EVALUATING POPULATION VIABILITY AND CONSERVATION OPTIONS FOR THE ENDANGERED PUAIOHI

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For my daughters, Olivia and Isabel,

who have grown up right along with this dissertation,

and my husband, Chris--

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Abstract

Evolution in the Hawaiian Islands has produced a unique assemblage of forest birds. Unfortunately, many of these species are highly endangered or extinct. Despite numerous threats and great effort aimed at saving endemic birds, we lack basic science necessary for understanding many species of concern, including the endangered puaiohi (*Myadestes palmeri*). Currently, the puaiohi's breeding population is estimated at 500 birds restricted to the Alakaʻi Wilderness Preserve on Kauaʻi. Given its small population and restricted range, understanding the conditions that affect the species' population dynamics is essential. Hence, the goals of this dissertation were to: investigate links between precipitation and temperature in the puaiohi's range and reproductive success; represent puaiohi population dynamics under current and potential management scenarios to determine management's potential efficacy in aiding species recovery; and, investigate which management activities might supply the most cost-effective species management. Management scenarios included rat management, habitat improvement (habitat restoration or supplemental feeding), provision of nest boxes, and translocation of an additional population to another island. Total rainfall in the previous wet season and mean rainfall during the breeding season positively correlated with most nest success variables. Female and juvenile survival most influenced puaiohi population viability, indicating that management should focus on increasing female and juvenile survival. Rat control, even at conservative levels, was the most effective method of increasing puaiohi abundance. While translocation offers hope of increasing puaiohi population and decreasing extinction risk, success depends on the conditions established at the release site. In addition, re-establishment of the puaiohi captive breeding program may be necessary to provide enough birds to translocate.

Management costs over the 25 years modeled ranged from $378,701 to $245,213,905, with translocation being one of the most cost-effective means of managing puaiohi and supplemental feeding the least. Cost-efficiency of rat control varied based on scale and method, and restoration of habitat was moderately cost-effective. Findings indicate that practical, attainable management activities can increase puaiohi and bring it back from the brink of extinction. These findings provide a model for other endangered species conservation efforts.

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CHAPTER 1

INTRODUCTION

The Hawaiian Islands are home to some of the most rapidly disappearing, rarest, and evolutionarily unique bird species in the world (Banko and Banko 2009, Pratt 2009). An island archipelago which evolved in relative isolation, its species have been devastated by the arrival of humans (Pratt 2009, Banko and Banko 2009). The rats, pigs, goats, cats, mosquitos and hosts of plants and insects humans have introduced to Hawaiʻi have indelibly altered its unique ecosystems. Once home to 152 land bird species, 110 of these have gone extinct since human arrival (Walther 2016). Thirty-three of its remaining 42 endemic birds are listed as endangered or threatened, making Hawaiʻi home to one of the most endangered avifaunas in the world (American Bird Conservancy 2016, Walther 2016). One such critically endangered Hawaiian bird species is the puaiohi, or small Kauaʻi thrush (*Myadestes palmeri*). Endemic to Kauaʻi, the puaiohi is one of only two extant (of the six historic) endemic Hawaiian birds in the thrush family, Turdidae. A fairly prominent white eye ring helps distinguish this relatively nondescript medium-sized brown and gray solitaire thrush from other Hawaiian thrushes. Males and females are similar in appearance, while juveniles show scalloping in their breast, belly and wing feathers (Snetsinger et al. 1999). Puaiohi are now the only native frugivore on Kauaʻi, and may play a major role in seed dispersal within their range (Pejchar, unpubl data). The only other extant thrush in Hawaiʻi is the ʻōmaʻo (*Myadestes obscurus*) which is endemic to the Island of Hawaiʻi. While ʻōmaʻo range and densities have declined, it still has a sizable and contiguous population (Gorresen et al. 2009, Scott et al. 1986) and is currently listed as vulnerable by the IUCN (2012). The remaining four thrushes originally present in the islands, (kāmaʻo [*Myadestes myadestinus*],

ʻāmaui [*Myadestes woahensis*], Lanaʻi ʻolomaʻo [*Myadestes lanaiensis lanaiensis*], and Molokaʻi ʻolomaʻo [*Myadestes lanaiensis rutha*]) are all extinct (Reynolds and Snetsinger 2001, Woodworth and Pratt 2009). The puaiohi is also one of the last six endemic forest bird species to remain in the Alakaʻi Swamp. Over the past 30 years, five other species disappeared from the swamp following Hurricanes ʻIwa (1982) and ʻIniki (1992) (Conant et al. 1998). Though some of these species were rare in the early 20th century (Perkins 1903), most were more common than the rare puaiohi. In fact, its congener, the kāmaʻo, was once the most common forest bird on Kauaʻi (Perkins 1903, Scott et al. 1986), yet the puaiohi has persisted while the kāmaʻo is extinct.

Currently, the puaiohi is restricted to about 40 km^2 of forest in the Alakaʻi Wilderness Preserve (Crampton et al., in review). Puaiohi live in forested ravines along streams above 1,050 m elevation (Snetsinger et al. 1999, U.S Fish and Wildlife Service 2006a), in wet native montane ʻōhiʻa (*Metrosideros polymorpha*) forest, with subdominant ʻōhia ha (*Syzygium sandwicensis*), and ʻōlapa (*Cheirodendron* spp.), and a rich understory of native plants including ʻōhelo (*Vaccinium calycinum*) and kanawao (*Broussaisia arguta*). The puaiohi has experienced range contraction since the 1960s (Scott et al 1986, U.S Fish and Wildlife Service 2006a), as it is no longer found at lower elevations (1000-1050 m) and is currently restricted to a forest remnant at 1050 to 1300 m. Surveys suggest the population is around 500 birds and appears to have remained relatively stable since 1973 (U.S. Fish and Wildlife Service 2006a, Crampton et al., in review).

While puaiohi are primarily frugivorous, arthropods form an important dietary component, particularly during the breeding season (Richardson and Bowles 1961, Kepler and Kepler 1983, Scott et al. 1986, Snetsinger et al. 1999). Fruit eaten include those from ʻōlapa species, ʻōhia ha, kanawao (*Broussaisia arguta*), ʻōhelo, paʻiniu (*Astelia* spp.), pūkiawe (*Styphelia tameiameiae*), kāwaʻu (*Ilex anomala*), and pilo (*Coprosma* spp.) (Snetsinger et al. 1999).

