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1 **Articles**

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

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20 **ABSTRACT:** Extinction rates for island birds around the world have been historically high. For
21 forest passerines, the Hawaiian archipelago has suffered some of the highest extinction rates and
22 reintroduction is a conservation tool that can be used to prevent the extinction of some of the
23 remaining endangered species. Population viability analyses can be used to assess risks to

24 vulnerable populations and evaluate the relative benefits of conservation strategies. Here we
25 present a population viability analysis to assess the long-term viability for Maui parrotbill(s)
26 (Kiwikiu) *Pseudonestor xanthophrys*, a federally endangered passerine on the Hawaiian island of
27 Maui. Contrary to indications from population monitoring, our results indicate Maui parrotbills
28 may be unlikely to persist beyond 25 years. Our modeling suggests female mortality as a primary
29 factor driving this decline. To evaluate and compare management options involving captive
30 rearing and translocation strategies we made a female-only stage-structured, meta-population
31 simulation model. Due to the low reproductive potential of Maui parrotbills in captivity, the
32 number of individuals (~ 20% of the global population) needed to source a reintroduction solely
33 from captive reared birds is unrealistic. A reintroduction strategy that incorporates a minimal
34 contribution from captivity and instead translocates mostly wild individuals was found to be the
35 most feasible management option. Habitat is being restored on leeward east Maui, which may
36 provide more favorable climate and habitat conditions and promote increased reproductive
37 output. Our model provides managers with benchmarks for fecundity and survival needed to
38 ensure reintroduction success, and highlights the importance of establishing a new population in
39 potentially favorable habitat to ensure long-term persistence.

40

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

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65 Running Head: Risk and Recovery options for Kiwikiu

66

67

Introduction

68 Bird species across the world are in peril; one in eight species is globally threatened
69 (BirdLife International 2014) and extinction rates are highest on islands (Gilpin and Soulé 1986;
70 Steadman 2006). Extinction risk to small populations is explained by a broad suite of ecological
71 characteristics; stochastic threats (e.g., environmental or catastrophic) and deterministic factors
72 (e.g., demographic or genetic; Shaffer 1981, 1987). While each characteristic or threat alone may

73 lead a population to extinction, together they produce interacting effects that can increase
74 extinction probabilities, the ‘extinction vortex’ (Gilpin and Soulé 1986; Soulé and Mills 1998;
75 Mills 2007).

76 Population viability analysis (PVA) is an analytical tool used to measure the processes that
77 can lead to extinction. Data can be applied to a suite of models that combine the effects of
78 deterministic and stochastic factors to estimate a population’s probability of future persistence
79 (Gilpin and Soulé 1986; Caughley 1994; Beissinger 2002). Historically, PVA was used to
80 quantify absolute risk of extinction and assess population sensitivity to model parameters, but
81 arguably its real value is in an applied context, to examine the relative benefits of alternative
82 management actions and estimate relative probability of extinction under different strategies
83 (Akçakaya and Sjögren-Gulve 2000; Ellner and Fieberg 2003). In recent years PVA-type models
84 have been applied to support specific endangered species management decisions such as
85 landscape planning and habitat acquisition decisions (Bonnott et al. 2011; Robinson et al. 2016),
86 allowing for mitigating incidental killings or harassment (McGowan and Ryan 2009; McGowan
87 et al. 2011a), reintroduction decisions (Converse et al. 2013; Converse and Armstrong 2016),
88 recovery planning (McGowan et al. 2014; Evans et al. 2016) and deciding whether species
89 warrant US Endangered Species Act (ESA 1973, as amended) protections (Regehr et al. 2015,
90 Reference S1; McGowan et al. 2017). Well-crafted PVA models can be designed and used to
91 assess future extinction risk and examine and inform specific management decisions for species
92 at risk (Runge 2011). Ideally, a PVA should incorporate the essential aspects of a population’s
93 biology, and when correctly parameterized it can provide insights into what factors constitute the
94 greatest threats to the population’s survival (Mills 2007). The species-specific information
95 needed to calculate a population’s absolute risk of extinction with precision and to compare

96 relative extinction risk under different management scenarios is rarely achievable for endangered
97 species, particularly those that exist at low density or have cryptic behaviors. However, in those
98 instances where endangered species have been sufficiently well studied, PVA is a useful tool for
99 conservation managers (Ralls et al. 2002). Indeed, predicting time to extinction under multiple
100 scenarios can inform conservation decisions, help guide management efforts and prioritize and
101 evaluate different management options (Clark et al. 1991; Cook et al. 2012).

102 The Maui parrotbill (Kiwikiu) *Pseudonestor xanthophrys* is listed as endangered pursuant to
103 the ESA and is of immediate conservation concern (USFWS 1967; IUCN 2012; Figure 1). The
104 Maui parrotbill is a feeding specialist with a parrot-like beak for extracting insect prey from bark
105 and decaying wood (Simon et al. 1997). Maui parrotbills are long-lived, strongly monogamous
106 passerines that can reproduce for at least 15 years (Becker et al. 2010; Mounce et al. 2013,
107 2014). Breeding pairs typically produce only one offspring per year, exhibit prolonged parental
108 care (5-17 months) and occupy relatively large home ranges averaging ~12 ha (Mounce et al.
109 2013; Simon et al. 2000; Warren et al. 2015). Adults typically show further delayed maturation
110 and do not breed until their third year, although second-year females may breed more commonly
111 than males (Maui Forest Bird Recovery Project, unpubl. data). These slow life-history traits
112 likely indicate that the species relies heavily on adult survival. Similar life history traits are seen
113 in 'Akiapola'au *Hemignathus wilsoni* the Maui parrotbill's closest living relative, but uncommon
114 in the Drepanidini tribe in general (Pratt et al. 2001). Maui parrotbills were once abundant on the
115 islands of Maui and Molokai (James & Olson 1991), but have undergone substantial declines
116 since the arrival of humans ~ 800-1000 years ago (Mounce et al. 2015). Today the wild
117 population comprises ~500 individuals, and occupies less than 50 km² on windward east Maui
118 (502 ± 116 [SE] reported from Scott et al. 1986; 590 ± 208 reported from Camp et al. 2009).

119 Population-wide surveys have not revealed a trend in the population since range-wide surveys
120 were begun in 1980, although abundance estimates have remained fairly consistent (Camp et al.
121 2009).

122 Due to an apparent lack of resistance by the native forest birds to mosquito-borne diseases,
123 such as avian malaria *Plasmodium relictum*, forests above 1500 m elevation provide the only
124 existing refuge for most native Hawaiian honeycreepers (Scott et al. 1986; Mountainspring 1987;
125 Simon et al. 1997) including the Maui parrotbill. Avian malaria is now moving into higher
126 elevations, coincident with increasing average temperatures in Hawaii and gradually eroding
127 available habitat for these species (Benning et al. 2002; Giambelluca et al. 2008; Harvell et al.
128 2002). Moreover, these high elevation windward habitats are suspected to be suboptimal for
129 Maui parrotbills. These habitats contain few koa *Acacia koa*, a historically observed Maui
130 parrotbill-preferred foraging substrate (Perkins 1903), and the prevalence of nest failures in these
131 areas are high, frequently attributable to severe weather (USFWS 2006, Reference S2; Becker et
132 al. 2010; Mounce et al. 2013). The historically forested island of Maui once provided almost
133 island-wide habitat for Maui parrotbills including lowland and leeward (southeast) forests (James
134 and Olson 1991). Little apparent habitat exists beyond the species' current range with the
135 exception of a few remnant forest tracts on leeward east Maui, such as those found in Nakula
136 Natural Area Reserve (NAR; 20.6°N, 156.3°W; 1097 – 2804 m in elevation; Figure 2), which is
137 currently being reforested specifically to provide habitat for Maui parrotbills and other native
138 forest birds. In addition to the wild population, there is a small captive flock of Maui parrotbills
139 (currently 15 individuals) that was established in 1997 and is managed by San Diego Zoo
140 Institute for Conservation Research. Together, the captive flock and habitat restoration efforts
141 have paved the way for several potential conservation strategies for this species.

