Articles

Extinction Risk and Conservation Options for Maui Parrotbill, an Endangered Hawaiian Honeycreeper

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ABSTRACT: Extinction rates for island birds around the world have been historically high. For forest passerines, the Hawaiian archipelago has suffered some of the highest extinction rates and reintroduction is a conservation tool that can be used to prevent the extinction of some of the remaining endangered species. Population viability analyses can be used to assess risks to vulnerable populations and evaluate the relative benefits of conservation strategies. Here we present a population viability analysis to assess the long-term viability for Maui parrotbill(s) (Kiwikiu) *Pseudonestor xanthophrys*, a federally endangered passerine on the Hawaiian island of Maui. Contrary to indications from population monitoring, our results indicate Maui parrotbills may be unlikely to persist beyond 25 years. Our modeling suggests female mortality as a primary factor driving this decline. To evaluate and compare management options involving captive rearing and translocation strategies we made a female-only stage-structured, meta-population simulation model. Due to the low reproductive potential of Maui parrotbills in captivity, the number of individuals (~ 20% of the global population) needed to source a reintroduction solely from captive reared birds is unrealistic. A reintroduction strategy that incorporates a minimal contribution from captivity and instead translocates mostly wild individuals was found to be the most feasible management option. Habitat is being restored on leeward east Maui, which may provide more favorable climate and habitat conditions and promote increased reproductive output. Our model provides managers with benchmarks for fecundity and survival needed to ensure reintroduction success, and highlights the importance of establishing a new population in potentially favorable habitat to ensure long-term persistence.

Key words: extinction risk, Hawai‘i, Maui parrotbill, population viability analysis, *Pseudonestor xanthophrys,* reintroduction, translocation

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Introduction

Bird species across the world are in peril; one in eight species is globally threatened (BirdLife International 2014) and extinction rates are highest on islands (Gilpin and Soulé 1986; Steadman 2006). Extinction risk to small populations is explained by a broad suite of ecological characteristics; stochastic threats (e.g., environmental or catastrophic) and deterministic factors (e.g., demographic or genetic; Shaffer 1981, 1987). While each characteristic or threat alone may lead a population to extinction, together they produce interacting effects that can increase extinction probabilities, the ‘extinction vortex’ (Gilpin and Soulé 1986; Soulé and Mills 1998; Mills 2007).

Population viability analysis (PVA) is an analytical tool used to measure the processes that can lead to extinction. Data can be applied to a suite of models that combine the effects of deterministic and stochastic factors to estimate a population’s probability of future persistence (Gilpin and Soulé 1986; Caughley 1994; Beissinger 2002). Historically, PVA was used to quantify absolute risk of extinction and assess population sensitivity to model parameters, but arguably its real value is in an applied context, to examine the relative benefits of alternative management actions and estimate relative probability of extinction under different strategies (Akçakaya and Sjogren-Gulve 2000; Ellner and Fieberg 2003). In recent years PVA-type models have been applied to support specific endangered species management decisions such as landscape planning and habitat acquisition decisions (Bonnott et al. 2011; Robinson et al. 2016), allowing for mitigating incidental killings or harassment (McGowan and Ryan 2009; McGowan et al. 2011a), reintroduction decisions (Converse et al. 2013; Converse and Armstrong 2016), recovery planning (McGowan et al. 2014; Evans et al. 2016) and deciding whether species warrant US Endangered Species Act (ESA 1973, as amended) protections (Regehr et al. 2015, Reference S1; McGowan et al. 2017). Well-crafted PVA models can be designed and used to assess future extinction risk and examine and inform specific management decisions for species at risk (Runge 2011). Ideally, a PVA should incorporate the essential aspects of a population’s biology, and when correctly parameterized it can provide insights into what factors constitute the greatest threats to the population’s survival (Mills 2007). The species-specific information needed to calculate a population’s absolute risk of extinction with precision and to compare relative extinction risk under different management scenarios is rarely achievable for endangered species, particularly those that exist at low density or have cryptic behaviors. However, in those instances where endangered species have been sufficiently well studied, PVA is a useful tool for conservation managers (Ralls et al. 2002). Indeed, predicting time to extinction under multiple scenarios can inform conservation decisions, help guide management efforts and prioritize and evaluate different management options (Clark et al. 1991; Cook et al. 2012).

The Maui parrotbill (Kiwikiu) *Pseudonestor xanthophrys* is listed as endangered pursuant to the ESA and is of immediate conservation concern (USFWS 1967; IUCN 2012; Figure 1). The Maui parrotbill is a feeding specialist with a parrot-like beak for extracting insect prey from bark and decaying wood (Simon et al. 1997). Maui parrotbills are long-lived, strongly monogamous passerines that can reproduce for at least 15 years (Becker et al. 2010; Mounce et al. 2013, 2014). Breeding pairs typically produce only one offspring per year, exhibit prolonged parental care (5-17 months) and occupy relatively large home ranges averaging ~12 ha (Mounce et al. 2013; Simon et al. 2000; Warren et al. 2015). Adults typically show further delayed maturation and do not breed until their third year, although second-year females may breed more commonly than males (Maui Forest Bird Recovery Project, unpubl. data). These slow life-history traits likely indicate that the species relies heavily on adult survival. Similar life history traits are seen in ‘Akiapola‘au *Hemignathus wilsoni* the Maui parrotbill’s closest living relative, but uncommon in the Drepanidini tribe in general (Pratt et al. 2001). Maui parrotbills were once abundant on the islands of Maui and Molokai (James & Olson 1991), but have undergone substantial declines since the arrival of humans ~ 800-1000 years ago (Mounce et al. 2015). Today the wild population comprises ~500 individuals, and occupies less than 50 km^2 on windward east Maui (502 ± 116 [SE] reported from Scott et al. 1986; 590 ± 208 reported from Camp et al. 2009).

Population-wide surveys have not revealed a trend in the population since range-wide surveys were begun in 1980, although abundance estimates have remained fairly consistent (Camp et al. 2009).

Due to an apparent lack of resistance by the native forest birds to mosquito-borne diseases, such as avian malaria *Plasmodium relictum*, forests above 1500 m elevation provide the only existing refuge for most native Hawaiian honeycreepers (Scott et al. 1986; Mountainspring 1987; Simon et al. 1997) including the Maui parrotbill. Avian malaria is now moving into higher elevations, coincident with increasing average temperatures in Hawaii and gradually eroding available habitat for these species (Benning et al. 2002; Giambelluca et al. 2008; Harvell et al. 2002). Moreover, these high elevation windward habitats are suspected to be suboptimal for Maui parrotbills. These habitats contain few koa *Acacia koa*, a historically observed Maui parrotbill-preferred foraging substrate (Perkins 1903), and the prevalence of nest failures in these areas are high, frequently attributable to severe weather (USFWS 2006, Reference S2; Becker et al. 2010; Mounce et al. 2013). The historically forested island of Maui once provided almost island-wide habitat for Maui parrotbills including lowland and leeward (southeast) forests (James and Olson 1991). Little apparent habitat exists beyond the species' current range with the exception of a few remnant forest tracts on leeward east Maui, such as those found in Nakula Natural Area Reserve (NAR; 20.6°N, 156.3°W; 1097 – 2804 m in elevation; Figure 2), which is currently being reforested specifically to provide habitat for Maui parrotbills and other native forest birds. In addition to the wild population, there is a small captive flock of Maui parrotbills (currently 15 individuals) that was established in 1997 and is managed by San Diego Zoo Institute for Conservation Research. Together, the captive flock and habitat restoration efforts have paved the way for several potential conservation strategies for this species.