Breeding typically occurs between March and August. Two eggs are laid per clutch, and a pair can nest up to five times during a breeding season (Snetsinger et al. 2005, Fantle-Lepczyk et al. 2016). Females build the nest, incubate the eggs, and brood and feed the nestlings (Snetsinger et al. 1999). After fledging, the male becomes the primary food provider to the young, while the female attempts a second brood (Snetsinger et al. 1999). Females will also re-nest if the first attempt fails (Snetsinger 2005). Pairs have potentially high, but quite variable productivity, with pairs producing 0.4 to 4.9 young per year (Snetsinger et al. 2005, Fantle-Lepczyk et al. 2016). Nests are concealed by mosses and ferns on cavities or cliff face ledges along streams, though tree cavities are also used (Kepler and Kepler 1983, Scott et al. 1986, Conant et al. 1998, Snetsinger 1999).

Although hurricanes have caused serious damage to puaiohi habitat, the species appears to recover relatively well, probably because their preferred ravines are better sheltered (Conant et al. 1998, Snetsinger et al. 1999). However, droughts appear to have a negative impact on reproductive output (Fantle-Lepczyk et al. 2016). Predation by native Short-eared Owls (*Asio flammeus*) and alien mammals (e.g., *Rattus* spp.) suppresses productivity and competition for food with introduced insects, birds, and mammals may also have negative impacts (Snetsinger et al. 1999, Snetsinger et al. 2005). Several plants, including blackberry (*Rubus argutus*), Australian tree fern (*Cyathea cooperi*), kahili ginger (*Hedychium gardnerianum*), daisy fleabane (*Erigeron annuus*), and strawberry guava (*Psidium cattleianum*) have significantly altered areas currently and recently occupied by puaiohi, and have the potential to convert the forest canopy, understory, and cliffs used for nesting substrate to unsuitable habitat (Crampton et al. in press). Malarial infection is also a concern, though the extent of its impact on the population remains unclear. Avian malaria (*Plasmodium relictum*) was detected in 22.7% of birds tested in 2007-2008 (Atkinson et al. 2014). This high prevalence may indicate that at least some puaiohi survive acute infection and have some tolerance of malaria (Atkinson et al. 2001).

The puaiohi was added to the United States Federal Endangered Species List on March 11, 1967 (U.S. Fish and Wildlife Service 2006b), and was included in the Kaua‘i Forest Bird Recovery Plan (US Fish and Wildlife Service 1983). Since 1995, ongoing research focusing on determining puaiohi population size and status, and assessing the influence of food availability, habitat structure and composition, predation, and introduced disease on survival and reproductive success (and ultimately abundance) have been carried out by the United States Geological Society (1995-2000) and the Kaua‘i Forest Birds Recovery project (KFBRP; 2001-present; Kaua‘i Forest Bird Recovery Project, 2016a). In addition, managers have been actively managing the puaiohi in hopes of increasing the population to sustainable levels. Early studies showed that poison bait stations around active puaiohi nests, reduced rat predation on nests and increased nest success (Snetsinger et al. 2005). In recent years, managers have begun controlling rats via 300 Goodnature A24 self-resetting rat traps across approximately 50 ha of remote forest (Kaua‘i Forest Birds Recovery Project 2016b). In addition, several types of nest boxes have been installed in puaiohi nesting habitat, to increase nest site availability, decrease nest predation, and expand puaiohi range (VanderWerf 2013). However, to date only a few pairs have been documented to successfully use nest boxes, and a preferred rat resistant design has yet to be identified. KFBRP continues to investigate the feasibility of using artificial nest boxes. Several NGOs have taken steps to control invasive alien plants in the Alaka‘i Wilderness

Preserve, and in 2010 a 810 ha unit was fenced with ungulate proof fencing and ungulates are being eradicated, with plans to fence three more adjacent units and protect an additional 1,215 ha in core puaiohi area (VanderWerf 2013). Finally, concerns about puaiohi's limited range and small population led to the establishment of a captive-bred population in 1996. From 1999 to 2012, a total of 222 birds were released into the Alakaʻi (Switzer et al. 2013). However, due to the relatively low recruitment and survival of released birds in later years of the program and signs of congenital abnormalities in captive bred chicks, the program was discontinued and the last of the captive flock was released in 2016 (DLNR 2016, VanderWerf et al. 2014, Switzer et al. 2013).

Despite the research and management activities directed at saving endemic birds like the puaiohi, some of the most basic science necessary for understanding them has never been done (Duffy and Krauss 2008). For instance, population models and population viability analyses (PVA) have not been conducted for 66% of Hawaiʻi's endangered avifauna, representing a critical gap in knowledge. This lack of knowledge is problematic, given that population viability is one of the criteria used for down listing (or de-listing) a species and that the draft recovery plan for Hawaiian Forest birds ranked PVA as an action necessary to prevent a significant decline in populations (U.S. Fish and Wildlife Service 2006c). To accurately assess the viability of these endangered species in the face of a changing climate, invasive species, and human population growth, and to provide the basis for conservation, population models and PVAs are urgently needed.

Population viability analysis

PVA (Ellner and Fieberg 2003) allows for incorporation of demographic and environmental variables to forecast population persistence and extinction risk. Though actual quantitative model results can be limited, PVA is useful for testing the relative power of model parameters via sensitivity analysis, evaluating management strategies, and identifying priorities for maximizing effective species recovery (Beissinger and Westphal 1998, Brook et al. 2000, Cross and Bessinger 2001, Reed et al. 2002). Given its utility, PVA has had a long and evolving history in conservation biology.

In the 1970s, Yellowstone National Park was embroiled in a heated debate over how to manage the Park's problem grizzly bears (*Ursus arctos*). To explore the outcomes of the proposed management options, researchers developed a model for the bears that incorporated random variability, and calculated extinction probabilities and minimum viable population size (Shaffer 1983, Shaffer and Samson 1985). This first attempt at modeling a species' or population's long term viability opened a whole new chapter in conservation biology research. Throughout the 1980s, researchers focused on calculating the minimum viable population (MVP) for species (Gilpin and Soulé 1986, Soulé and Mills 1992). However, this idea drew criticism as it is unlikely that a minimum number of individuals can persist indefinitely and the number of individuals required to carry out ecological functions may be much larger than the minimum number needed for a species to persist (Soulé et al. 2003). To address these criticisms, Gilpin and Soulé (1986) broadened the concept of MVP to what they called population vulnerability analysis and used it as a heuristic to examine the many forces that can affect the viability of a population.

Eventually the concept of population *vulnerability* analysis evolved into population *viability* analysis (PVA) which embraced the ideas behind MVP while removing the idea of focusing on a single population size. This evolution allowed for the development of a much more constructive and reliable model which can evaluate a range of effects under a range of possibilities. Hence, the modern iteration of PVA is the process of identifying the viability requirements of and threats faced by a species and estimating the likelihood it will persist into the future (Akçakaya and Sjögren-Gulve 2000, Boyce 1992). In essence, PVA is a marriage of ecology and statistics that brings together species characteristics and environmental variability (stochasticity) to forecast population persistence and extinction risk.