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

154

155

Methods

Base models

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

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

177 Our model was a stage-structured model that included a young of the year age class (0-1 yrs
178 old), an immature age class (2-3 yrs old) and a breeding adult age class to reflect known age at
179 maturation (≥ 3 yrs old). We incorporated a dispersal function between sub-populations and
180 different survival rates for juvenile (0.3 ± 0.05 [Woodworth and Pratt 2009]) and adult birds
181 (0.72 ± 0.02 [Mounce et al. 2014]; see equations below) modeled as beta distributed random
182 variables. Fecundity rate was incorporated as the number of female offspring fledged per
183 breeding female and was modeled as a log-normally distributed random variable. Mean annual
184 fecundity was set at 0.2415 with a 0.15 standard error to incorporate environmental variability
185 into the reproductive rate (Mounce et al. 2013; see equation below). For some parameters where
186 the source data did not include an estimate of variance we used a CV of 15%, an accepted
187 practice in PVA models when no estimate of variance is available (Morris and Doak 2002). In

188 our model we also included an estimate of carrying capacity, whereby if a specified abundance
189 threshold (432 females) was exceeded, the fecundity rate for that year was set to 0. Carrying
190 capacity (K) was calculated using the Maui parrotbill range used in Camp et al (2009), 51.07
191 km², and pair home range size from Warren et al. (2015), 0.118 km². This approximates the
192 number of pairs (females) given total saturation in the entire range. Carrying capacity was set at
193 92 females for the future Leeward population based on 10.9 km² of habitat that is being restored.
194 We set the population ceiling very high compared to current estimated abundance. Informal
195 sensitivity analysis indicates that unless the population is currently very close to, or in excess of,
196 carrying capacity selecting the population carrying capacity has little influence on population
197 predictions since all of our simulations decline and are not limited by K. If model predictions
198 were sensitive to carrying capacity, more sophisticated approaches to estimating carrying
199 capacity could be implemented, such as estimating available habitat and dividing by estimated
200 female home range. This is a simplistic and fairly severe effect of abundance on demographic
201 rates, however the density dependent mechanisms for this species are not known and a ceiling
202 type function allows us to prevent exponential population growth without speculating on the
203 functional form of density dependence (Morris and Doak 2002; McGowan and Ryan 2009). We
204 modeled these processes as population level stochastic processes, not as individual based
205 processes, where binomial functions are more appropriate for survival and Poisson are more
206 appropriate for fecundity. The initial population of 292 females was calculated using the most
207 recent available density estimate, 11.41 Maui parrotbill per km² (Brinck et al. 2011), estimated
208 within a subset of the species range and extrapolated to the entire 51.07 km² range.

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

$$212 \quad N_{t+1}^J = N_t^A \times F_t^A \times S_t^Y.$$

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

$$216 \quad N_{t+1}^A = N_t^A \times S_t^A + N_t^J \times S_t^J.$$

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

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

232 0.03; Woodworth and Pratt 2009). The Mounce et al. (2014) estimate was generated from only
233 10 individuals and had a large standard error (± 0.15). Second, the estimate of annual
234 reproductive success (ARS) presented in Mounce et al. (2013) was derived from the core-
235 breeding season for Maui parrotbills (January-June). Breeding attempts for this species have
236 been observed in 11 months of the year. Therefore, it is probable that while this ARS estimate
237 may capture the majority of the success in a given year, it is likely to be an underestimate of the
238 true ARS over the entire calendar year. Third, an annual decline in carrying capacity (K) in their
239 current habitat is inevitable because of predicted climate change and the associated upslope
240 movement of avian malaria and its vector (Benning et al. 2002; Giambelluca et al. 2008; Harvell
241 et al. 2002). Fourth, genetic analysis has shown that the Maui parrotbill population is not
242 contiguous across its range likely because of limited dispersal between two subpopulations
243 (Mounce et al. 2015).

244 To address these issues, we modified our base model by (1) increasing juvenile survivorship
245 from 17% to 32% to reflect values found in the other Hawaiian passerines (equal to 39-44% of
246 adult survival), (2) increasing the percentage of breeding females each year by 10% to account
247 for a reasonable estimate of less well-documented ARS in the months outside of January-June,
248 (3) decreasing K by 1% per year to account for the influx of avian malaria resulting from climate
249 changes (Giambelluca et al. 2008), and (4) dividing the population into two sub-populations with
250 an associated K for each calculated using home range data from Warren et al. (2015). Further,
251 we allowed for the possibility of dispersal between sub-populations with the number of
252 dispersers each year (D) modeled as Poisson distributed random variables with a mean I (set to
253 2% of the size of each subpopulation; Modified Base Model in Table 1). We do not have enough
254 data on movements to estimate these rates of movement empirically. We set mean I between the

255 two extant wild populations to be a low annual rate (2%), because we know that movement
256 between the populations does occur but it appears to be very uncommon (H. Mounce,
257 unpublished data). Thus the number of juveniles in each time period (t), i.e., year, were added to
258 each population was modeled as follows:

$$D_t^{i,j} \sim \text{Poisson}(I_t^i \times N_t^{A+I,i})$$
$$N_{t+1}^I = N_t^A \times F_t^A \times S_t^Y + \sum D_t^{j,i} - \sum D_t^{i,j}$$

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

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

268

269 **Sensitivity Analyses**

270 **Measures of viability**

271 Population viability analyses are limited by the quality of the input parameters available for a
272 given species under each given scenario and do not identify absolute probabilities of extinction
273 in a given time frame (Akçakaya and Sjogren-Gulve 2000; Reed et al. 2002). Viability measures
274 most commonly presented in PVA studies include extinction probability, population size and
275 estimates of time to extinction. However, it is important to evaluate the full suite of quantitative

276 measures that PVAs produce to evaluate population viability across all models rather than
277 relying solely on these most common measures (Pe'er et al. 2013). Consequently, for each model
278 we present mean finite rate of growth (λ), probability of quasi-extinction ($N < 10$; PE), median
279 population size from all iterations (N -all) and median population size from extant populations (N
280 ≥ 10 ; N -extant). Quasi-extinction is somewhat arbitrary in nature but here we used $N \geq 10$ as our
281 threshold because we expect that when the population falls to single digit abundance drastic
282 changes in management approach would be enacted and demographic stochasticity, rather than
283 environmental stochasticity, would become the predominate force driving population annual
284 changes in abundance.

285

286 **Testing demographic sensitivity**

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

293

294 **Population viability with management**

295 A working group of researchers and managers (Maui Parrotbill Reintroduction Working
296 Group) has developed a plan to reintroduce Maui parrotbills to Nakula NAR over a three-year
297 period, a strategy designed to balance probability of success with efficient use of resources.
298 Based on Maui parrotbill home range size (Warren et al. 2015), Nakula NAR may be able to

299 support ~12 Maui parrotbill pairs in the first few years of a reintroduction program. Considering
300 these restrictions in the total numbers of individuals the area can immediately support, we
301 therefore tested a variety of reintroduction scenarios whereby six pairs were released each year.
302 While there are many possible scenarios that could be tested, we selected six that we thought
303 were realistic given current management opportunities:

- 304 *i.* Release only the captive birds currently available to establish a second population;
- 305 *ii.* Augment the captive flock with wild birds such that the captive flock alone would
306 source a second population;
- 307 *iii.* Augment the captive flock with wild birds such that the captive flock would provide
308 half the individuals needed for reintroduction with the other half from translocated
309 wild individuals;
- 310 *iv.* Augment the captive flock with wild birds such that the captive flock would provide 1
311 female per year in combination with translocated wild individuals;
- 312 *v.* Release only the captive birds currently available in combination with wild
313 translocations to establish a second population; and,
- 314 *vi.* Release wild translocated individuals to establish a second population with no input
315 from the captive population.