We applied PVA models using detailed data from demographic, genetic and ecological studies recently completed for this species (Mounce et al. 2013, 2014, 2015; Warren et al. 2015), to assess long-term viability of Maui parrotbills and evaluate potential conservation strategies. We used a custom-made simulation model to understand key limiting factors for the current population by determining which demographic variable(s) were most influential for population growth and long-term viability. We also expanded upon this model to examine the effects of (1) different management strategies to improve productivity and survival in the species' current range, (2) removing individuals from the wild for reintroduction elsewhere, and (3) establishing an additional geographically-distinct population in the leeward forests, currently unoccupied by Maui parrotbills, which may provide a long-term refuge for the species. We use our findings for the Maui parrotbill to illustrate the broader value of using PVA models to help guide the decision-making needed to plan future conservation strategy for endangered species.

Methods

Base models

Our base model was parameterized using estimates of Maui parrotbill vital rates from Mounce et al. (2013, 2014, 2015; Table 1). This base model was designed to represent the Maui parrotbill population in its current state without incorporation of any change in threats (besides normal demographic and stochastic effects of small population size) and thus produces simulations of a probable population trajectory without additional management actions. The effect of environmental variation on the annual reproduction and survival probabilities was not separately included in the model as these parameters were derived from long-term data sets that already averaged temporal variation (Table 1).

To explore different viability scenarios on the current wild populations we created a female-only stage-structured population model in R 3.4.2 (R Core Team 2017). We designed this model to incorporate demographic values (including variance) from field studies and to predict population dynamics as discrete, sequential events that incorporate environmental and demographic stochasticity through random draws from probability distributions. The model was designed to run 1,000 simulations to generate a distribution of possible fates that a population might experience under a given set of parameters. We did not model parametric uncertainty directly into our simulations using Bayesian PVA or double loop structures to incorporate hyper-parameters for demographic rates (e.g., McGowan et al. 2011b) but rather explored the effects of parametric uncertainty on model predictions though specific simulations, similar to Goodman et al. (2003). Each simulation steps through a series of events that describes an annual cycle (reproduction, mortality, and dispersal among populations,).

Our model was a stage-structured model that included a young of the year age class (0-1 yrs old), an immature age class (2-3 yrs old) and a breeding adult age class to reflect known age at maturation (≥ 3 yrs old). We incorporated a dispersal function between sub-populations and different survival rates for juvenile (0.3 ± 0.05 [Woodworth and Pratt 2009]) and adult birds (0.72 ± 0.02 [Mounce et al. 2014]; see equations below) modeled as beta distributed random variables. Fecundity rate was incorporated as the number of female offspring fledged per breeding female and was modeled as a log-normally distributed random variable. Mean annual fecundity was set at 0.2415 with a 0.15 standard error to incorporate environmental variability into the reproductive rate (Mounce et al. 2013; see equation below). For some parameters where the source data did not include an estimate of variance we used a CV of 15%, an accepted practice in PVA models when no estimate of variance is available (Morris and Doak 2002). In our model we also included an estimate of carrying capacity, whereby if a specified abundance threshold (432 females) was exceeded, the fecundity rate for that year was set to 0. Carrying capacity (K) was calculated using the Maui parrotbill range used in Camp et al (2009), 51.07 km^2, and pair home range size from Warren et al. (2015), 0.118 km^2. This approximates the number of pairs (females) given total saturation in the entire range. Carrying capacity was set at 92 females for the future Leeward population based on 10.9 km^2 of habitat that is being restored. We set the population ceiling very high compared to current estimated abundance. Informal sensitivity analysis indicates that unless the population is currently very close to, or in excess of, carrying capacity selecting the population carrying capacity has little influence on population predictions since all of our simulations decline and are not limited by K. If model predictions were sensitive to carrying capacity, more sophisticated approaches to estimating carrying capacity could be implemented, such as estimating available habitat and dividing by estimated female home range. This is a simplistic and fairly severe effect of abundance on demographic rates, however the density dependent mechanisms for this species are not known and a ceiling type function allows us to prevent exponential population growth without speculating on the functional form of density dependence (Morris and Doak 2002; McGowan and Ryan 2009). We modeled these processes as population level stochastic processes, not as individual based processes, where binomial functions are more appropriate for survival and Poisson are more appropriate for fecundity. The initial population of 292 females was calculated using the most recent available density estimate, 11.41 Maui parrotbill per km^2 (Brinck et al. 2011), estimated within a subset of the species range and extrapolated to the entire 51.07 km^2 range.

Future juvenile bird abundance (N^I) per year was modeled as the product of the number of breeding adults (N_t^A), the fecundity rate (F_t^A) and the survival rate of young of the year (S_t^Y), as follows:

$$N_{t+1}^I = N_t^A \times F_t^A \times S_t^Y.$$

The number of adults in future years was a product of the number of adults (N_t^A) and their annual survival rate (S_t^A), plus the product of the number of juvenile birds (N_t^I) and their annual survival rate (S_t^I), as follows:

$$N_{t+1}^A = N_t^A \times S_t^A + N_t^I \times S_t^I.$$

Adult and juvenile survival rates in the simulations were environmentally stochastic and drawn from a beta distribution, where the alpha and beta shape parameters were derived from the survival estimates reported in Mounce et al. (2014) using the method of moments calculations (see Morris & Doak 2002).

We modified the base model in four ways to increase demographic rates above the estimates from field studies. We used these modifications to capture parametric uncertainty in our estimated demographic parameters, following the recommendations of Goodman (2002) who demonstrated that structured changes in demographic rates within models can allow researchers to explore the effects of parametric uncertainty. Because our base model predicted rapid and near certain extinction for the population in contrast to the observed patterns in density estimates over the last 20 years (Camp et al. 2009), there is the possibility that some of the parameter estimates were not accurate in either the PVA simulations or in the count data analyses. As such, we investigated four suspect parameter estimates in detail that may have been driving the projected decline in population size. First, the estimate of juvenile survival (0-1 yrs old) presented in Mounce et al. (2014; 0.17) was markedly lower than other Hawaiian passerines (average 0.32 ±

0.03; Woodworth and Pratt 2009). The Mounce et al. (2014) estimate was generated from only 10 individuals and had a large standard error (± 0.15). Second, the estimate of annual reproductive success (ARS) presented in Mounce et al. (2013) was derived from the core-breeding season for Maui parrotbills (January-June). Breeding attempts for this species have been observed in 11 months of the year. Therefore, it is probable that while this ARS estimate may capture the majority of the success in a given year, it is likely to be an underestimate of the true ARS over the entire calendar year. Third, an annual decline in carrying capacity (K) in their current habitat is inevitable because of predicted climate change and the associated upslope movement of avian malaria and its vector (Benning et al. 2002; Giambelluca et al. 2008; Harvell et al. 2002). Fourth, genetic analysis has shown that the Maui parrotbill population is not contiguous across its range likely because of limited dispersal between two subpopulations (Mounce et al. 2015).

To address these issues, we modified our base model by (1) increasing juvenile survivorship from 17% to 32% to reflect values found in the other Hawaiian passerines (equal to 39-44% of adult survival), (2) increasing the percentage of breeding females each year by 10% to account for a reasonable estimate of less well-documented ARS in the months outside of January-June, (3) decreasing K by 1% per year to account for the influx of avian malaria resulting from climate changes (Giambelluca et al. 2008), and (4) dividing the population into two sub-populations with an associated K for each calculated using home range data from Warren et al. (2015). Further, we allowed for the possibility of dispersal between sub-populations with the number of dispersers each year (*D*) modeled as Poisson distributed random variables with a mean *I* (set to 2% of the size of each subpopulation; Modified Base Model in Table 1). We do not have enough data on movements to estimate these rates of movement empirically. We set mean *I* between the two extant wild populations to be a low annual rate (2%), because we know that movement between the populations does occur but it appears to be very uncommon (H. Mounce, unpublished data). Thus the number of juveniles in each time period (*t*), i.e., year, were added to each population was modeled as follows:

$$D_t^{i,j} \sim Poisson\left(I_t^i \times N_t^{A+I,i}\right)$$

$$N_{t+1}^I = N_t^A \times F_t^A \times S_t^Y + \sum D_t^{j,i} - \sum D_t^{i,j}$$

where *i* represents the current sub-population being projected, and *j* indicates the other sub-populations to or from which individuals can be translocated.