PVA has become one of the most powerful and widely used tools in conservation biology over the past two decades (Reed et al. 2002). In fact, PVA has been called one of the cornerstones of modern conservation biology and credited with being partly responsible for conservation biology's emergence as a credible science (Beissinger and Westphal 1998). Across the United States, PVA has become a common approach in species management as federal agencies and ecologists required methods to evaluate the risk of extinction and possible outcomes of management decisions, particularly in accordance with the Endangered Species Act of 1966, and the National Forest Management Act of 1976, which require that biologists manage species for "viable populations" (Boyce 1992, Reed et al. 2002). Furthermore, as personal computers advanced and software packages became more readily available in the late 1980s and early 1990s (Lindenmayer et al. 1995), use of PVA increased dramatically. Currently, the types of PVA vary widely and there are a variety of modeling programs available to assess population viability, which is particularly important for rare and threatened species.

Uses of population viability analysis in conservation

PVA is often oriented towards the conservation and management of rare and threatened species, with the goal of applying the principles of population ecology to improve their chances of survival. In particular, PVA is often used to quantify the risk of extinction and to examine the relative benefits of alternative management actions (Ellner and Fieberg 2003, Beissinger and Westphal 1998). Predicting the risk of and time to extinction under a variety of scenarios can inform conservation decisions and management efforts (Clark et al. 1990). In general, threatened species management has two broad objectives. The short-term objective is to minimize the risk of extinction, while the long term objective is to promote conditions in which species retain their potential for evolutionary change without intensive management (Akçakaya et al. 1999). PVA can be used by conservation biologists to address several specific areas in which they may need more information, especially in targeting essential research and data needed to better assess population status, assessing the population or species vulnerability, and evaluating and ranking management options and impact of human activities (Morris et al. 2002, Akçakaya and Sjögren-Gulve 2000). In addition, PVA can be applied to validate focal or umbrella species to guide conservation efforts for entire nested species groups (Fleishman et al. 2000).

Perhaps the most undervalued aspect of PVA's utility in conservation biology is that it may reveal that population viability is strongly linked to particular model parameters. Such model insights provide conservation biologist with insights into where they need to devote resources in order to develop the best possible parameter estimates and into which demographic characteristics of the population are the most efficacious to manage in terms of conserving the population. For instance, if the PVA shows that population numbers are most strongly affected by juvenile mortality, and managers know that they can increase juvenile survival by controlling rats, the model can help guide them to manage for increased survival of this age class. In addition to providing information on specific demographic factors, PVA can be used to rank management options amongst a suite of possible activities (e.g., Duca et al. 2009, Garcia-Ripolles and Lopez-Lopez 2011, Proctor et al. 2004). For instance, PVA may be used to predict the likely response of species to reintroduction, captive breeding, predator control, habitat rehabilitation, or different nature reserve or corridor network designs. This predictive power allows managers to explore the possible outcomes of a suite of management options without risking potentially ineffectual ones on a species that needs immediate help. Analogously, PVA can also be used to assess the impact of human activities, such as development or exploitation of resources, by comparing results of models with and without the consequences of the activity. Finally, PVA can be used to assess the overall vulnerability of a species or population by putting hard numbers and graphical representations to a species' potential trajectory and thus be used to illustrate the dangers the species faces. Together with cultural priorities, economic imperatives, and taxonomic uniqueness, PVA may be used to set policy and priorities for allocating scarce conservation resources.

Because resources are often a limiting factor for conservation efforts, one benefit of using PVAs is that they can be integrated with decision support tools. By integrating these two approaches, it is possible to evaluate and compare conservation strategies (Clark et al. 1991, Drechsler and Burgman, 2004) before investing in implementing them, thereby allowing managers to make more insightful decisions. For instance, incorporating realistic economic costs can aid in determining how different conservation actions or management options provide the best or most optimal viability for a given financial expenditure (Noon and McKelvey 1996, Possingham et al. 2001, Yokomizo et al. 2003, Haight et al. 2004, Yokomizo et al. 2004, 2007).

While valuable, the integration of PVAs and economic assessments has been quite rare (e.g., Larson et al. 2003, Tisdell et al. 2005). Such rarity is particularly disconcerting in light of the fact that funding available for conserving many threatened and endangered species is often very limited. By failing to integrate economic considerations in PVA modeling efforts, less efficient management plans may be implemented which ultimately divert resources away from more cost-efficient conservation actions (Baxter et al. 2006). Given the large numbers of threatened and endangered species in places like Hawaiʻi, less efficient use of resources is particularly problematic (Baillie et al. 2004), as optimizing conservation spending requires tightly focused research agendas having benefits (answers) clearly linked to costs (Duffy and Kraus 2008).

Modeling population viability analysis

Every PVA is different, because every species and every situation is different. However, all good PVAs should follow some general steps to develop a sound and accurate model. A good model begins with the identification of a question to be investigated, after which a model is constructed to explore the question. Once constructed, model parameters are estimated and entered into the model, and the model is run through a variety of iterations. After the model is run, sensitivity analysis can be run to account for variability in the data and to identify which parameters are most sensitive to change. Finally, the model can be used to implement efficacious management activities or shape management policy (Akçakaya et al. 1999, see Fig. 1.1). Though not all PVAs will have all of the components identified in Fig. 1.1, and some will have additional ones, general steps and options are discussed below in more detail.

As with any good scientific study, a PVA should start with a specific question of interest. Depending on what is known about the species, the question may be very general, though with more data it can become more specific and informative. Some examples of appropriate questions would entail: 1) what a species extinction risk is over the next 50 years; 2) whether it would be more appropriate to protect a species from hunting or procure more habitat for it; 3) whether reintroduction of captive bred individuals to the wild is a viable strategy for conserving a species; and, 4) if captive reintroduction is viable, whether or not it’s better to introduce all the individuals into one or over several patches?