316 We modified the female-only stage-structured, meta-population simulation model in R to
317 evaluate and compare management options involving captive rearing and translocation strategies
318 tailored to the recovery requirements for this species. This model was based on a spatially
319 implicit meta-population structure of four separate sub-populations in the simulations. Two
320 populations represent the existing east (Hanawi NAR) and west (TNC Waikamoi Preserve)
321 populations (Mounce et al. 2015) on the windward slopes of Haleakala (Figure 2). Another

322 population represents the proposed third population that will be established on the leeward slopes
323 of Haleakala (Nakula NAR; Figure 2), and a fourth population represents a captive breeding
324 population that may serve as a source of individuals for release into the wild populations. The
325 two wild populations were modeled with the demographic parameters described above for the
326 Modified Base PVA Model. For the third (not yet established) reintroduced population we tested
327 the effects of increased survival and fecundity rates on the probability of successfully
328 establishing a wild self-sustaining population and on overall species extinction probability. To
329 account for the potential that leeward habitats may be higher quality due to fewer storms and
330 overall less precipitation than windward habitats, we used demographic rates that were 5%, 10%
331 and 20% greater than those documented for Maui parrotbills to model the new population. In
332 many cases these increased demographic values are more aligned with those of other Hawaiian
333 honeycreepers (Woodworth and Pratt 2009). For example, a 20% increase in annual adult Maui
334 parrotbill survivorship is 0.92 and annual adult survivorship of other Maui species have been
335 estimated as high as 0.95. Although, a 20% increase in juvenile survivorship from the modified
336 base model may be optimistic given that this parameter was already taken from the average from
337 all honeycreeper species (0.32) and this parameter has not been found to be quite this high (20%
338 increase in juvenile Maui parrotbill survivorship = 0.52) in other species.

339 We used the most recent density estimate from Brinck et al. (2011), 11.41 Maui
340 parrotbill/km², and extrapolated to generate initial abundance in the east and west populations
341 using range sizes of 41.8 km² and 9.3 km², respectively. These range sizes are based on the 51.07
342 km² Maui parrotbill range map used in Camp et al. (2009) and divided at the Ko‘olau Gap, a
343 large topographic feature thought to limit gene flow between the populations (Mounce et al.
344 2015). Based on an initial abundance of 583 and these spatial parameters, we set the initial

345 abundance in the east wild population at 239 females, the west wild population at 53 females,
346 and the third wild, yet to be established population at 0. With these populations combined, we set
347 initial abundance for the entire current range at 292 female Maui parrotbills.

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

$$N_t^B \sim \text{Poisson}(2)$$

$$N_t^D \sim \text{Poisson}(2)$$

355
$$N_{t+1}^C = N_t^C + N_t^B - N_t^D.$$

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

362 Movements between the sub-populations were restricted to translocations in captive and the
363 future leeward populations. Movements involving the current wild populations included
364 translocations amongst all populations and natural dispersal between the east and west
365 populations only. The projected abundance in a subpopulation was a function of natural

366 population dynamics (as described above), and the number of individuals added to and
367 subtracted from the population as follows:

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

368 where T indicates the number of birds moved by management intervention and $D = 0$ in the
369 leeward and captive populations. The model was written in a generalized form so that birds could
370 be moved from any sub-population to another (Text S1), but in our simulations management
371 actions were limited to establishing a new sub-population and/or contributing to the small
372 captive population. Translocations of birds between sub-populations was specified for a limited
373 number of years such that if abundance in the west and east sub-populations fell below 25% of
374 their starting population size, removing individuals from that sub-population was prohibited.
375 Lastly, individuals introduced to the wild from captivity are typically less successful (Fischer and
376 Lindenmayer 2000). The fact that Maui parrotbills will be re-established in a different habitat
377 type increases the uncertainty regarding their survival. To reflect that uncertainty rather than use
378 the estimated survival rates from the empirical studies on the windward populations (Mounce et
379 al. 2014) in our model, we made first-year survival of captive-released birds an annually varying
380 uniformly distributed random number bounded between 0.3 and 0.9. There is no data available to
381 characterize the form and shape of the post release survival function so using a uniform
382 distribution is appropriate in this case. The lower-bound value is based on success of Palila
383 (*Loxioides bailleui*) translocated to the north slope of Mauna Kea on Hawaii Island (Banko et al.
384 2009).

385 The reintroduction scenarios differed mainly based on the source of birds (i.e., the east and
386 west wild populations, and the captive population). The goal of the captive breeding program
387 from its onset has been to develop a sustainable breeding program for the species in the event of

388 a collapse of the wild populations and/or to act as a source for reintroduction as new habitat
389 became available. However, the captive program has only been moderately successful. As of
390 2015, the captive population consisted of seven females and eight males, which together produce
391 an average of one bird each year. Given a sex ratio of 50:50 this represents a rate of 0.07 females
392 produced per female per year. Realistic options for sourcing birds for reintroduction from the
393 captive population include:

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

400

401

Results

402 All population viability models predicted a negative population growth rate (Table 2) in the
403 wild populations, with none of the trajectories for the east and west subpopulations as well as the
404 meta-population persisting beyond 25 years (Figure 3, Figure 3A and 3B). As expected the
405 sensitivity analyses identified female mortality, followed by fecundity and juvenile mortality as
406 the main contributors to the overall population trajectory (Table 3). There are a number of
407 constraints to carrying out the proposed reintroduction scenarios given demographic variables in
408 the captive and wild populations. Assuming no changes to the fecundity among the captive flock,
409 sourcing the reintroduction using only captive birds would require either using six available
410 females (leaving one female in captivity; *i*), or moving 68 females from the wild into captivity to

411 increase the captive populations' productivity (*ii*). The third option (*iii*) would still require 30
412 additional females to be brought into captivity to supplement the captive flock in order to source
413 50% of the translocations (Table 4). The fourth option (*iv*) requires that eight additional birds are
414 brought into captivity so that the captive flock could consistently supply one female per year for
415 reintroduction efforts. Population trajectories among the last three scenarios (*iv*, *v* and *vi*) are
416 similar as they use the same input parameters, but the scenarios differed with regards to the
417 origin of individuals (Table 4; Figure 4).

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

425

426 Discussion

427 Our PVA models provide a tool to evaluate management scenarios and generate demographic
428 benchmarks necessary for a sustainable Maui parrotbill population. The rapid decline projected
429 by these models highlights the fact that certain aspects of the species' biology, ecology and life
430 history traits (e.g., mainly single egg clutches, prolonged parental investment) make this species
431 in its current state (e.g., small, contracting range, occupying potentially suboptimal habitat)
432 highly vulnerable to extinction. Our models allowed us to identify the demographic rates most
433 limiting the species, to explore potential management solutions, and identify the most promising
434 scenarios for reintroducing the species to previously occupied leeward mesic forests. Given the

435 assumptions in our model and current restraints in captive Maui parrotbill productivity, we found
436 that a reintroduction scenario that incorporates a minimal contribution from captivity and instead
437 translocates mostly wild individuals to be the most practicable strategy.

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

447 Weather has been identified as a key, limiting factor to reproductive success of Maui
448 parrotbills, with high incidence of nest failure in heavy rain events (Mounce et al. 2013).
449 Although weather cannot be manipulated, there have been numerous other unsuccessful attempts
450 to manage Maui parrotbills within their current forest habitat. These efforts have included trying
451 to increase productivity, survival, or both by providing supplemental food to wild individuals,
452 decreasing predation risk through control of invasive mammalian predators, and decreasing nest
453 predation by protecting nest trees from mammalian predation (suspected rat depredation on Maui
454 parrotbill nests; HL Mounce, personal observation). The forest currently occupied by Maui
455 parrotbills is native Hawaiian rainforest that is already protected (i.e., fenced and free of
456 ungulates) and actively managed by the National Park Service, the State of Hawaii, and The
457 Nature Conservancy. Thus, the vegetation community is in prime condition, and there are limited

458 options for other management interventions that can improve vital rates in Kiwikiu. It is
459 particularly concerning that the models presented here predict a rapid decline in the species given
460 that the species primarily occupies areas with such a high degree of protection. This leaves few
461 options beyond landscape-scale management actions (e.g., aerial broadcast rodenticide) in the
462 current range. Therefore, establishing an additional population that may appreciate increased
463 vital rates represents a measure that may ensure long-term persistence of the species.

