Santa Cruz Island or increased drought frequency, low quasi-extinction risk was only consistently achieved with both vaccination and a large Santa Rosa population (Figure 5).

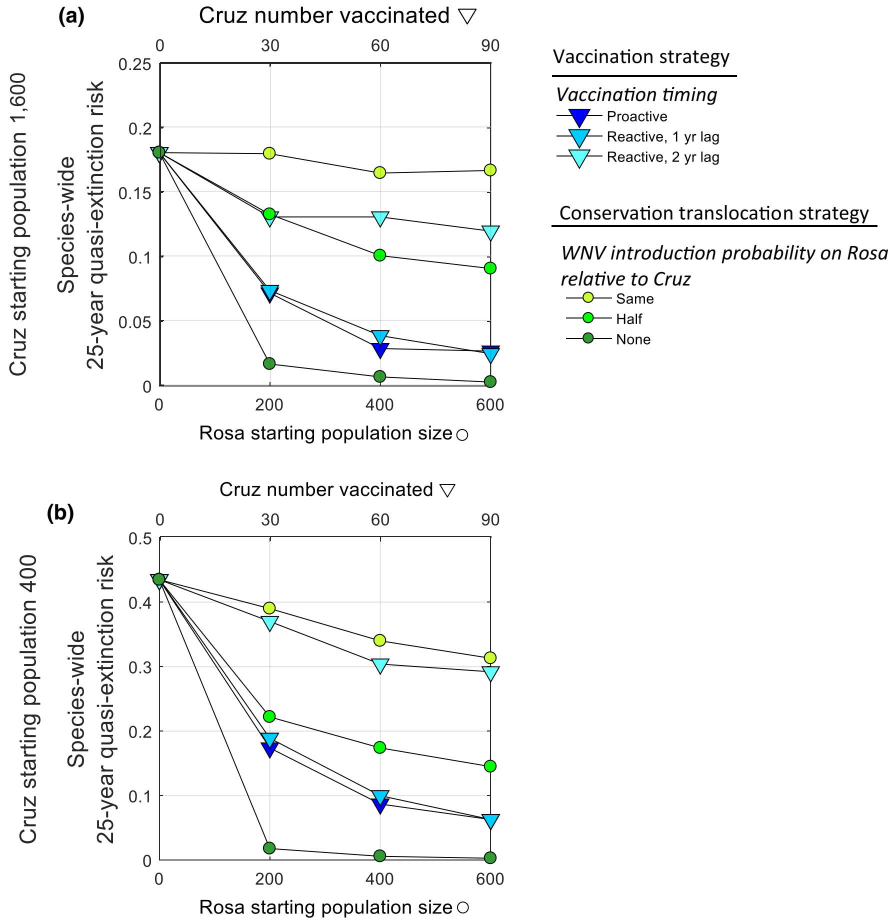

FIGURE 4 Predicted 25-year quasi-extinction risk for island scrub-jays under alternative scenarios for WNV disease management. We compared extinction risk when simulating vaccination of jays on Santa Cruz Island to extinction risk when simulating conservation translocations to establish a second jay population on Santa Rosa Island. For the vaccination strategy, we considered different timing for vaccinations (proactive, reactive with 1-year lag, reactive with 2-year lag) and three vaccination levels (30, 60 or 90 individuals, depicted by blue triangles, as indicated in upper *x*-axis for each panel). For the translocation strategy, we considered different WNV introduction probabilities (same, half, none, or P_{epi} = 0.3, 0.15, or 0) on Santa Rosa relative to Santa Cruz Island and different starting population sizes (200, 400 and 600 individuals, depicted by green circles, as indicated in lower *x*-axis for each panel) on Santa Rosa Island. We assessed the effectiveness of each strategy (a) when the starting population size on Santa Cruz Island was large (1,600 individuals) and (b) small (400 individuals). For all simulations, we assumed the same annual probability of WNV introductions on Santa Cruz Island (P_{epi} = 0.3) and complete correlation in the timing of WNV introductions (r = 1). We simulated 1,000 replicate runs for each scenario and used a quasi-extinction threshold of 30 individuals. See Figure S3.4 for scenarios varying drought frequency, inter-island correlation in WNV introduction and Santa Rosa Island habitat area

4 | DISCUSSION

4.1 | Island scrub-jay viability and West Nile virus

Our model highlights the risk posed by WNV to the persistence of the island scrub-jay, the most range-restricted bird species in the continental USA. Although the jay's predicted risk of quasi-extinction is currently very low (~0%) if future populations adhere to past dynamics, an outbreak of WNV on Santa Cruz Island markedly increases risk (22% at current population sizes, 44%–82% at smaller population sizes of 400–100, Figure 3). If its population size declines due to habitat loss or other factors, the jay risk of quasi-extinction within a relatively short timeframe increases substantially.