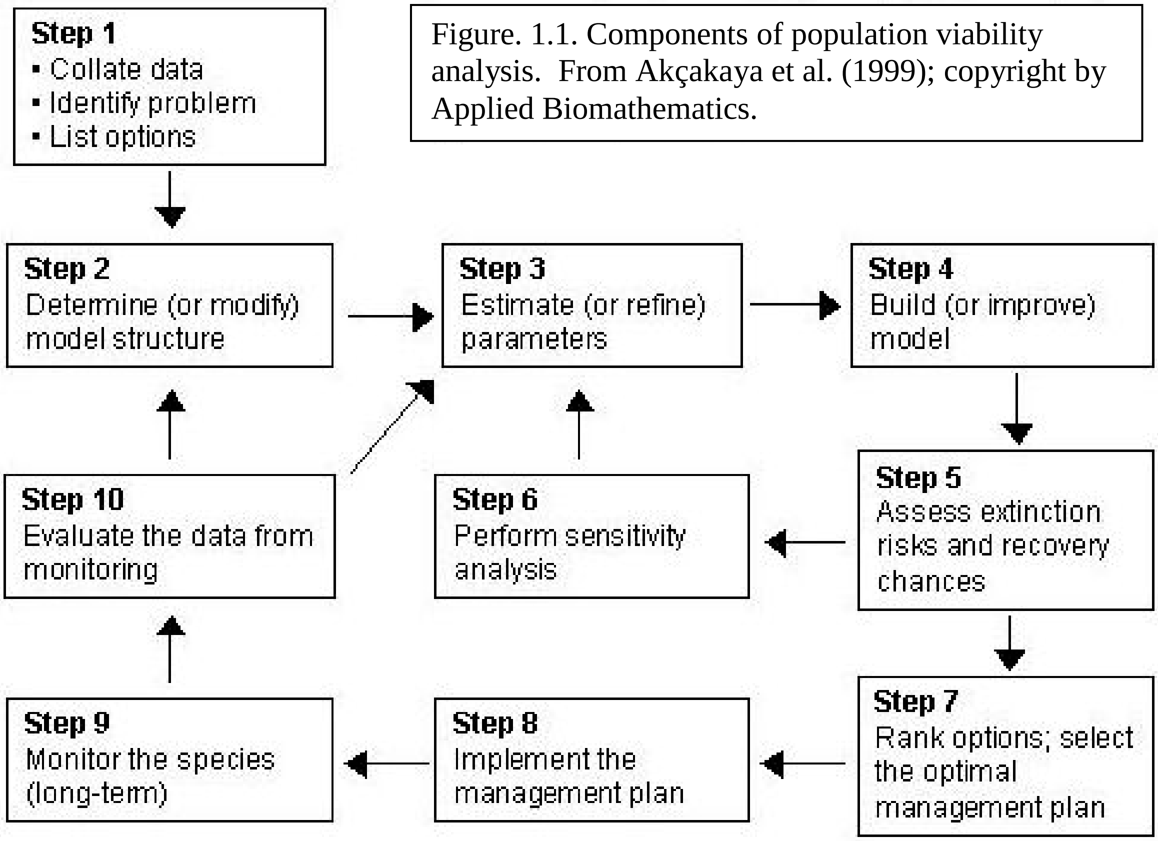

Figure. 1.1. Components of population viability analysis. From Akçakaya et al. (1999); copyright by Applied Biomathematics.

In order to develop study questions, the PVA should concentrate on the identification of natural factors and human impacts that are important in dynamics of the specific populations, as well as potential conservation and management options (Step 1, Fig. 1.1). Available data and demographic information should be reviewed and collated. Depending on the available data and questions to be addressed, this collation might include statistical analysis of historical data, comparison of populations that are declining with those that are stable, and correlating recent changes in the environment, such as those due to climate change, habitat loss or invasive species, with changes in the target species.

Once questions have been articulated and data collected, the next step is to determine the model structure (Step 2, Fig. 1.1). The most appropriate model structure for a PVA will depend on what data are available, the species' natural history and ecology, and the kinds of questions that the biologists wish to answer. Depending upon the biological facts known for the population in question, PVAs can be based on exponential, density-dependent, interactive multi-species (generally, predator-prey), metapopulation, or other types of spatially-implicit models, or even age/stage dependent models (Boyce 1992, Morris and Doak 2002). Since many of the populations of endangered species for which PVA is utilized are so small, they are unlikely to experience any changes in net recruitment due to increasing density. As a result, density-independent exponential models are reasonable to use for these populations. Furthermore, depending upon the quality of the available data, the PVA may be demographically explicit, based on time series data, or based on presence/absence data for a multi-population approach (Morris and Doak 2002). While the time series approach is acceptable and can competently predict a population's viability, in many ways demographically explicit models are preferable as they have the benefit of being able go beyond simply predicting viability and actually point towards actions that will most effectively reverse a declining population (Beissinger and Westphal 1998, Reed et al. 2002).

Following model construction, parameter estimation (Step 3, Fig. 1.1) is conducted with data collected from field studies and/or laboratory experiments. The better the data available, the more detailed a model can be, which allows for a detailed and realistic model that can address more specific questions. Of particular importance is that the model should have a parameter related to the question being investigated (Akçakaya and Sjögren-Gulve 2000). For instance, if the research question involves the effects of development on a population, the model should include at least one parameter that realistically reflects development. The amount and type of data needed for a PVA depends primarily on the question addressed and the ecology of the species. For most PVA studies, this is the limiting step, because data are often insufficient. This lack of data is also one of the most criticized and controversial steps of the analysis, as many conservation biologists are concerned with the effects of the estimation error on the overall model (Taylor 1995, Beissinger and Westphal 1998). In cases where data are unavailable, model parameters can be estimated from those known for similar species (i.e. congeners) or situations. In order to control for error in the estimation of the data, a range of numbers can be used for that parameter instead of a single number. These ranges can then be assessed via sensitivity analysis as described later in this paper.

Once the model structure is chosen and all the parameters estimated, the model can be constructed and estimated.   Constructing a model combines the existing data into predictions about the persistence of species under different assumptions of environmental conditions and under different conservation and management options (Steps 4 and 5, Fig. 1.1). Regardless of structural details, all PVAs use estimated variation in demographic parameters to add stochasticity to simulated populations. By simulating models hundreds or thousands of times using an approach such as Monte Carlo models, one can assess the probability of falling below an arbitrary critical value termed the quasi-extinction threshold. This quasi-extinction threshold is almost always set above zero to reflect the fact that any population that drops below a given low level is likely doomed to extinction even if can persist at such low levels for an extended period and the fact that at small population sizes many models behave differently than at large population sizes (Sinclair et al. 2006). Thus, at the model construction stage the assumptions that go into the model must be clearly defined and be reasonable for the species being studied. The structure of the model and the questions addressed usually determine how the results will be presented. Since these models generally include stochasticity, in addition to the potential variations or errors in parameters, results are generally presented as probabilities or likelihoods.

Sensitivity analysis (Step 6, Fig. 1.1) can be used to complement the predictions that arise from running the model by providing insights into which parameters most affect the quasi-extinction probabilities of the population (Reed et al. 2002). Several approaches can be used to assess parameter sensitivity, ranging from analytical sensitivity and elasticity analysis to PVA-based modeling (Cross and Beissinger 2001, Mills and Lindberg 2002). Often, the model must be run many times, with different combinations of the low and high values of each parameter to ensure that all uncertainty in parameter values is accounted. Similarly, if a parameter is not given a range, a modeler often varies it by 10-20% above and below the given value and evaluates the model outcome as another approach to sensitivity analysis. Sensitivity analysis is particularly useful for two reasons. First, it helps researchers identify which parameter estimates are most critical for population studies (Reed et al. 1993). For instance, if the extinction probability is very different based on variations in the value of adult survival rate, then the results are sensitive to this parameter. Hence, we can surmise that future field studies should concentrate on estimating adult survival rate more accurately (this feedback is represented by an arrow from Step 6 to Step 3, Fig. 1.1). Second, sensitivity analysis provides insights into the most efficient ways to increase growth in a declining population (Reed et al. 1993). When simulations include different management options, sensitivity analysis gives information about the effectiveness of these options, and these can be used to further inform management decisions.