464 Our model simulations and predicted extinction probabilities are limited by the precision of
465 the demographic parameters estimates. While this study has used the most comprehensive data
466 available on the Maui parrotbill, there is still uncertainty in several critical parameter estimates.
467 The variables with the most uncertainty included initial population size and annual habitat loss as
468 predicted through climate change models. However, our sensitivity analysis identified female
469 mortality at all ages as the parameter most responsible for driving the observed population
470 changes, with juvenile survivorship and fecundity playing a lesser role – yet (with the exception
471 of juvenile survivorship) these are all parameter estimates that we have high confidence in from
472 empirical studies (e.g., Mounce et al. 2015). Our model predictions contrast with the estimated
473 population estimates based on point counts over the last 20 years (Camp et al. 2009). These
474 disparities could be the result of un-modeled observation error in the count data, inaccurate
475 parameter estimates in the PVA model, or a variety of other analytic or sampling issues. It is
476 possible that the PVA is predicting a decline that has not yet been observed in the count data but
477 something we may see in the near future. All abundance estimates for this species are associated
478 with extremely large confidence intervals reflecting the low number of detections typically
479 recorded for the species on these counts. As a result, significant trends have not been found and,
480 although it has been tempting to say that the population is stable given similar abundance

481 estimates between years, we do not know whether the wild population is stable with any
482 certainty. It would be a mistake to ignore model predictions based solely on how well the output
483 conforms to count estimates for such a cryptic species. We suggest that a productive path
484 forward would be to implement an integrated population model that incorporates both
485 demographic data and count data, applies observation error models to both data sets and
486 integrates the analysis to estimate key demographic parameters using all available data (e.g.,
487 Schaub and Abadi 2011; Rushing et al. 2017).

488 Given the lack of management actions for increasing population viability in currently
489 occupied habitat, an alternative is to establish new populations, particularly in areas with high-
490 quality habitat. Historically, Maui parrotbills were observed to prefer koa as a foraging substrate
491 (Perkins 1903) and it stands to reason that habitats containing a higher proportion of koa, which
492 tend to occur in drier, leeward areas on Maui, were important areas for the species. Furthermore,
493 sub-fossil records show a distribution of this species across the island, not restricted to the high
494 elevation wet windward forests where they are found currently (James and Olson 1991). Today,
495 there are no Maui parrotbills in koa-dominated forests on Maui. We do not know whether Maui
496 parrotbills were historically distributed at higher densities in the wet windward forests, but it
497 may be that these areas were always marginal habitat. Regardless, if managers do not have the
498 tools to successfully manage this species in currently occupied habitats, then increasing the range
499 of occupied habitats may provide a viable long-term conservation strategy. Furthermore,
500 establishing geographically disjunct populations is good conservation practice, as having an
501 entire global population of a species within one 51 km² area (such as the Maui parrotbill) puts it
502 at greater risk of extinction in the event of a severe hurricane or other weather event.

503 Given the apparent limitation of management options in currently occupied habitats, moving
504 birds from existing populations to the leeward side of Haleakala, Nakula NAR, a drier, koa-
505 dominated habitat, as modeled here, may be necessary. Furthermore, the birds in this new habitat
506 may be able to benefit from increased survival and productivity, key to the species long-term
507 success. Options for moving birds include moving birds from the wild, using captive-bred birds,
508 and a combination of these alternatives. Using captive-bred individuals can have ecological
509 consequences such as behavioral deficiencies, high susceptibility to starvation and disease, high
510 post-release depredation rates and overall low reintroduction success rates that have been widely
511 documented (Curio 1996; Fischer and Lindenmayer 2000; Jule et al. 2008; Rantanen et al. 2010).
512 Captive Maui parrotbills have the additional disadvantage of reduced genetic variation and
513 significant genetic differentiation compared to some wild individuals (pairwise F_{st} and R_{st}
514 between west and captive populations [$F_{st} = 0.1$; $R_{st} = 0.16$] Mounce et al. 2015). Furthermore,
515 given the low reproduction rate of captive Maui parrotbills, using only captive-bred birds would
516 1) render the current captive population ineffective, 2) establish a new population with genetic
517 variation from just a few females (*i*) or 3) require that a large number of wild individuals be
518 brought into captivity (*ii* and *iii* requiring 23% or 10%, respectively, of all wild females).
519 Without considering potential effects on the wild populations, the resources necessary to capture
520 and care for these high numbers of an endangered species in captivity is unrealistic with current
521 conservation support available in Hawaii (Leonard 2008). Conversely, if the availability of
522 resources for this type of hands-on management substantially increased, there may be some
523 advantages, namely that captive birds may possibly anchor any wild birds to the release area,
524 which would facilitate monitoring (Banko et al. 2009). A major obstacle in translocations of wild
525 individuals is that they often reject the habitat close to release sites and travel long distances

526 before settling (Stamps and Swaisgood 2007), exhibiting preferences that captive individuals
527 may not have.

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

544 We further explored scenario *iv* by looking at the reintroduced population's viability using
545 parameter values from the current wild population (Figure 5; Mounce et al. 2013, Mounce et al.
546 2014) as well as predicted trends in annual fecundity, female survivorship and juvenile
547 survivorship increased by 5%, 10% and 20%. These changed demographics were examined
548 based on potential benefits that the leeward mesic habitat may have for the species. These

549 potential increased Maui parrotbill vital rates are not outside what has been estimated for other
550 honeycreeper species, including other Maui endemics (Woodworth and Pratt 2009). The exact
551 limitations of the wetter windward habitats are unknown but Maui parrotbills in the mesic forest
552 may have increased nest success, increased foraging success, or both in the drier habitat. Maui
553 parrotbills may also have reduced predation pressure in a habitat with lower invasive mammal
554 densities (HL Mounce, personal observation). No Maui parrotbills currently occupy koa-
555 dominated habitats, thus it is impossible to predict if the demography of released birds and their
556 offspring will differ from that of the windward population. Our results demonstrate that the
557 persistence of the reintroduced population is largely predicated on there being an increase in key
558 demographic parameters in the new and potentially favorable environment. Given the importance
559 of higher demographic rates for a new leeward population, a reintroduction strategy that includes
560 an adaptive management plan is likely the most successful approach, where elevated parameter
561 values in the leeward release sites serve as an alternative management hypothesis that can be
562 evaluated through management actions and system monitoring (Williams et al. 2007, Reference
563 S3). Managers could use the demographic parameter values we present here as benchmarks to
564 strive for in future populations to ensure that the populations are successful and viable.

565

566

Supplemental Materials

567

568 **Text S1.** The code for the custom-made model in Program R for the Maui parrotbill
569 557 (*Pseudonestor xanthophrys*) population viability analyses conducted. This is a female-only,
570 558 stochastic model assuming multiple, isolated populations. Notes are indicated with the
571 pound 559 symbol (#) and Program R will not read these as part of the code.

572 Found at DOI: <http://dx.doi.org/10.3996/072017-JFWM-059.S1> (11 KB DOCX).

573

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581 actions for Maui Parrotbills; Part II, pages 77-85.