Vector abundance and distribution and island scrub-jay morbidity and mortality rates are important uncertainties in our disease model parameterization. However, we based our model inputs on well-documented patterns of WNV disease dynamics and impacts on corvid populations, including patterns observed on the nearby mainland. The ongoing imperilment of other range-restricted species, especially island biota, in the face of novel diseases linked to climate change underscores the wisdom of precautionary stewardship. Yet, aside from regular survival monitoring of colour-banded individuals, no active management plan currently exists for island scrub-jays.

Our simulations predict that a vigilant and large-scale vaccination strategy provides island scrub-jays with substantial protection against WNV threats across a range of conditions. If the Santa

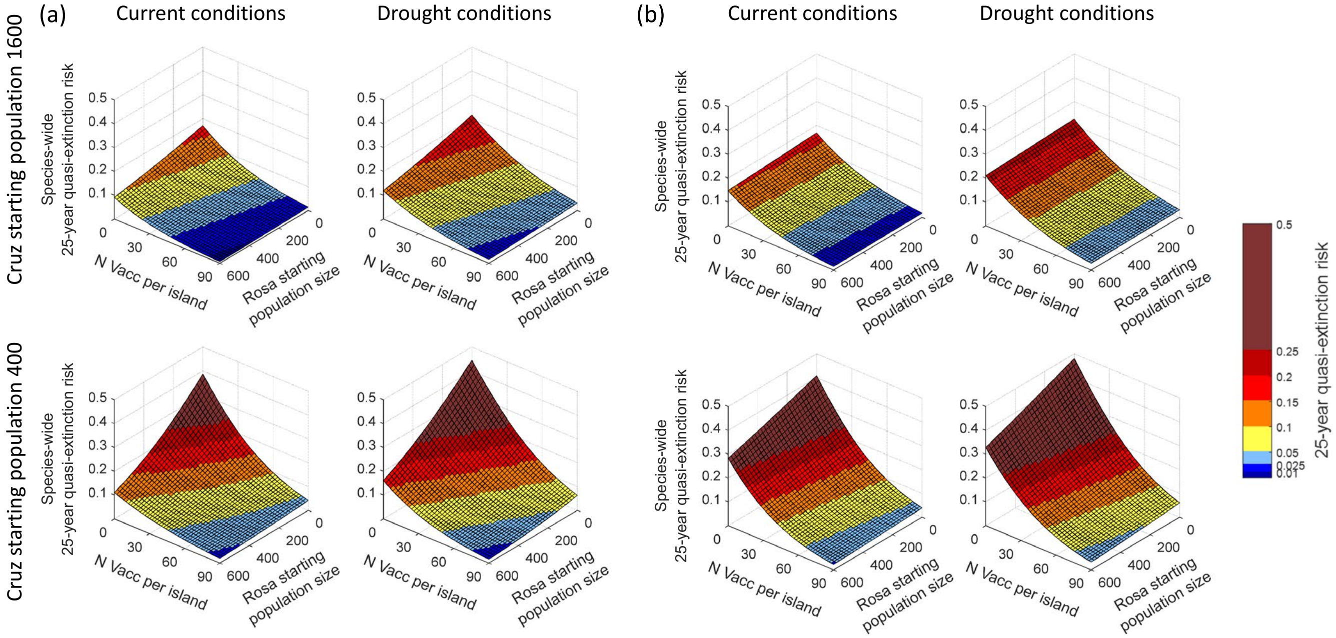

FIGURE 5 Hybrid approaches: trade-offs in strategies to reduce quasi-extinction risk of island scrub-jay due to WNV with a population on Santa Rosa Island and vaccinations on both islands, assuming current conditions or increased drought frequency. Plots show trade-offs in species-wide extinction risk of island scrub-jay for a range of starting population sizes on Santa Rosa Island (0, 200, 400 and 600) and proactive vaccination strategies on both islands at four vaccination levels (0, 30, 60 or 90 individuals) for large (1,600) or small (400) starting population sizes on Santa Cruz Island. Plots compare risk predictions when WNV introduction probability on Santa Rosa Islandis (a) equal (*Pepi* = 0.3) that of Santa Cruz Island and (b) half (P_{epi} = 0.15) that of Santa Cruz Island. Inter-island correlation in the timing of WNV introductions is 1. We simulated 1,000 replicate runs for each scenario and used a quasi-extinction threshold of 30 individuals (see Table S3.2)