With the selection of the best course of action under a given set of conditions (Step 7, Fig. 1.1), the modeling is completed, and the most effective plan can be implemented (Step 8, Fig. 1.1). Field monitoring can continue to yield data (Step 9, Fig. 1.1) which can be used to refine and improve the model parameters, and give valuable information about the response of the species to management (Step 10, Fig. 1.1). While these steps provide an idealization of how PVA can be used, many criticisms and caveats of the method exist.

Criticisms and limitations of population viability analysis

In spite of its obvious utility to the field, debates exist and remain unresolved over the appropriate uses of PVA in conservation biology and PVA's ability to accurately assess extinction risks. One of the pervasive criticisms of PVA is the amount and quality of data needed for accurate population projections. We rarely have precise estimates of demographic parameters for most species, and minor errors in these can be compounded over time, leading to inaccurate estimates of extinction risk (Ludwig 1999, Fieberg and Ellner 2000). Projection of extinction risks beyond about 10-20% of the length of the data time series can be so uncertain that extinction risk values have little value (Fieberg and Ellner 2000). PVA for threatened and endangered species is especially problematic as the predictive power of PVA plummets dramatically due to the minimal amount of data often associated with these species. In fact, Ellner et al. (2002) argued that PVA has little value under the circumstances often faced by threatened and endangered species. Others, however, argue that PVA remains the best tool available for estimations of extinction risk, especially with the use of sensitivity analysis (Brook et al. 2002).

Even with an adequate dataset, a PVA may still have large errors in extinction rate predictions. Most PVAs rely on the idea that conditions like climate, habitat availability and human interference will remain relatively constant far into the future. Unfortunately, this is rarely true and cannot be incorporated all future possibilities into a PVA: habitats may change, catastrophes may occur, and new diseases may be introduced (Coulson et al. 2001). Nature is dynamic and disturbance is the norm, not equilibrium or constant states. Though such variability can be controlled for to some degree by running models multiple times with varying sets of assumptions based on potential future forecasts, this will always cause some degree of error in the analysis.

In light of these issues, some critics have argued that PVA is virtually meaningless (Ludwig 1999, Coulson et al. 2001), and that being preoccupied with the stochastic and demographic dynamics of a population or species ignores the more important, ultimate causes of population decline, particularly anthropomorphic causes (Caughley 1994, Harcourt 1995). While this is true to some degree, many PVAs do incorporate pressures such as habitat loss (e.g., Akçakaya and Raphael 1998) and overharvest (e.g., Ebenhard 2000) into the model. Furthermore, even the most avid proponents of PVA would not argue that management decisions should be based solely on a model. Rather, a model should be used as a guiding factor to making a sound judgment within the social and political decision making context for the species.

Strengths of population viability analysis

Despite these criticisms, overall the strengths and utility of PVA definitely outweigh the weaknesses. While not infallible, PVA can still be of great use as a means of comparing relative extinction risks, either between subpopulations of a species or between alternative management actions (Lindenmayer and Possingham 1996, Brook et al. 2000, Morris and Doak 2002). One of the important aspects of PVA is that it is rigorous and quantitative, and results can be replicated and validated as necessary. Over time, predicted values can be compared to those observed in the field to confirm appropriateness of the original model and inform the development of future models (e.g., McCarthy et al. 2000). In fact, Brook et al. (2000) found that for 21 populations with PVAs, the predictions of the model were concordant with real world population trends. Specifically, the risk of population decline closely matched observed outcomes, no significant bias was found and population size projections did not differ significantly from reality. Furthermore, the predictions of five PVA software packages yielded similar results (Lindenmayer et al. 1995). In addition, PVAs are also rigorous in terms of what can be included into the model. A PVA can use various types of data sets, including presence-absence data, habitat relationships, GIS data on landscape characteristics, mark-recapture data, as well as survey and census data. Thus, all the data available for the species or population of interest can generally be incorporated into the assessment. Obviously, this thoroughness has many advantages over methods such as reserve selection, habitat suitability or gap analysis methods which can only use a limited range of data types such as presence/absence.

Another advantage of PVA is that it allows uncertainty to be incorporated into the model, which is something ignored by most other methods of assessment (Akçakaya and Sjögren-Gulve 2000). If data are uncertain, as they usually are, ranges of parameter values can be used. Various methods of propagating such uncertainties into calculations and simulations exist, but perhaps the best and simplest way is to simply build best- and worst-case scenario models (Akçakaya and Raphael 1998). Combining the results of the two models gives a range of estimates of extinction risk or management outcomes and allows conservation biologists to understand wherein lies the uncertainty in their parameters and make decisions with full knowledge of the uncertainties (Akçakaya and Sjögren-Gulve 2000). Not only does PVA give us the flexibility to incorporate uncertainty in parameters into the analysis, it gives us the ability to explore the uncertain outcomes of several different management activities. By manipulating parameters to reflect proposed management, researcher can explore the possible outcomes of their activities without the potential waste of time and resources necessary to experiment with management outcomes in the real world. By focusing on models of species viability instead of relying only on subjective guidelines and opinions, a scientific risk assessment approach can directly relate the maintenance of viable populations of imperiled species to the management options that can sustain them. These models simply have to be used with some caution.

Future directions for population viability analysis

PVA has advanced greatly in the 20 years since it was first implemented and has become one of the strongest and most useful tools in the conservationist's tool box. However, as mentioned above, it is not without faults and issues, and a great deal of room still exists for improvements and strengthening of the method. One of the next steps needed in the development of this method is to create a fixed definition of PVA and scientific standards of quality by which all PVA are judged. Several researchers have argued that the definition of PVA be narrowed to quantitative modeling (Reed et al. 2002, Ralls et al. 2002), though as yet little discussion has been devoted to unifying quality criteria. To date, developing reliable PVA for plants has been a challenge, given lack of good data and complications due to plants' life cycles, episodic recruitment and other issues like dormancy (Reed et al. 2002). As these issues are recognized and researchers are developing ways to deal with them in the model, PVA is becoming a more realistic option for plants. Several recent advances in conservation studies, including the use of genetics and spatial analysis, are also emerging issues in PVA (Burgman and Possingham 2000, Reed et al. 2002). As we understand more about how these issues affect the ecology and thus, viability, of species we are also devising ways to quantify and parameterize these into models, through the use of things like inbreeding coefficients and models of movement based on GIS maps. Finally, we need to begin to use more sophisticated methods for dealing with uncertainties in model construction, parameter estimation, and output. Detailed sensitivity analyses techniques exist to deal with most of these issues, but are not yet incorporated into most PVAs (Burgman and Possingham 2000).