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588

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770

771 **FIGURE LEGENDS**

772

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

776

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

782

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

791

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

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

802
803 **Figure 5.** Maui parrotbill (*Pseudonestor xanthophrys*) population trajectories for the proposed
804 future reintroduced leeward population (Nakula Natural Area Reserve) based on a realistic
805 proposed reintroduction scenario (scenario *iv*, wherein the captive flock sources 1 female/year
806 and additional translocations from wild populations [Hanawi Natural Area Reserve and The
807 Nature Conservancy's Waikamoi Preserve]). Panel A demonstrates a population trajectory
808 predicting trends in the reintroduced population with annual fecundity, female survivorship, and
809 young of the year set as in Mounce et al. (2013, 2014; A). The other panels demonstrate
810 trajectories for the same population with parameters increased by 10% (B), 15% (C), and 20%
811 (D) based on potential benefits of the leeward mesic habitat. Solid lines indicate mean number of
812 adult females in the population from 1000 model runs. Dashed lines indicate 95% CI around
813 mean values.

814 **Table 1.** Parameter input values for the base and modified base PVA model used for Maui
815 parrotbills (*Pseudonestor xanthophrys*). Input parameters derived from Mounce et al. (2013,
816 2014, 2015), Warren et al. (2015), and unpublished data from Maui Forest Bird Recovery
817 Project. Values in bold highlight changes between the Base and Modified Base models.
818 Percentage of breeding females and survival rates are presented with estimates of environmental
819 variation (EV; \pm 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 (\pm 0.25)	56 (\pm 0.25)	56 (\pm 0.25)
% 1 offspring (% 2 offspring)	95 (5)	95 (5)	95 (5)
% survival rates 0-1, S_y	17 (\pm 0.15)	32 (\pm 0.02)	32 (\pm 0.02)
% survival rates after age 1, S_a	72 (\pm 0.02)	72 (\pm 0.02)	72 (\pm 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

820

821

822 **Table 2.** Population viability analysis model results for the base and modified base model for the