For all individual simulations in R we used 1,000 iterations spanning 25 years. Although longer time frames are more appropriate for assessing the predicted longevity of a species, for this exercise our focus was on the immediate viability risk and the effects of conservation actions that can be implemented to prevent imminent extinction. Due to persistent problems associated with introduced predators, continued loss of habitat, invasive species and the inherent risks of a critically endangered organism, modeling population dynamics for this species on a longer timeframe would not provide any additional insight for critical management needs.

Sensitivity Analyses

Measures of viability

Population viability analyses are limited by the quality of the input parameters available for a given species under each given scenario and do not identify absolute probabilities of extinction in a given time frame (Akçakaya and Sjogren-Gulve 2000; Reed et al. 2002). Viability measures most commonly presented in PVA studies include extinction probability, population size and estimates of time to extinction. However, it is important to evaluate the full suite of quantitative measures that PVAs produce to evaluate population viability across all models rather than relying solely on these most common measures (Pe'er et al. 2013). Consequently, for each model we present mean finite rate of growth (λ), probability of quasi-extinction ($N < 10$; PE), median population size from all iterations (*N*-all) and median population size from extant populations ($N \geq 10$; *N*-extant). Quasi-extinction is somewhat arbitrary in nature but here we used $N \geq 10$ as our threshold because we expect that when the population falls to single digit abundance drastic changes in management approach would be enacted and demographic stochasticity, rather than environmental stochasticity, would become the predominate force driving population annual changes in abundance.

Testing demographic sensitivity

Demographic sensitivity and elasticity are common metrics to report in PVA analyses (Morris and Doak 2002; Reed et al. 2002). To test the demographic sensitivity and elasticity of the current wild populations we used the ‘popbio’ package in R (Stubben and Milligan 2007). We applied the sensitivity and elasticity functions in the ‘popbio’ package to the deterministic projection matrix for the Base Model. The sensitivity and elasticity analyses use the Modified Base Model parameter as a deterministic matrix (Table 1).

Population viability with management

A working group of researchers and managers (Maui Parrotbill Reintroduction Working Group) has developed a plan to reintroduce Maui parrotbills to Nakula NAR over a three-year period, a strategy designed to balance probability of success with efficient use of resources. Based on Maui parrotbill home range size (Warren et al. 2015), Nakula NAR may be able to support ~12 Maui parrotbill pairs in the first few years of a reintroduction program. Considering these restrictions in the total numbers of individuals the area can immediately support, we therefore tested a variety of reintroduction scenarios whereby six pairs were released each year. While there are many possible scenarios that could be tested, we selected six that we thought were realistic given current management opportunities:

i. Release only the captive birds currently available to establish a second population;

ii. Augment the captive flock with wild birds such that the captive flock alone would source a second population;

iii. Augment the captive flock with wild birds such that the captive flock would provide half the individuals needed for reintroduction with the other half from translocated wild individuals;

iv. Augment the captive flock with wild birds such that the captive flock would provide 1 female per year in combination with translocated wild individuals;

v. Release only the captive birds currently available in combination with wild translocations to establish a second population; and,

vi. Release wild translocated individuals to establish a second population with no input from the captive population.

We modified the female-only stage-structured, meta-population simulation model in R to evaluate and compare management options involving captive rearing and translocation strategies tailored to the recovery requirements for this species. This model was based on a spatially implicit meta-population structure of four separate sub-populations in the simulations. Two populations represent the existing east (Hanawi NAR) and west (TNC Waikamoi Preserve) populations (Mounce et al. 2015) on the windward slopes of Haleakala (Figure 2). Another population represents the proposed third population that will be established on the leeward slopes of Haleakala (Nakula NAR; Figure 2), and a fourth population represents a captive breeding population that may serve as a source of individuals for release into the wild populations. The two wild populations were modeled with the demographic parameters described above for the Modified Base PVA Model. For the third (not yet established) reintroduced population we tested the effects of increased survival and fecundity rates on the probability of successfully establishing a wild self-sustaining population and on overall species extinction probability. To account for the potential that leeward habitats may be higher quality due to fewer storms and overall less precipitation than windward habitats, we used demographic rates that were 5%, 10% and 20% greater than those documented for Maui parrotbills to model the new population. In many cases these increased demographic values are more aligned with those of other Hawaiian honeycreepers (Woodworth and Pratt 2009). For example, a 20% increase in annual adult Maui parrotbill survivorship is 0.92 and annual adult survivorship of other Maui species have been estimated as high as 0.95. Although, a 20% increase in juvenile survivorship from the modified base model may be optimistic given that this parameter was already taken from the average from all honeycreeper species (0.32) and this parameter has not been found to be quite this high (20% increase in juvenile Maui parrotbill survivorship = 0.52) in other species.

We used the most recent density estimate from Brinck et al. (2011), 11.41 Maui parrotbill/km^2, and extrapolated to generate initial abundance in the east and west populations using range sizes of 41.8 km^2 and 9.3 km^2, respectively. These range sizes are based on the 51.07 km^2 Maui parrotbill range map used in Camp et al. (2009) and divided at the Koʻolau Gap, a large topographic feature thought to limit gene flow between the populations (Mounce et al. 2015). Based on an initial abundance of 583 and these spatial parameters, we set the initial abundance in the east wild population at 239 females, the west wild population at 53 females, and the third wild, yet to be established population at 0. With these populations combined, we set initial abundance for the entire current range at 292 female Maui parrotbills.

The captive population was modeled differently from the wild populations since in captivity the birds are not subject to the same ecological processes. We modeled the captive populations as an individual based model, which is common for captive populations (Lacy and Pollak 2014) because the conditions are more controlled. Instead, once established, the future abundance in captivity (N_{t+1}^{C}) is the current number of individuals (N_t^C), plus the number successfully reared (N_t^B), minus the number that died (N_t^D), which were modeled as Poisson distributed random variables with a mean of 2.0 and incorporated into the projection as follows:

$$N_t^B \sim Poission(2)$$

$$N_t^D \sim Poission(2)$$

$$N_{t+1}^{C} = N_t^C + N_t^B - N_t^D.$$

We set initial abundance in captive population at 7 females to reflect current conditions of the captive flock. We set the captive population to be approximately stable with no increase or decrease on average (without inputs from the wild or outputs to the wild) with equal mean number of births and deaths each year (2). The captive breeding program thus far is very small and has limited production (i.e., births each year) so our rates of two births and deaths reflect the production capacity and limited space for the captive population.