In the end, PVA should be treated as a model. Techniques to improve the model exist and the methods will continue to evolve, but models are simplification of the real world and as such, are never entirely correct. However, these models can provide valuable approximations and insights into alternative management options (Burgman et al. 1993). While they may not be without fault, being guided by scientific evidence, even if it is not as precise as we might wish, is better than to throwing away what knowledge we do have. The final management decisions for any species must depend upon human judgment, but we need to use the best tools available to come to those decisions. In fact, PVA may arguably be one of the best conservation management tools we have available to us, and has certainly helped put conservation biology on the map.

Goals and objectives

Given the ongoing and increasing threats facing Hawaiian forest birds, evaluating their long-term viability and the management actions needed to ensure their continued persistence is essential. To begin addressing this gap, the overarching goal of this dissertation is to model puaiohi populations under current and potential future management scenarios to determine efficacy in aiding in the recovery of this rare and ecologically important species. As such, this work will directly inform conservation by providing comparisons of management options and analyzing aspects of puaiohi biology that are poorly understood, but may prove crucial to modeling and, by extension, successfully conserving the species.

To address the overarching goal, I evaluated the following objectives:

1. Investigate potential links between prevailing weather conditions in the puaiohi's range and breeding success, as measured by the numbers of fledglings/attempt, of nest attempts/season, of young fledged/pair/year, and the length of breeding season (Chapter 2, published in the *Wilson Journal of Ornithology*).
2. Model puaiohi populations under current and potential future management scenarios to determine their potential efficacy in aiding in the recovery of this rare and ecologically important species (Chapter 3, submitted to *Condor*)
3. Model potential outcomes of translocating puaiohi to another population and identified optimal levels of effort and support necessary to successfully create the new population, while minimizing effects on the current population, to evaluate whether translocation offers a feasible tool for recovering puaiohi, and if so, identify how success can be maximized (Chapter 4, in prep for *Endangered Species Research*)
4. Compare the cost-effectiveness of potential management options, and to use these comparisons to recommend management practices which offer the greatest likelihood of maintaining the species based on available budgets. (Chapter 5, in prep for *Conservation Biology*)

This dissertation addresses currently missing information and provides managers with a framework from which to make conservation decisions. While the project focuses solely on one species, the puaiohi, most of the endangered forest birds in Hawaiʻi are similarly underfunded and lacking in data supported management decisions, and the methods and procedures developed in this project could be applied to many other Hawaiian species.

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CHAPTER 2

WEATHER INFLUENCES ON NEST SUCCESS OF THE ENDANGERED PUAIOHI (*MYADESTES PALMERI*)

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ABSTRACT**---**The endangered Puaiohi (*Myadestes palmeri*) endemic to Kaua‘i is the island’s only remaining native thrush. Given its small population of ca. 500 birds, it is essential to understand conditions that affect the species’ recruitment and survival. Previous observations of Puaiohi suggested that weather may influence nest success and productivity, but no studies investigated this relationship empirically. Our goal was to investigate potential links between weather conditions (precipitation and temperature) in the Puaiohi’s range (~20 km^2) and several measures of reproductive success, using published data from 1996-1998 and new data collected by the Kaua‘i Forest Bird Recovery Project from 2007-2009. Total rainfall in the previous wet season strongly and positively correlated with the majority of the nest success variables (3 of 4). Mean rainfall during the breeding season positively correlated with reproductive effort (attempts/season and length of breeding season) and with total reproductive output, but there was some evidence that too many rainy days during the peak breeding season associated with fewer young fledged per nesting attempt. Although there seem to be clear implications that weather affects Puaiohi reproductive output, results from longer time series will be useful in refining this relationship. Given that prevailing weather conditions of the Puaiohi’s range may shift with anthropogenic climate change, which in turn may alter the severity and frequency of ENSO events, our findings provide insight into future trends in reproductive output, and thus, population of this endangered species.

KEYWORDS---Climate change, Hawaiian forest birds**,** *Myadestes palmeri*, reproductive success, Small Kauaʻi Thrush, weather effects

INTRODUCTION

The Hawaiian Islands are home to some of the most rapidly disappearing, as well as rarest and evolutionarily unique bird species in the world (Banko and Banko 2009, Pratt 2009b). Of the more than 110 endemic land bird species currently known to have occurred in Hawaiʻi prior to human colonization, only about 6% are extant and face no immediate threats of extinction (Pratt 2009a). Furthermore, of the 71 endemic species or subspecies persisting after western contact (ca. 1778), 51 are listed as endangered or worse, with 43 of these on the brink of extinction (i.e. critically endangered, extinct in the wild, or possibly extinct) or already extinct (IUCN 2012; James 1995).

The endangered Puaiohi, or Small Kauaʻi Thrush, (*Myadestes palmeri*) is one of these critically endangered species. Endemic to Kauaʻi, the Puaiohi is the only remaining species in the thrush family, Turdidae, and the only remaining native frugivore on the island. At present, there is only one other thrush species extant in the Hawaiian Islands, the Island of Hawaiʻi endemic ʻŌmaʻo (*Myadestes obscurus*). While ʻŌmaʻo range and densities have declined, it still has a sizable and contiguous population (Scott et al. 1986, Gorresen et al. 2009) and is listed as vulnerable by the IUCN (2012). The other four thrush species or subspecies originally present in the Islands, (Kāmaʻo [*Myadestes myadestinus*], ʻĀmaui [*Myadestes woahensis*], Lanaʻi ʻOlomaʻo [*Myadestes lanaiensis lanaiensis*], and Molokaʻi ʻOlomaʻo [*Myadestes lanaiensis rutha*]) are all now extinct (Reynolds and Snetsinger 2001, Woodworth and Pratt 2009). The

Puaiohi is also one of the last six endemic forest bird species to remain in the Alakaʻi Wilderness. Over the past three decades, five other species disappeared from the swamp following Hurricanes ʻIwa (1982) and ʻIniki (1992) (Conant et al. 1998). Although some of these species were rare at the turn of the 20th century (Perkins 1903), most were more common than the Puaiohi. In fact, its larger congener, the Kāmaʻo, was once the most common forest bird on Kauaʻi (Perkins 1903, Scott et al. 1986), yet the Puaiohi has persisted while the Kāmaʻo is now extinct.