823 Maui parrotbill (*Pseudonestor xanthophrys*) population(s) with the viability measures of λ
824 (median rate of population change), PQE (probability of quasi-extinction [$N < 10$] at 25 years), N-
825 all (median population size from all iterations at year 25), N-extant (median population size from
826 extant populations at year 25). * N-extant is defined as $N > 10$, thus in the base model with N-
827 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

828

829 **Table 3.** Results of the sensitivity and elasticity analysis for the Maui parrotbill (*Pseudonestor*
830 *xanthophrys*) meta-population based on parameter changes in the “modified base model.”
831 Demographic parameters included were juvenile survival (% survival rates 0-1; S_y), adult
832 survivorship (% survival rates after age 1; S_a), and fecundity (F). Lambda (λ) for this model was
833 0.866

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

834

835

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

842

	Scenario <i>i</i>					Scenario <i>ii</i>			
	East	West	Leeward	Captive		East	West	Leeward	Captive
# to captivity	0	0	-	-	# to captivity	51	17	-	-
# to Leeward	0	0	-	7	# to Leeward	0	0	-	15
PQE	0.990	1.000	1.000	0.089	PQE	0.966	1.000	1.000	0.000
N-all	1	1	0	9	N-all	1	0	1	66
SD N-all	2.157	0.599	0.422	4.469	SD N-all	1.701	0.528	0.475	4.127
N-extant	14	-	-	12	N-extant	11	-	-	66
SD N-extant	1.805	-	-	2.36	SD N-extant	3.559	-	-	4.127

	Scenario <i>iii</i>					Scenario <i>iv</i>			
	East	West	Leeward	Captive		East	West	Leeward	Captive
# to captivity	23	8	-	-	# to captivity	6	2	-	-
# to Leeward	4.5	3	-	7.5	# to Leeward	7.5	4.5	-	3
PQE	0.991	1.000	1.000	0.000	PQE	0.988	1.000	1.000	0.000
N-all	1	1	0	32	N-all	1	1	0	18
SD N-all	1.936	0.555	0.483	4.263	SD N-all	1.884	0.556	0.477	4.230
N-extant	11	-	-	32	N-extant	10	-	-	18

SD N-extant	1.59	-	-	4.263
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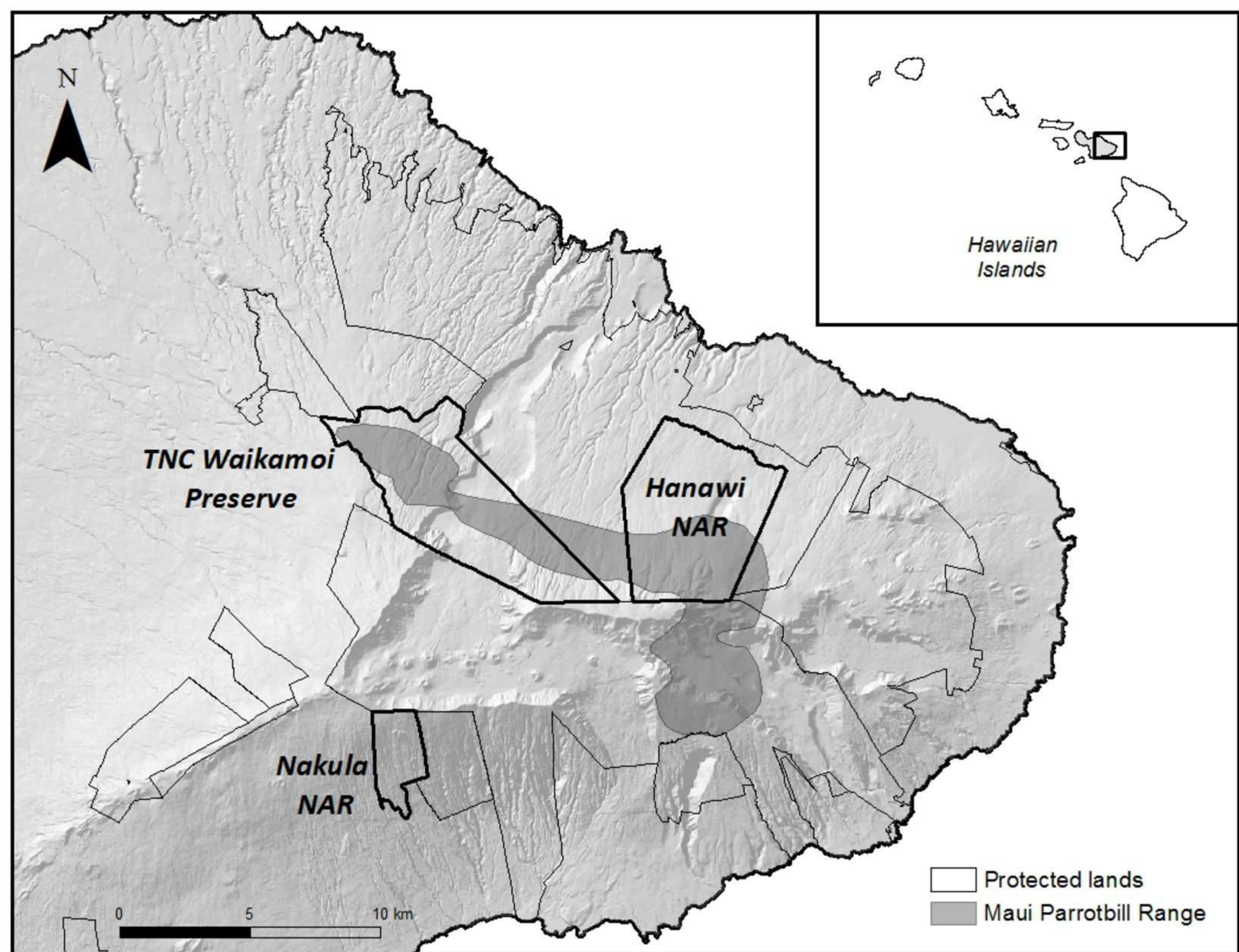
SD N-extant	2.348	-	-	3.972
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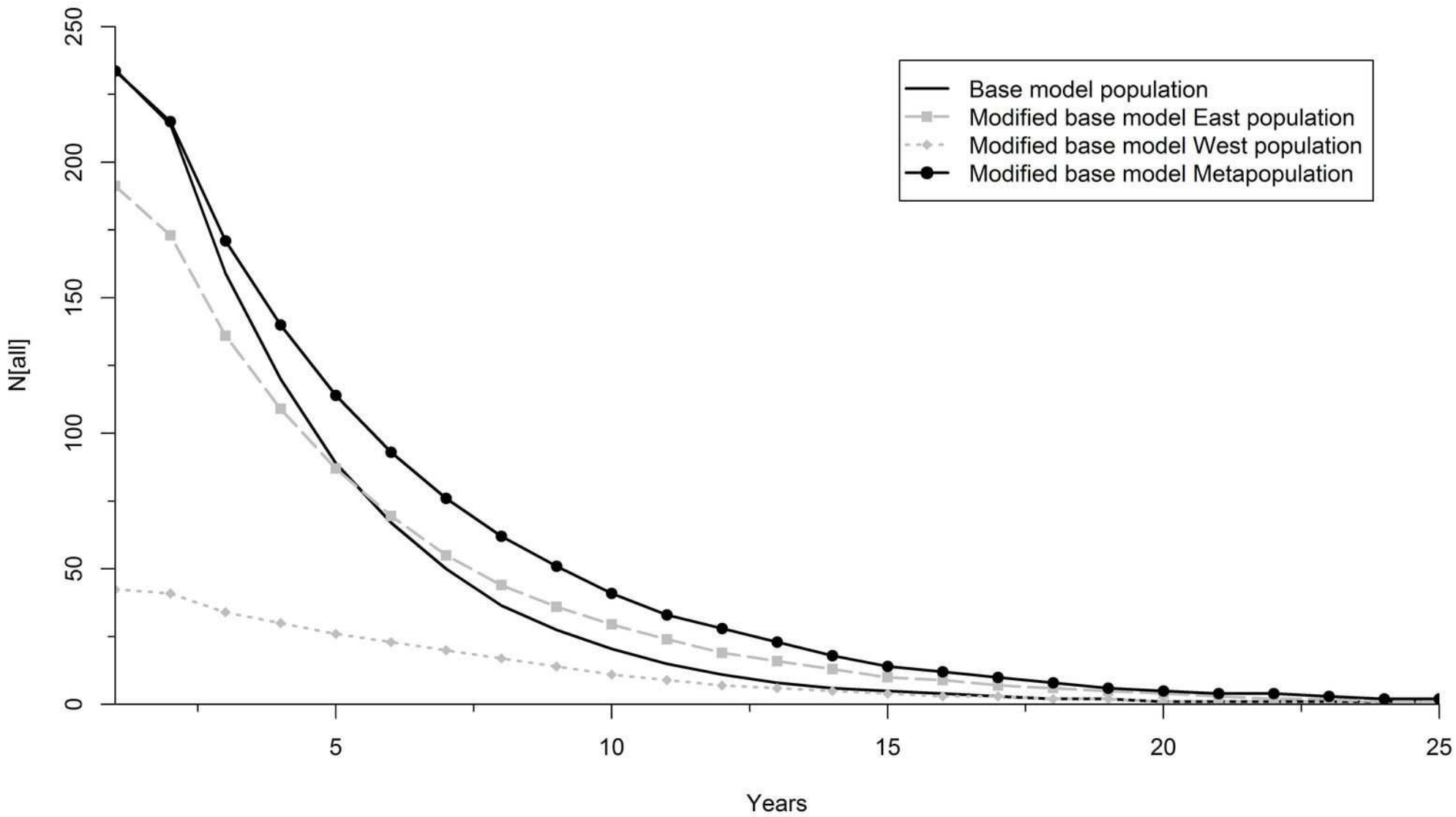
Scenario <i>v</i>				
	East	West	Leeward	Captive
# to captivity	0	0	-	-
# to Leeward	4.5	3	-	7.5
PQE	0.989	1.000	1.000	0.045
N-all	1	1	0	10
SD N-all	2.018	0.563	0.455	4.443
N-extant	12	-	-	12
SD N-extant	1.859	-	-	2.762