Movements between the sub-populations were restricted to translocations in captive and the future leeward populations. Movements involving the current wild populations included translocations amongst all populations and natural dispersal between the east and west populations only. The projected abundance in a subpopulation was a function of natural population dynamics (as described above), and the number of individuals added to and subtracted from the population as follows:

$$N_{t+1}^{A,i} = (N_t^{A,i} \times S_t^A) + (N_t^{I,i} \times S_t^I) + \sum T_t^{j,i} - \sum T_t^{i,j} + \sum D_t^{j,i} - \sum D_t^{i,j}$$

where T indicates the number of birds moved by management intervention and $D = 0$ in the leeward and captive populations. The model was written in a generalized form so that birds could be moved from any sub-population to another (Text S1), but in our simulations management actions were limited to establishing a new sub-population and/or contributing to the small captive population. Translocations of birds between sub-populations was specified for a limited number of years such that if abundance in the west and east sub-populations fell below 25% of their starting population size, removing individuals from that sub-population was prohibited. Lastly, individuals introduced to the wild from captivity are typically less successful (Fischer and Lindenmayer 2000). The fact that Maui parrotbills will be re-established in a different habitat type increases the uncertainly regarding their survival. To reflect that uncertainty rather than use the estimated survival rates from the empirical studies on the windward populations (Mounce et al. 2014) in our model, we made first-year survival of captive-released birds an annually varying uniformly distributed random number bounded between 0.3 and 0.9. There is no data available to characterize the form and shape of the post release survival function so using a uniform distribution is appropriate in this case. The lower-bound value is based on success of Palila (*Loxioides bailleui*) translocated to the north slope of Mauna Kea on Hawaii Island (Banko et al. 2009).

The reintroduction scenarios differed mainly based on the source of birds (i.e., the east and west wild populations, and the captive population). The goal of the captive breeding program from its onset has been to develop a sustainable breeding program for the species in the event of a collapse of the wild populations and/or to act as a source for reintroduction as new habitat became available. However, the captive program has only been moderately successful. As of 2015, the captive population consisted of seven females and eight males, which together produce an average of one bird each year. Given a sex ratio of 50:50 this represents a rate of 0.07 females produced per female per year. Realistic options for sourcing birds for reintroduction from the captive population include:

a) Releasing a large proportion of the existing captive birds (e.g., 7 females and 7 males) in a single year;
b) Releasing a minimal subset of the captive population (e.g., 1 female and 1 male) over the course of a few years; and
c) Augmenting the captive flock with wild birds, allowing for the release of a larger number of captive birds over the course of a few years.

Results

All population viability models predicted a negative population growth rate (Table 2) in the wild populations, with none of the trajectories for the east and west subpopulations as well as the meta-population persisting beyond 25 years (Figure 3, Figure 3A and 3B). As expected the sensitivity analyses identified female mortality, followed by fecundity and juvenile mortality as the main contributors to the overall population trajectory (Table 3). There are a number of constraints to carrying out the proposed reintroduction scenarios given demographic variables in the captive and wild populations. Assuming no changes to the fecundity among the captive flock, sourcing the reintroduction using only captive birds would require either using six available females (leaving one female in captivity; *i*), or moving 68 females from the wild into captivity to increase the captive populations' productivity (*ii*). The third option (*iii*) would still require 30 additional females to be brought into captivity to supplement the captive flock in order to source 50% of the translocations (Table 4). The fourth option (*iv*) requires that eight additional birds are brought into captivity so that the captive flock could consistently supply one female per year for reintroduction efforts. Population trajectories among the last three scenarios (*iv*, *v* and *vi*) are similar as they use the same input parameters, but the scenarios differed with regards to the origin of individuals (Table 4; Figure 4).

The increase of demographic parameters based on the assumption that leeward forests will provide higher quality habitat for Maui parrotbills resulted in different population trajectories (under reintroduction scenario *iv*) after the initial three-year reintroduction timeframe (Figure 5). All reintroduction scenario models show that a 10% increase in key demographic rates is not expected to be sufficient to maintain the reintroduced population ($\lambda = 0.96$). However, a 15% increase results in a likely stable population ($\lambda = 1.0$) and a 20% increase results in a growing population ($\lambda = 1.1$; Figure 5).

Discussion

Our PVA models provide a tool to evaluate management scenarios and generate demographic benchmarks necessary for a sustainable Maui parrotbill population. The rapid decline projected by these models highlights the fact that certain aspects of the species' biology, ecology and life history traits (e.g., mainly single egg clutches, prolonged parental investment) make this species in its current state (e.g., small, contracting range, occupying potentially suboptimal habitat) highly vulnerable to extinction. Our models allowed us to identify the demographic rates most limiting the species, to explore potential management solutions, and identify the most promising scenarios for reintroducing the species to previously occupied leeward mesic forests. Given the assumptions in our model and current restraints in captive Maui parrotbill productivity, we found that a reintroduction scenario that incorporates a minimal contribution from captivity and instead translocates mostly wild individuals to be the most practicable strategy.

Our population models highlight the strength and weakness of several conservation strategies that managers could implement given existing resources and capabilities in attempts to recover the wild population. Given that the population model does not reach carrying capacity, simply increasing available habitat in the current Maui parrotbill range may not increase the total population. Alternatively, if managers are able to augment the current habitat (e.g., through threat management, such as predator control) to increase quality, and thus increase some of the more sensitive parameters (i.e., female survival) within the current populations, they may be able to increase the population viability. Unfortunately, these options appear to be quite limited for Maui parrotbills for several reasons.

Weather has been identified as a key, limiting factor to reproductive success of Maui parrotbills, with high incidence of nest failure in heavy rain events (Mounce et al. 2013). Although weather cannot be manipulated, there have been numerous other unsuccessful attempts to manage Maui parrotbills within their current forest habitat. These efforts have included trying to increase productivity, survival, or both by providing supplemental food to wild individuals, decreasing predation risk through control of invasive mammalian predators, and decreasing nest predation by protecting nest trees from mammalian predation (suspected rat depredation on Maui parrotbill nests; HL Mounce, personal observation). The forest currently occupied by Maui parrotbills is native Hawaiian rainforest that is already protected (i.e., fenced and free of ungulates) and actively managed by the National Park Service, the State of Hawaii, and The Nature Conservancy. Thus, the vegetation community is in prime condition, and there are limited options for other management interventions that can improve vital rates in Kiwikiu. It is particularly concerning that the models presented here predict a rapid decline in the species given that the species primarily occupies areas with such a high degree of protection. This leaves few options beyond landscape-scale management actions (e.g., aerial broadcast rodenticide) in the current range. Therefore, establishing an additional population that may appreciate increased vital rates represents a measure that may ensure long-term persistence of the species.

Our model simulations and predicted extinction probabilities are limited by the precision of the demographic parameters estimates. While this study has used the most comprehensive data available on the Maui parrotbill, there is still uncertainty in several critical parameter estimates. The variables with the most uncertainty included initial population size and annual habitat loss as predicted through climate change models. However, our sensitivity analysis identified female mortality at all ages as the parameter most responsible for driving the observed population changes, with juvenile survivorship and fecundity playing a lesser role – yet (with the exception of juvenile survivorship) these are all parameter estimates that we have high confidence in from empirical studies (e.g., Mounce et al. 2015). Our model predictions contrast with the estimated population estimates based on point counts over the last 20 years (Camp et al. 2009). These disparities could be the result of un-modeled observation error in the count data, inaccurate parameter estimates in the PVA model, or a variety of other analytic or sampling issues. It is possible that the PVA is predicting a decline that has not yet been observed in the count data but something we may see in the near future. All abundance estimates for this species are associated with extremely large confidence intervals reflecting the low number of detections typically recorded for the species on these counts. As a result, significant trends have not been found and, although it has been tempting to say that the population is stable given similar abundance estimates between years, we do not know whether the wild population is stable with any certainty. It would be a mistake to ignore model predictions based solely on how well the output conforms to count estimates for such a cryptic species. We suggest that a productive path forward would be to implement an integrated population model that incorporates both demographic data and count data, applies observation error models to both data sets and integrates the analysis to estimate key demographic parameters using all available data (e.g., Schaub and Abadi 2011; Rushing et al. 2017).