Although this historically rare species has outlasted many others, it appears to have experienced range contraction since the 1960s (Scott et al 1986, U.S Fish and Wildlife Service, 2006). Specifically, the Puaiohi no longer is found at the lower elevations (1000-1050 m) of its historic range and is currently restricted to a remnant of the Alakaʻi Wilderness Preserve at 1050 to 1300 m, with 75% of its breeding population occurring in just 10 km^2 of forest (Richardson and Bowles, 1964, U.S. Fish & Wildlife Service 2006). As of 2012, population size was estimated at ca. 500 birds (Kaua'i Forest Birds Recovery Project 2013) and surveys suggest the population has remained stable since 1973 (U.S. Fish & Wildlife Service 2006). A number of factors may affect population vulnerability, including drought, hurricanes, mammalian predation at all life stages, and habitat degradation due to feral livestock (pigs and goats) and weeds (Snetsinger et al. 2005, U.S. Fish & Wildlife Service 2006, Woodworth & Pratt 2009). Given the species' small population size and range, it is essential to gain a better understanding of the conditions which affect recruitment and survival.

Previous work on Puaiohi has suggested that climate may be related to nest success (Snetsinger at al. 2005), but no studies have yet explicitly investigated this possible relationship. Specifically, Snetsinger et al. (2005) noted that in years with higher reproductive output, female

Puaiohi successfully reared two to four broods of one to two young each. However, in other years recruitment was much lower, with less than one brood being successfully produced. This interannual variability suggests that environmental variables may drive reproductive success. Snetsinger et al. (2005) hypothesized that decreased reproductive success occurred in years of low rainfall during the wet season preceding breeding, which reduced food availability. Thus, not only was the condition of adult birds and their ability to successfully rear young affected, but also depredation by rats increased as birds were forced to search more widely for food sources.

Considering predictions of anthropogenic climate change and the associated changes in weather variables, understanding how the Puaiohi's nest success is related to weather may become critical. Although changes in trade wind inversions complicate predictions of temperature and rainfall changes at higher altitudes (Cao et al. 2007, Giambelluca et al. 2008; Timm & Diaz 2009), over the past 20 years the Alakaʻi has already experienced increasing mean air temperatures, declining precipitation, and changes in stream flow (Atkinson et al. 2014) that will likely continue and will impact remaining forest bird populations. In good years the Puaiohi has high reproductive potential, which may be the key to its continued persistence in the face of its long term rarity and all the factors negatively impacting its survival and reproduction. However, if the frequency or timing of precipitation and temperature patterns change, and in turn hampers reproductive success, the Puaiohi's outlook could be quite different. The goal of this research, therefore, was to investigate potential links between prevailing weather conditions in the Puaiohi's range and breeding success, as measured by the numbers of fledglings/attempt, of nest attempts/season, of young fledged/pair/year, and the length of breeding season. Specifically, we hypothesized that increasing rain during the wet season which directly precedes the breeding season would result in more young fledged per nest, a longer breeding season which allows for more breeding attempts per season, and as a result, more young fledged/pair/season. Furthermore, increased rain during the breeding season and extreme minimum and maximum temperatures should result in fewer young fledged per attempt, shorter breeding seasons which allow for fewer nesting attempts, resulting in fewer young fledged/pair/season.

METHODS

Puaiohi inhabit native wet and mesic forests in the Alakaʻi Wilderness Preserve, which in managed by Hawaii's Department of Land and Natural Resources, Division of Forestry and Wildlife. Study sites range in elevation from 1,123-1,303 m. Forest canopy is dominated by ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa*), ōlapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ʻōhiʻa ha (*Syzygium sandwicensis*), kāwaʻu (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), with a diverse understory of native plants including ʻōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) (U.S. Fish & Wildlife Service 2006). Annual rainfall in the area follows a steep rainfall gradient ranging from around 3.5 m in the northewest to over 8 m in the southeast (Giambelluca et al. 2013).

To address the research objectives, we used the only two Puaiohi data sets available. The first was collected from 1996-1998 in the upper and lower Mohihi and upper Kawaikōī streams (Mohihi study area; Snetsinger et al. 2005). Researchers surveyed potential habitat during September 1995-January 1996, and areas of suitable nesting habitat were identified at 1250 m elevation along the upper stretches of Mohihi Stream and its tributaries as well as in the neighboring Koaie drainage. At sites where they observed pairs (1996—12 pairs, 26 nests; 1997—14 pairs, 44 nests; 1998—22 pairs, 24 nests) actively developing territories, researchers searched for nests at least once every three days from the onset of breeding in March through the end of breeding in August or September. Weather permitting, nests were checked every other day and nesting stage was recorded. Eggs or nestlings were counted when possible and nest failures recorded and cause identified, if possible. Based on these observations, researchers calculated the mean fledglings/territory, nesting attempts/territory, fledglings/attempt, and length of breeding season for each of the three years. Snetsinger et al. (2005) calculated length of breeding season as the period from the mean first egg laid that year through the mean final fledge or fail date.

We collected the second dataset over the 2007-2009 breeding seasons along the upper reaches of Halepaʻakai and Halehaha streams (Halepaʻakai study area). As with Snetsinger et al. (2005), we surveyed sites in which we observed pairs (2007—14 pairs, 30 nests; 2008—13 pairs, 20 nests; 2009—11 pairs, 16 nests) actively developing territories at least once every three days from March through August or September, and, as feasible, checked nests every other day. We recorded nesting stage, counted eggs and/or nestlings when possible and recorded nest failures and identified cause if possible. From these data, we calculated annual numbers of offspring/female/nesting attempt, nesting attempts/year, offspring/female/year and length of breeding season, and pooled these with the data from Snetsinger et al. (2005).

Weather information was collected from the National Climatic Data Center (NCDC, 2013) of the National Oceanic and Atmospheric Association (NOAA). The NCDC's Global Historical Climatology Network (GHCND) is a public access database of historical monthly temperature, precipitation, and snow records over global land areas. The values are a composite of climate records from numerous sources that are merged and subjected to a suite of quality assurance reviews. The GHCND-Monthly Summaries database includes 18 meteorological elements from more than 40,000 stations distributed across all continents.

The weather-data station used for this analysis is located at 1,097 m elevation near Koke‘e State Park (ID: Kanalohuluhulu 1075, HI US GHCND:USC00513099 at [22.12972°, -159.65861°]). The Kanalohuluhulu station is the only station in the area with a recording period which covers the study period (1996-2009) and exhibits nearly continuous monthly data points at an elevation comparable to Puaiohi habitat. Of the 18 meteorological elements available, we selected five: number of days per month with ≥ 1 mm precipitation, total monthly precipitation (mm), mean maximum temperature (°C) by month, mean minimum temperature (°C) by month, and mean temperature (°C) by month.

We used several *a priori* assumptions to select these five elements. First, given the subtropical nature of the birds' habitat and its relatively moderate elevation, it was reasonable to eliminate certain elements pertaining to snow, cooling, and/or extreme minimum or maximum temperatures. Furthermore, we eliminated computed elements that measured the number of days per month that met a specific rain or temperature level, as means or presence/absence were more parsimonious. We averaged the remaining five monthly elements over three periods thought to be meaningful to Puaiohi reproduction: peak breeding season (April-June), full breeding season (March-August), and previous wet season (November of the preceding year-March of the current year). Weather elements are correlated with each other, particularly within the temperature and precipitation measures by season (Fig. 2.1).