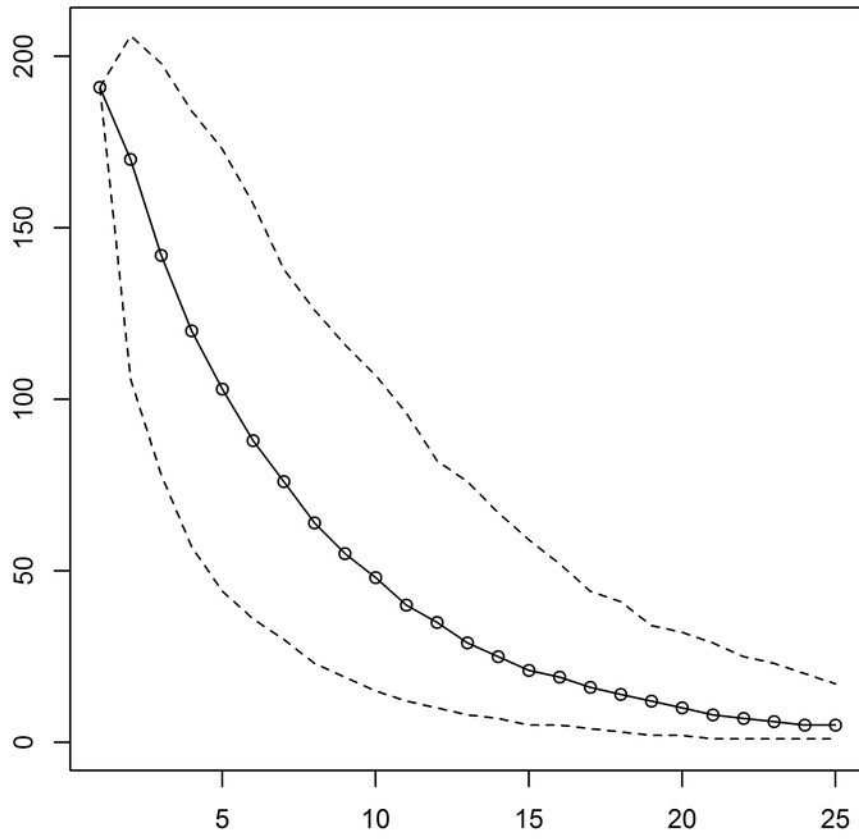
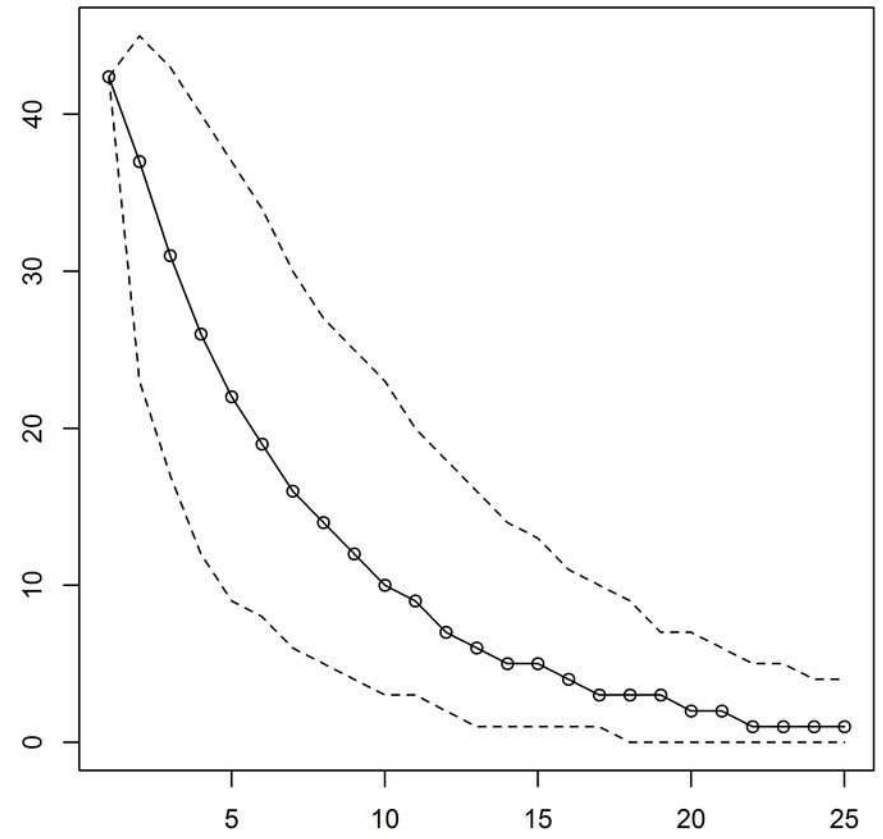
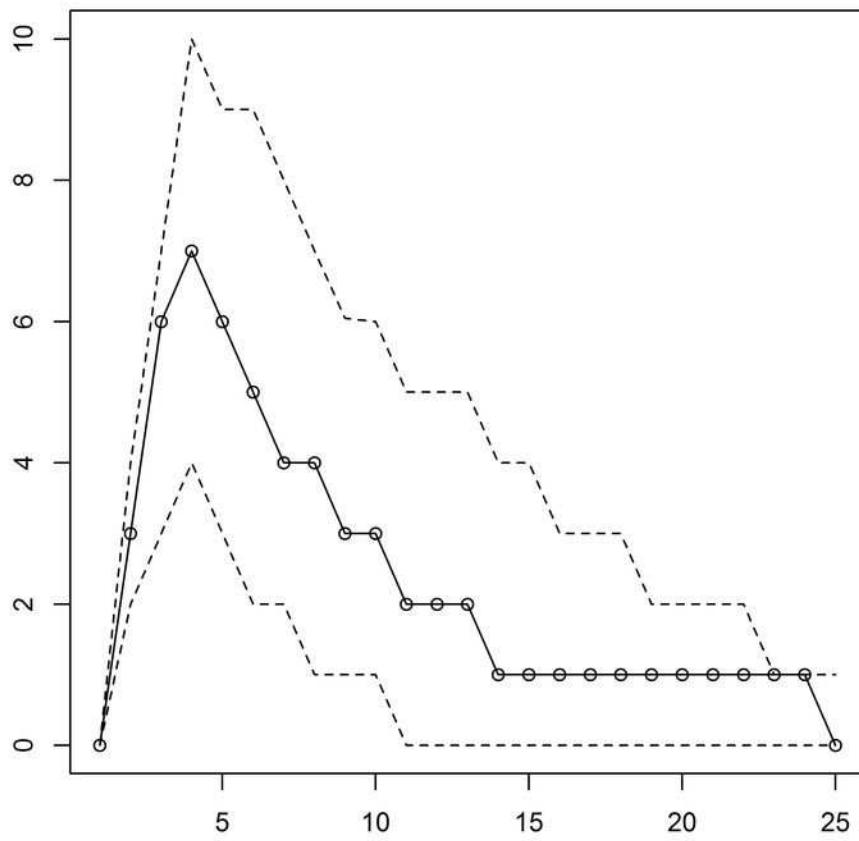
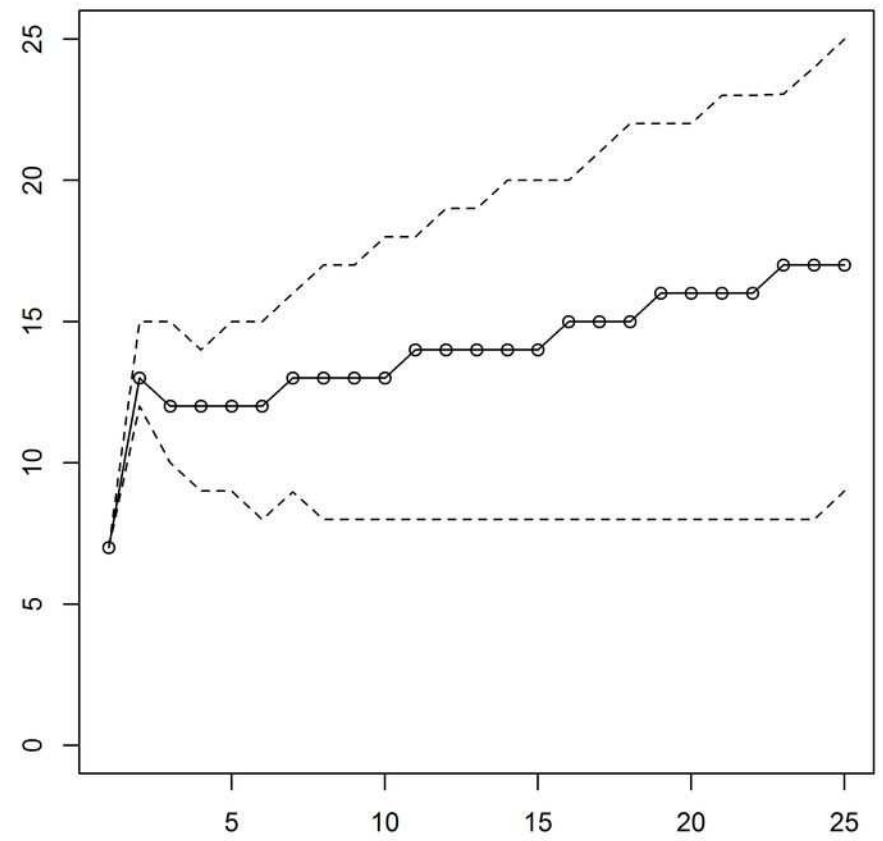
Scenario <i>vi</i>				
	East	West	Leeward	Captive
# to captivity	0	0	-	-
# to Leeward	9	6	-	0
PQE	0.980	1.000	1.000	0.006
N-all	1	1	0	13
SD N-all	2.367	0.640	0.465	4.241
N-extant	12	-	-	14
SD N-extant	3.832	-	-	3.311