Given the lack of management actions for increasing population viability in currently occupied habitat, an alternative is to establish new populations, particularly in areas with high-quality habitat. Historically, Maui parrotbills were observed to prefer koa as a foraging substrate (Perkins 1903) and it stands to reason that habitats containing a higher proportion of koa, which tend to occur in drier, leeward areas on Maui, were important areas for the species. Furthermore, sub-fossil records show a distribution of this species across the island, not restricted to the high elevation wet windward forests where they are found currently (James and Olson 1991). Today, there are no Maui parrotbills in koa-dominated forests on Maui. We do not know whether Maui parrotbills were historically distributed at higher densities in the wet windward forests, but it may be that these areas were always marginal habitat. Regardless, if managers do not have the tools to successfully manage this species in currently occupied habitats, then increasing the range of occupied habitats may provide a viable long-term conservation strategy. Furthermore, establishing geographically disjunct populations is good conservation practice, as having an entire global population of a species within one 51 km^2 area (such as the Maui parrotbill) puts it at greater risk of extinction in the event of a severe hurricane or other weather event.

Given the apparent limitation of management options in currently occupied habitats, moving birds from existing populations to the leeward side of Haleakala, Nakula NAR, a drier, koa-dominated habitat, as modeled here, may be necessary. Furthermore, the birds in this new habitat may be able to benefit from increased survival and productivity, key to the species long-term success. Options for moving birds include moving birds from the wild, using captive-bred birds, and a combination of these alternatives. Using captive-bred individuals can have ecological consequences such as behavioral deficiencies, high susceptibility to starvation and disease, high post-release depredation rates and overall low reintroduction success rates that have been widely documented (Curio 1996; Fischer and Lindenmayer 2000; Jule et al. 2008; Rantanen et al. 2010). Captive Maui parrotbills have the additional disadvantage of reduced genetic variation and significant genetic differentiation compared to some wild individuals (pairwise F_{st} and R_{st} between west and captive populations [F_{st} = 0.1; R_{st} = 0.16] Mounce et al. 2015). Furthermore, given the low reproduction rate of captive Maui parrotbills, using only captive-bred birds would 1) render the current captive population ineffective, 2) establish a new population with genetic variation from just a few females (*i*) or 3) require that a large number of wild individuals be brought into captivity (*ii* and *iii* requiring 23% or 10%, respectively, of all wild females). Without considering potential effects on the wild populations, the resources necessary to capture and care for these high numbers of an endangered species in captivity is unrealistic with current conservation support available in Hawaii (Leonard 2008). Conversely, if the availability of resources for this type of hands-on management substantially increased, there may be some advantages, namely that captive birds may possibly anchor any wild birds to the release area, which would facilitate monitoring (Banko et al. 2009). A major obstacle in translocations of wild individuals is that they often reject the habitat close to release sites and travel long distances before settling (Stamps and Swaisgood 2007), exhibiting preferences that captive individuals may not have.

Scenario *iv* models a reintroduction that incorporates a minimal contribution from captive individuals and has the advantage of potentially being among the least expensive scenarios. The ultimate monetary costs of many of the key steps involved in these scenarios remain unknown and in some cases are impossible to predict (e.g., the amount of field time required to capture 68 females [scenario *ii*]). Without these figures, a cost comparison among all scenarios is impossible at this time. However, scenario *iv* calls for the least amount of effort devoted to capturing wild individuals to be added to the captive population, a benefit over *ii* and *iii*, while also making use of the investment already made toward maintaining the captive population, an advantage over *vi*. This scenario also does not deplete the already small captive population, unlike *i* and *v*, and minimizes the addition of new birds to captivity and thus the costs in maintaining the larger captive population. In order for the leeward population to be considered genetically viable (Foose 1993) birds from both the east and the west need to be incorporated into the releases, yet captive birds were sourced only from the east population. Therefore, scenario *iv* would also likely provide any new populations with the most comprehensive genetic foundation considering the genetic differentiation observed between the east (including captive) and west wild Maui parrotbill populations (Mounce et al. 2015).

We further explored scenario *iv* by looking at the reintroduced population's viability using parameter values from the current wild population (Figure 5; Mounce et al. 2013, Mounce et al. 2014) as well as predicted trends in annual fecundity, female survivorship and juvenile survivorship increased by 5%, 10% and 20%. These changed demographics were examined based on potential benefits that the leeward mesic habitat may have for the species. These potential increased Maui parrotbill vital rates are not outside what has been estimated for other honeycreeper species, including other Maui endemics (Woodworth and Pratt 2009). The exact limitations of the wetter windward habitats are unknown but Maui parrotbills in the mesic forest may have increased nest success, increased foraging success, or both in the drier habitat. Maui parrotbills may also have reduced predation pressure in a habitat with lower invasive mammal densities (HL Mounce, personal observation). No Maui parrotbills currently occupy koa-dominated habitats, thus it is impossible to predict if the demography of released birds and their offspring will differ from that of the windward population. Our results demonstrate that the persistence of the reintroduced population is largely predicated on there being an increase in key demographic parameters in the new and potentially favorable environment. Given the importance of higher demographic rates for a new leeward population, a reintroduction strategy that includes an adaptive management plan is likely the most successful approach, where elevated parameter values in the leeward release sites serve as an alternative management hypothesis that can be evaluated through management actions and system monitoring (Williams et al. 2007, Reference S3). Managers could use the demographic parameter values we present here as benchmarks to strive for in future populations to ensure that the populations are successful and viable.

Supplemental Materials

Text S1. The code for the custom-made model in Program R for the Maui parrotbill 557 (Pseudonestor xanthophrys) population viability analyses conducted. This is a female-only, 558 stochastic model assuming multiple, isolated populations. Notes are indicated with the pound 559 symbol (#) and Program R will not read these as part of the code.
Found at DOI: http://dx.doi.org/10.3996/072017-JFWM-059.S1 (11 KB DOCX).

Reference S1. Regehr EV, Wilson RR, Rode KD, Runge MC. 2015. Resilience and risk: a demographic model to inform conservation planning for polar bears. Reston, VA: U.S. Geological Survey, Open-File Report 2015-1029:1-56.
Found at DOI: http://dx.doi.org/10.3996/072017-JFWM-059.S2 (2005 KB PDF).

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Found at DOI: http://dx.doi.org/10.3996/072017-JFWM-059.S3 (6 KB PDF).

Reference S3. Williams BK, Szaro RC, Shapiro CD. 2007. Adaptive Management: the US Department of the Interior Technical Guide. Washington, D.C.: US Department of the Interior, Adaptive Management Working Group.
Found at DOI: http://dx.doi.org/10.3996/072017-JFWM-059.S4 (38,192 KB PDF).

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FIGURE LEGENDS

Figure 1. Female Maui parrotbill *Pseudonestor xanthophrys*. Photo taken on 6 May 2017 in The Nature Conservancy's Waikamoi Preserve, Maui, HI by Zach Pezzillo used with permission by Maui Forest Bird Recovery Project.

Figure 2. Map of land protections that benefit native forest birds in east Maui, HI (Haleakala Volcano) and the Maui parrotbill (*Pseudonestor xanthophrys*) range. The Maui parrotbill range overlays the windward (northeast) reserves, Hanawi Natural Area Reserve and The Nature Conservancy's Waikamoi Preserve. The reserve where Maui parrotbills will be reintroduced, Nakula NAR, is shown on the leeward (southern) slope.

Figure 3. Projected mean final female population sizes (*N*-all) for Maui parrotbill (*Pseudonestor xanthophrys*) under base and modified base models in R 3.4.2. Solid black line represents the "Base Model Population Metapopulation", solid black line with dots represents the "Modified Base Model Metapopulation", and broken gray line with box represents the "Modified Base Model East Population", and dotted gray line with diamond represents the "Modified Base Model West Population". Population projections are presented for the East population (i.e., Hanawi Natural Area Reserve), West (i.e., The Nature Conservancy's Waikamoi Preserve), and the Metapopulation (i.e., East and West combined).