Cruz island scrub-jay population remains large, annual vaccinations (proactive or reactive with one-year lag) of ≥60 individuals reduce its WNV-associated extinction risk to <5%, although this risk doubles if population size decreases and escalates further if drought frequency increases. The favourable performance of this strategy is not surprising—we have analysed and currently employ a similar vaccine-based approach to disease threats for island foxes (Doak et al., 2013). However, we have access to safe, inexpensive and effective vaccines for these canids, which are routinely trapped and handled for annual monitoring—conditions that do not exist for island scrub-jays.

Conservation translocation to establish a second population on Santa Rosa Island is also predicted to reduce island scrub-jay extinction risk. With this approach, risk reduction is attained through the increase in global population size, the creation of spatial population structure and the possibility of asynchronous disease dynamics. The predicted effectiveness of a Santa Rosa population was strongly influenced by the probability of WNV establishment, which is hypothesized to be lower than on Santa Cruz Island due to the island's colder temperatures and lower mosquito densities. If Santa Rosa Island is inhospitable to WNV establishment, a second population outperforms all vaccination scenarios considered.

One surprising result of our simulations was the ineffectiveness of inter-island transfers as a response to population declines on either or both islands. This dynamic occurred due to simulated parameter uncertainty; parameter sets that predicted lower population growth rates often led to diminished populations on both islands. Consequently, drawing down the larger population to augment, the more threatened population increased extinction risk for the larger population without successfully averting extinction of the smaller population. Because we did not account for potential added mortality associated with translocations, metapopulation management scenarios are also likely to overestimate to some extent the effectiveness of active translocations during WNV outbreaks. These results urge caution in relying on "metapopulation management" in response to populations in active decline. Once the threat is controlled (e.g. if WNV threat abates in the longer term), however, inter-island transfers may be appropriate to bolster or re-establish a two-population system. Monitoring demographic rates on each island could support more informed decisions about such transfers.

We expect WNV risk to increase in the coming decades due to warming and to remain indefinitely once established on an island. WNV's effects may moderate over time, as has been observed in its spread across North America (Kilpatrick & Wheeler, 2019). The likelihood of this occurring on the Channel Islands is unknown, but our simulations suggest that such moderation only modestly lowers WNV-associated extinction risk (≤10%, Figure S3.2c). Even under this scenario, however, the principal management concern remains island scrub-jay persistence during the initial phases of the epizootic. In addition, ongoing exposure to WNV, either with full or reduced virulence, depresses population sizes (Figure S3.3), thereby decreasing the resilience of island scrub-jay to other threats.

4.2 | Interacting threats

Although WNV was our principal focus, island scrub-jays face myriad threats, including the potential for habitat loss or degradation (e.g. from wildfires or island invasion by nest predators or oak pests and pathogens, Coleman et al., 2011; Erickson & Halvorson, 1990; Westerling & Bryant, 2008), and many potential threats are likely to be exacerbated by climate change (Morrison et al., 2011). Increases in weather extremes precipitated by climate change may lead to greater fluctuations in jay demographic rates through a variety of direct or indirect (e.g. food availability) effects. Increased drought frequency could also facilitate habitat alteration and loss, reducing island scrub-jay carrying capacity. Recent drought conditions contributed to widespread die-off of the island's bishop pine forests (Taylor et al., 2020), an important habitat for island scrub-jays (Langin et al., 2015). Given that full recovery of jay habitats from overgrazing during the ranching era is expected to take decades under ideal conditions (Pesendorfer et al., 2018), climate-related habitat change would interact with WNV threats to elevate island scrub-jay extinction risk. As previously noted, the relative efficacy of a translocation strategy increases when small populations are exposed to interacting threats. Finally, our simulations assumed WNV risk is unchanged in drought years, but the effect of drought is unknown and some evidence suggests it may enhance WNV vector-based transmission rates (Paull et al., 2017).