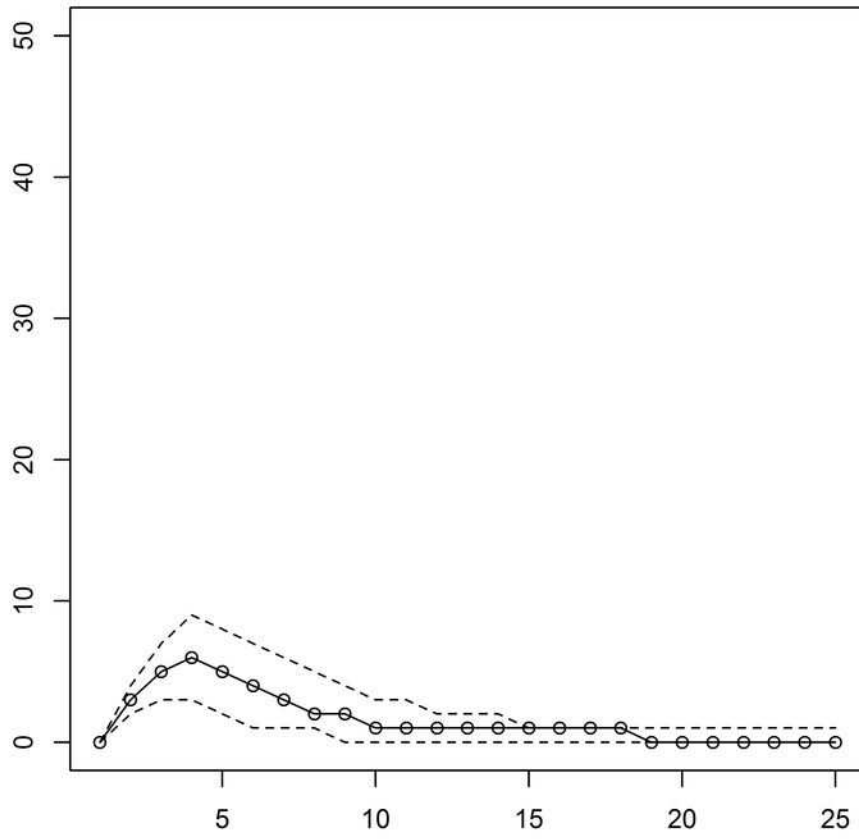
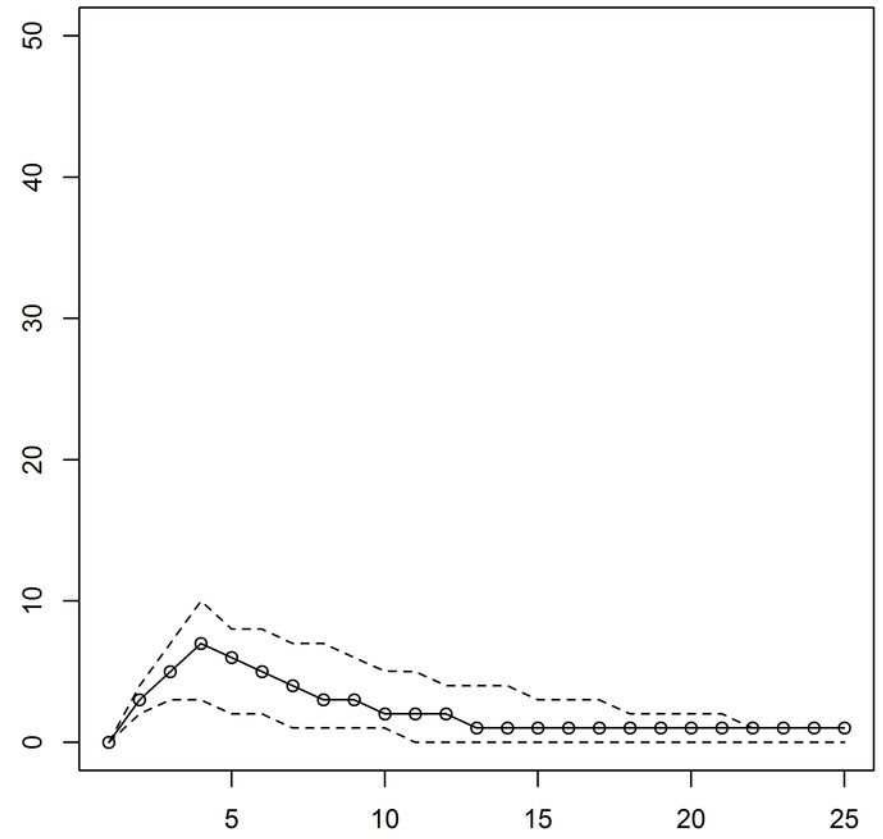
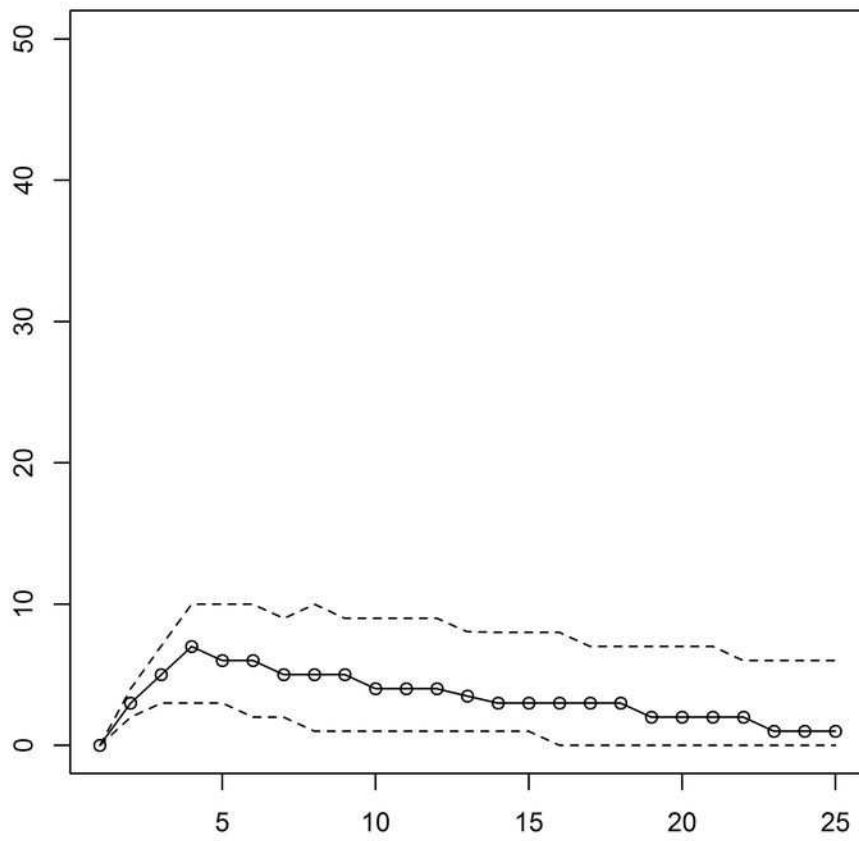
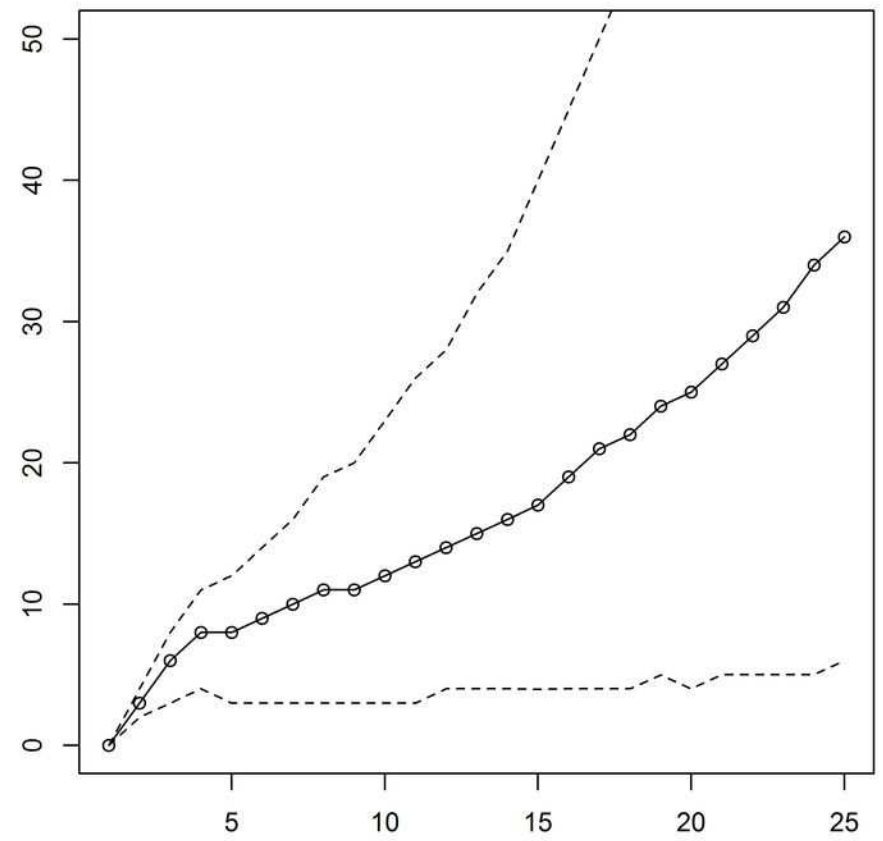
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A) East**B) West****C) Leeward****D) Captive****Year**

A) +0%**B) +5%****C) +10%****C) +20%****Year**