Figure 4. Female Maui parrotbill (*Pseudonestor xanthophrys*) population trajectories for the three existing populations (A- East [Hanawi Natural Area Reserve], B- West [The Nature Conservancy's Waikamoi Preserve], and D- Captive [San Diego Zoo Global facilities]) and the

proposed reintroduced leeward population (C- Leeward [Nakula Natural Area Reserve]). Population estimates for (A), (B), (C), and (D) are based on a proposed three-year reintroduction scenario wherein the captive flock is augmented to source 1 female/year in combination with translocations from existing wild populations (scenario *iv*). Demographic parameters for wild populations are set to values from Mounce et al. (2013, 2014). Solid lines indicate mean number of adult females in the population from 1000 model runs. Dashed lines indicate 95% CI around mean values.

Figure 5. Maui parrotbill (*Pseudonestor xanthophrys*) population trajectories for the proposed future reintroduced leeward population (Nakula Natural Area Reserve) based on a realistic proposed reintroduction scenario (scenario *iv*, wherein the captive flock sources 1 female/year and additional translocations from wild populations [Hanawi Natural Area Reserve and The Nature Conservancy's Waikamoi Preserve]). Panel A demonstrates a population trajectory predicting trends in the reintroduced population with annual fecundity, female survivorship, and young of the year set as in Mounce et al. (2013, 2014; A). The other panels demonstrate trajectories for the same population with parameters increased by 10% (B), 15% (C), and 20% (D) based on potential benefits of the leeward mesic habitat. Solid lines indicate mean number of adult females in the population from 1000 model runs. Dashed lines indicate 95% CI around mean values.

Table 1. Parameter input values for the base and modified base PVA model used for Maui parrotbills (*Pseudonestor xanthophrys*). Input parameters derived from Mounce et al. (2013, 2014, 2015), Warren et al. (2015), and unpublished data from Maui Forest Bird Recovery Project. Values in bold highlight changes between the Base and Modified Base models. Percentage of breeding females and survival rates are presented with estimates of environmental variation (EV; ± SD).

	Base Model	**Modified Base Model**	
		East Pop (1)	West Pop (2)
Dispersal	No	**Yes**	**Yes**
Age range of dispersers	.	**0-1**	**0-1**
% survival of dispersers	.	**40-90**	**40-90**
Mean % dispersing between pops	.	**2**	**2**
Age of 1st breeding	2	2	2
% adult females breeding (EV)	46 (± 0.25)	**56 (± 0.25)**	**56 (± 0.25)**
% 1 offspring (% 2 offspring)	95 (5)	95 (5)	95 (5)
% survival rates 0-1, S_y	17 (± 0.15)	**32 (± 0.02)**	**32 (± 0.02)**
% survival rates after age 1, S_a	72 (± 0.02)	72 (± 0.02)	72 (± 0.02)
Initial population size	292	239	53
Carrying capacity (K)	432	354	78
Future change in K?	No	**Yes**	**Yes**
% annual increase	.	**-1**	**-1**

Table 2. Population viability analysis model results for the base and modified base model for the Maui parrotbill (*Pseudonestor xanthophrys*) population(s) with the viability measures of λ (median rate of population change), PQE (probability of quasi-extinction [N<10] at 25 years), N-all (median population size from all iterations at year 25), N-extant (median population size from extant populations at year 25). * N-extant is defined as N > 10, thus in the base model with N-extant = 10, no SD can be calculated as the model considers the population extinct.

	Base model	Modified base model
λ	0.784	0.866
PQE	0.999	0.992
N-all	1	2
SD N-all	0.75	3.04
N-extant	10	12
SD N-extant	*	6.317

Table 3. Results of the sensitivity and elasticity analysis for the Maui parrotbill (*Pseudonestor xanthophrys*) meta-population based on parameter changes in the "modified base model." Demographic parameters included were juvenile survival (% survival rates 0-1; S_y), adult survivorship (% survival rates after age 1; S_a), and fecundity (F). Lambda (λ) for this model was 0.866

	S_y	S_a	F
Sensitivity .	0.316	0.856	0.39
Elasticity .	0.144	0.712	0.144

Table 4. Reintroduction scenarios indicating the total number female Maui parrotbill (*Pseudonestor xanthophrys*) would be needed to move between the East (Hanawai Natural Area Reserve), West (The Nature Conservancy's Waikamoi Preserve), Leeward (Nakula Natural Area Reserve), and Captive (San Diego Zoo Global) populations over three years. For each scenario are population viability analysis model results for the modified base model with the viability measures of PQE (probability of quasi-extinction [N<10] at 25 years), N-all (median population size from all iterations at year 25), N-extant (median population size from extant populations at year 25). (-) indicates N/A.

Scenario *i*

	East	West	Leeward	Captive
# to captivity	0	0	-	-
# to Leeward	0	0	-	7
PQE	0.990	1.000	1.000	0.089
N-all	1	1	0	9
SD N-all	2.157	0.599	0.422	4.469
N-extant	14	-	-	12
SD N-extant	1.805	-	-	2.36

Scenario *ii*

	East	West	Leeward	Captive
# to captivity	51	17	-	-
# to Leeward	0	0	-	15
PQE	0.966	1.000	1.000	0.000
N-all	1	0	1	66
SD N-all	1.701	0.528	0.475	4.127
N-extant	11	-	-	66
SD N-extant	3.559	-	-	4.127

Scenario *iii*

	East	West	Leeward	Captive
# to captivity	23	8	-	-
# to Leeward	4.5	3	-	7.5
PQE	0.991	1.000	1.000	0.000
N-all	1	1	0	32
SD N-all	1.936	0.555	0.483	4.263
N-extant	11	-	-	32