4.3 | Management recommendations

Under current conditions, vaccination strategies provide the greatest reduction in predicted extinction risk from WNV. However, proactive vaccination currently has low feasibility, and if managers opt for a reactive vaccination strategy, they will need to institute a robust monitoring program to detect and respond to a disease outbreak within 1 year, a time period when WNV outbreaks are expected to produce few mortalities, and before the peak of the outbreak. Although we assumed vaccinated individuals were distributed randomly across the island, targeted vaccinations in the warmest areas most susceptible to WNV could maximize efficacy. Vaccination strategies may be improved further by targeting younger individuals, which have higher survival, targeting individuals in areas where mosquitoes are more likely to transmit WNV, or targeting established pairs to minimize widowing effects. Investment in vaccination strategies will not offer protection against most other diseases or other threats to jays or their habitat.

Conservation translocation to re-establish a second population of jays provides the broadest insurance for species viability because it can abate threats beyond just WNV. It is also least reliant on ongoing active intervention but can work synergistically with such interventions. The ability of the Santa Rosa population to moderate extinction risk is positively associated with its starting population size. Thus, if a translocation strategy were pursued, prompt initiation would increase its efficacy by maximizing growth potential prior to the introduction of WNV or other threats (McDonald-Madden, Runge, Possingham, & Martin, 2011). A Santa Rosa population is predicted to grow rapidly, with starting populations of 50 reaching 400 in 20 years (Figure S3.1). If habitat increases on Santa Rosa Island due to the recent removal of exotic ungulates and to the seed dispersal activities of island scrub-jay (Pesendorfer et al., 2018), the island could support an even larger island scrub-jay population, further reducing species-wide extinction risk. The rapid growth predicted by the model relies on the applicability of habitat-based demographic rates from Santa Cruz Island to Santa Rosa Island and assumes no detrimental Allee effects due to widowing, disruption of spatial structure, or other factors. The decision to proceed with jay translocation would require analyses of factors beyond viability trade-offs, including a focus on the potential for unintended consequences resulting from biotic interactions (Morrison et al., 2011) as well as issues of cost and feasibility.

The best approaches across the broad range of potential scenarios are likely to be hybrid strategies, which include the use of conservation translocation to establish a second population and vaccination of individuals if extinction risk rises due to population declines. With this bet-hedging approach, extinction risk is ameliorated by the Santa Rosa population alone if WNV introduction probabilities are very low on that island. Across the range of potential future conditions, only options that include a Santa Rosa population and vaccinations on both islands consistently achieve a low species-wide extinction risk (Figure 5).

The history of conservation management on the California Channel Islands highlights how rapidly population threats can endanger endemic taxa. Four of six subspecies of island fox faced extinction in recent decades due to catastrophic disease from invasive pathogens and novel predation (Bakker et al., 2009). The reactive management required to recover those populations was intensive and costly, and managers today proactively manage disease risk to help prevent future such crises (Doak et al., 2013). As we seek effective and affordable methods to protect species in the face of climate-related threats, proactive interventions such as establishing additional populations are increasingly called for in the conservation literature (e.g. Fortini et al., 2015). Our analysis can help conservation managers evaluate novel strategies to improve the long-term viability of the island scrub-jay in an era of climate change, while providing a template for carefully assessing conservation translocation proposals for other species and threats. While many such scenarios will play out on far larger geographic stages, the approaches we outline to assessing alternative management strategies will remain the same and can provide clear and quantitative ways to decide between management methods.

ACKNOWLEDGEMENTS

We thank the many researchers whose determined and careful work enabled this study, especially Luke Caldwell, Michelle Desrosiers, Katie Langin and Mario Pesendorfer. Also instrumental were island colleagues from The Nature Conservancy, Colorado State University and the University of California Field Station, including Jennifer Baker, Christie Boser, David Dewey, Cameron Ghalambor, Chris Funk and Lyndal Laughrin. We also thank colleagues, particularly Kate Faulkner (retired), at Channel Islands National Park for their partnership. We are grateful for the assistance of Michael Tercek, who analysed the temperature data. This work was funded by The Nature Conservancy, the Smithsonian Institution and the U.S. National Science Foundation (DEB award 1754821).

DATA AVAILABILITY STATEMENT

Simulated territory shapefiles and island scrub-jay reproductive and resighting data are available on Dryad at https://doi.org/10.5061/dryad.vdncjsxr4.

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BIOSKETCH

Dr. Bakker is a quantitative conservation biologist at Montana State University. She is interested in understanding and modelling population dynamics and offering managers a robust and user-friendly means of comparing the effects of alternative actions on the future resilience of populations of concern.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bakker VJ, Sillett TS, Boyce WM, et al. Translocation with targeted vaccination is the most effective strategy to protect an island endemic bird threatened by West Nile virus. *Divers Distrib*. 2020;26:1104–1115. https://doi.org/10.1111/ddi.13109