Scenario *iv*

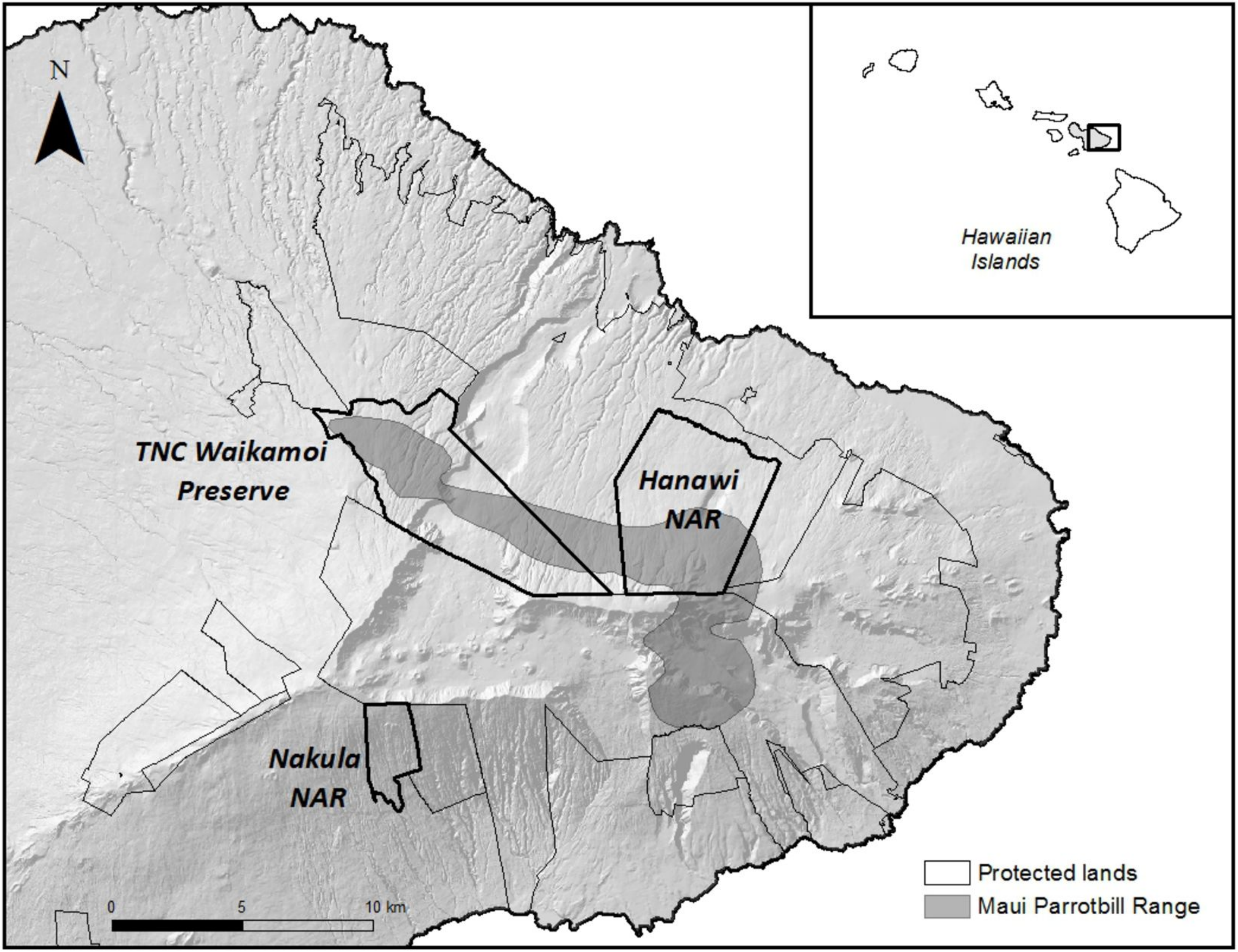
	East	West	Leeward	Captive
# to captivity	6	2	-	-
# to Leeward	7.5	4.5	-	3
PQE	0.988	1.000	1.000	0.000
N-all	1	1	0	18
SD N-all	1.884	0.556	0.477	4.230
N-extant	10	-	-	18

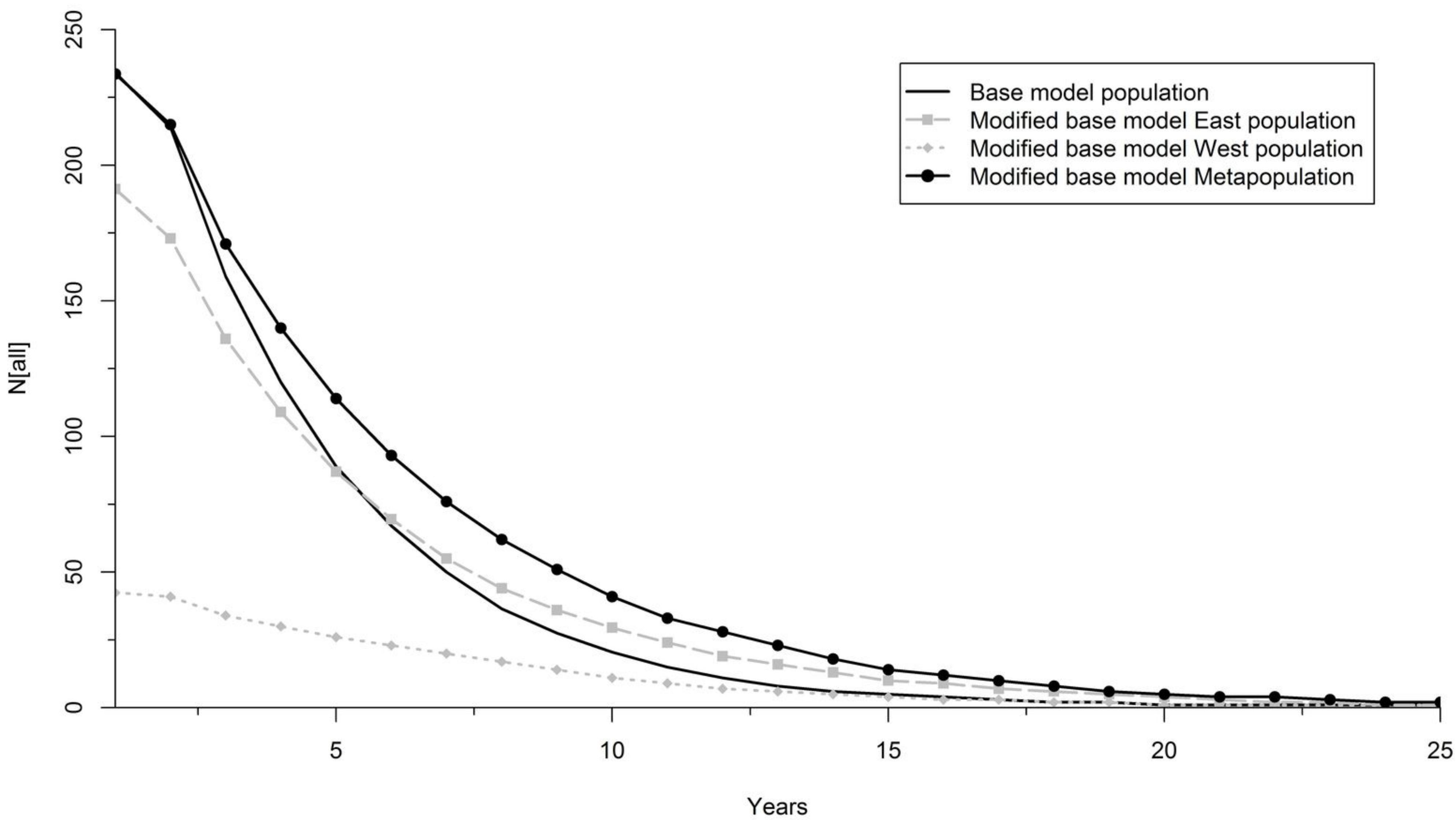
SD N-extant	1.59	-	-	4.263

SD N-extant	2.348	-	-	3.972

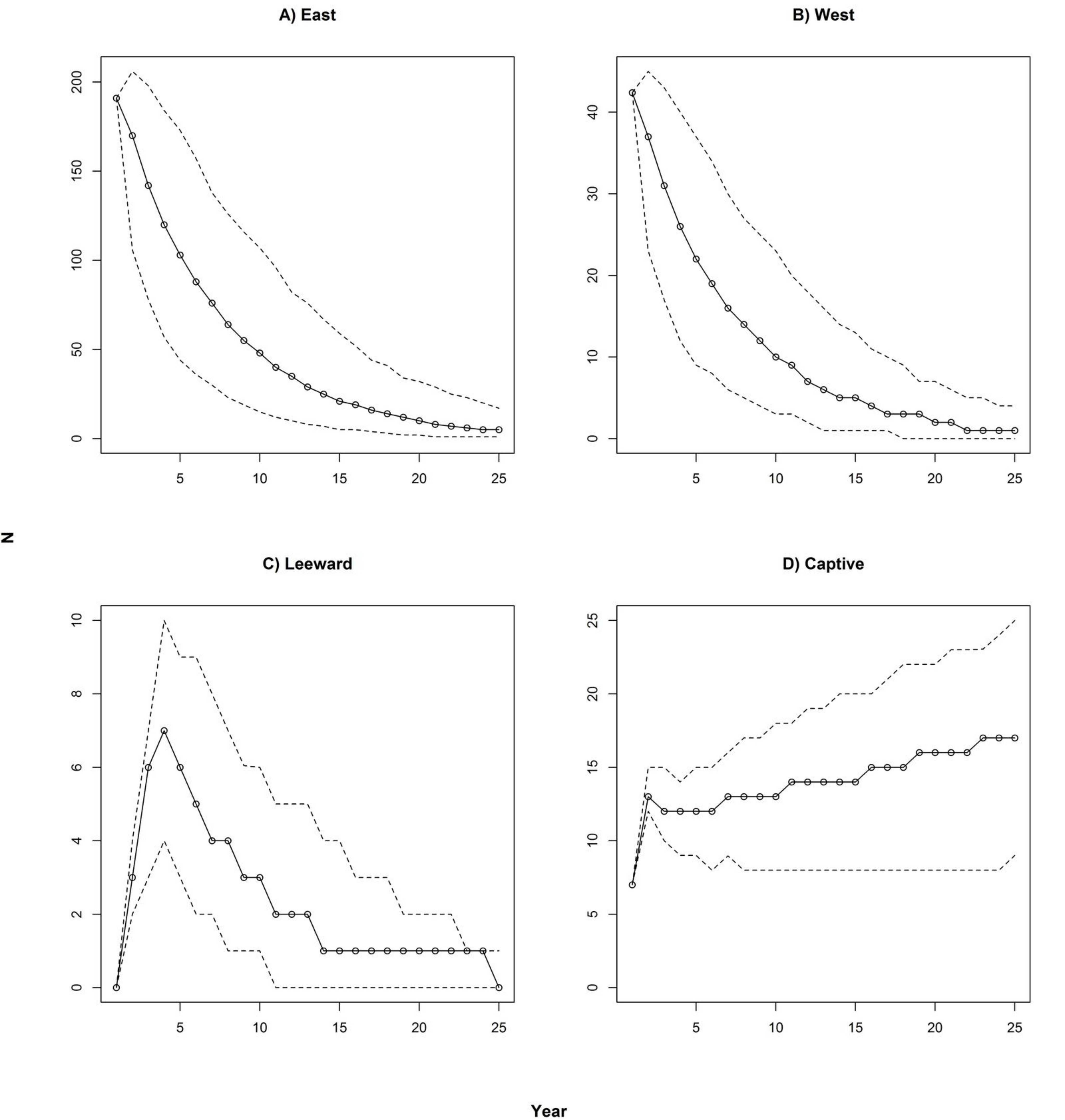
Scenario *v*				
	East	West	Leeward	Captive
# to captivity	0	0	-	-
# to Leeward	4.5	3	-	7.5
PQE	0.989	1.000	1.000	0.045
N-all	1	1	0	10
SD N-all	2.018	0.563	0.455	4.443
N-extant	12	-	-	12
SD N-extant	1.859	-	-	2.762

Scenario *vi*				
	East	West	Leeward	Captive
# to captivity	0	0	-	-
# to Leeward	9	6	-	0
PQE	0.980	1.000	1.000	0.006
N-all	1	1	0	13
SD N-all	2.367	0.640	0.465	4.241
N-extant	12	-	-	14
SD N-extant	3.832	-	-	3.311

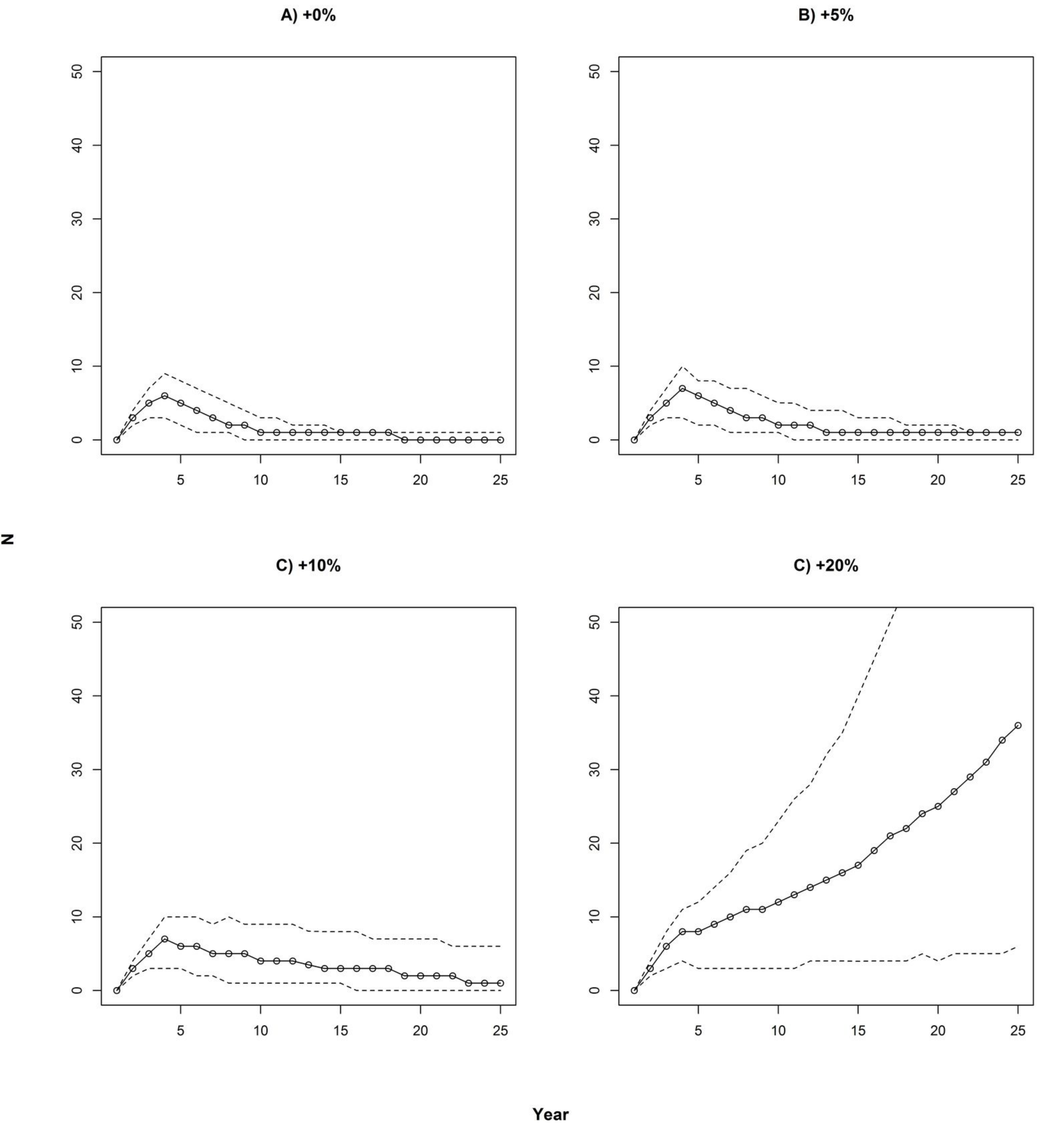

N
Hawaiian Islands
TNC Waikamoi Preserve
Hanawi NAR
Nakula NAR
0
5
10 km
Protected lands
Maui Parrotbill Range



Base model population
Modified base model East population
Modified base model West population
Modified base model Metapopulation
N[all]
0
50
100
150
200
250
5
10
15
20
25
Years



A) East
B) West
C) Leeward
D) Captive
N
Year
0
50
100
150
200
0
10
20
30
40
0
2
4
6
8
10
0
5
10
15
20
25
5
10
15
20
25


A) +0%
B) +5%
C) +10%
C) +20%
N
Year
0
10
20
30
40
50
5
10
15
20
25