To investigate how nest success variables associated with weather variables, we evaluated simple linear regressions using Akaike's information criterion, corrected for small sample size (AIC*c*; Burnham & Anderson 2002). For each of the four dependent reproductive variables (fledglings/attempt, attempts/season, fledglings/female/season, and length of breeding season), we fit fifteen regression models; each model used one of the five weather variables within one of the three time periods as the explanatory variable. Because of the very small sample size (6 years), models with more than one independent variable could not be fit reliably; reflecting this, the penalty for small sample size rendered the AIC*c* of all multivariable models too large to be competitive. We considered models with the smallest ΔAIC*c* as compared to the best fit model to be supported by the data and are reported below.

RESULTS

Puaiohi nest success, by all measures, appears to exhibit some degree of variability from year to year. While birds produce two to three young per pair most seasons (1996; 2007-2009), some years appear to be much more (1997; 4.9 fledged/pair/year) or much less (1998; 0.4 young fledged/pair/year) successful. The length of the breeding season is similarly variable, ranging from 132 days during the very successful 1997 breeding season, to just 50 days in 2008 (Table 2.1).

All four nest-success variables had strong relationships with at least one weather variable (Table 2.2). The number of young fledged per nesting attempt strongly related ($r^2 > 0.59$ and ΔAIC*c* < 2.3) to six weather variables: number of rainy days during peak breeding season, both peak breeding and full breeding season mean maximum temperature, previous wet season mean monthly rainfall, previous wet season mean minimum temperature, and full breeding season mean temperature. Frequent rainy days during the peak breeding season associated with fewer young fledged per nesting attempt (Fig. 2.2), although, interestingly, total rainfall during the breeding season was not. Specifically, each additional rainy day per month during the peak breeding season associated with a decrease of 0.148 young fledged/attempt. The other weather variables all positively related to the number of young fledged per nest attempt. With each 1° C increase in the monthly mean high temperature and the mean temperature during the full breeding season, corresponded with an additional 0.616 and 0.719 young fledged per attempt, respectively (Figs. 2.3, 2.4). Furthermore, we saw an additional 0.337 young fledged per attempt for each 1° C increase in the monthly mean high temperature during the peak breeding season (Fig. 2.3), and 0.354 additional young fledged per attempt where associated with each 1° C increase in the monthly mean low temperature during the previous wet season (Fig. 2.5). Although too many rainy days during the peak breeding season negatively associated with number of young fledged, greater rainfall in the previous wet season associated with increased young fledged per attempt (Fig. 2.6), such that each additional 1 cm of mean monthly rain during the previous wet season associated with an increase of 0.04 young fledged per attempt.

The number of nest attempts per season strongly positively associated with rainfall both during the full breeding season and in the previous wet season (Fig. 2.7). An additional 1 cm of average monthly rain during the full breeding season corresponded with 0.25 additional nest attempts per season, while each additional 1 cm of average monthly rain during the previous wet season corresponded with 0.07 additional nest attempts per season. Number of young fledged per season and attempts per season were not the only measures of reproductive success for which previous wet season total rain was meaningful. Indeed, previous wet season was the only weather variable that fit the model for number of young fledged per pair per year (Fig. 2.8). Each additional 1 cm of average monthly rain during the previous wet season associated with an additional 0.15 young fledged per pair per breeding season.

The only measure of Puaiohi reproduction that did not include total rainfall in previous wet season as a best fit model was length of the breeding season. Average total rainfall during the full breeding season was the only weather variable strongly correlated with the length of breeding season (Fig. 2.9), such that an additional 1 cm of average monthly rain during the full breeding season associated with a breeding season which lasted 11.1 days longer. The second-best variable for predicting the length of the breeding season was total rainfall in the previous wet season, though this relationship was considerably weaker than that of length of breeding season with rainfall during the breeding season ($\Delta AICc > 3.5$).

DISCUSSION

Overall, support for our hypotheses was mixed. The first hypothesis, that increased rain during the wet season prior to the breeding season is correlated with greater reproductive success, was supported, with more young fledged per nest, more nesting attempts per season, and hence, more fledglings/pair/season associated with more rain in the previous wet season. Rain during the previous wet season also was the second best explanatory variable for length of breeding season, though this relationship was substantially weaker than that between length of breeding season and rainfall during the breeding season. In contrast, results did not support our second hypothesis, that increased rain and extreme temperatures during the breeding season would correlate with reduced reproductive success. Though we saw some indication that too many rainy days during the peak breeding season may be detrimental, the total amount of rain during the breeding season positively correlated with the number of attempts per season and length of the breeding season.

Although all four nesting parameters exhibited some degree of relationship to weather variables, only the number of young fledged per attempt model was well supported by multiple weather variables. Of greater note is that one weather variable, rain prior to the breeding season, is positively and moderately to very strongly related to all four measures of nest success, including overall nest success (number of young fledged per pair per year), and may serve as the primary explanatory value for Puaiohi nest success. More rain in the previous wet season associated with increased reproductive output for all models in which it appeared (Figs. 5, 6, 7), with rainfall during the wet season preceding the breeding season being the single most important weather factor in predicting a season's nest success. More rain in the preceding wet season likely results in increased production of the fruits Puaiohi rely upon as a major food source, thereby increasing their ability to successfully rear and fledge young. In addition, the greater food availability may lessen predation pressure, as predatory rats may be fulfilled by the relatively easy to find fruit and not invest increased effort in hunting. Alternatively, rat populations may decline following cold and wet winters, thereby posing less threat to nesting Puaiohi.

Though rain in the previous wet season was the primary factor related to measures of nest success, other factors seem to be at play as well. For instance, too many rainy days during the peak breeding season may decrease reproductive successes, perhaps due to decreased ability of parents to forage during prolonged rainy periods as well the potentially higher energetic expenditures necessary for both parents and nestlings to stay warm. At the same time, however, sufficient rain during the full breeding season may be necessary to sustain a longer breeding season and increase number of nest attempts. Specifically, sufficient rainfall is likely needed to sustain fruit production, both supplying ample food to Puaiohi parents and young, as well as rats, thereby lessening predation pressures. Additionally, more young fledged per nesting attempt with warmer temperatures during the breeding season, a pattern which had not been previously suggested or hypothesized.

Although the weather-reproductive success relationships identified in this study show a significant correlation, it is important to keep in mind that most of the trends identified here are driven by two years (1997 and 1998), and there is little to no relationship between weather variables and reproductive success in the other four years. Given the small dataset, it is possible that relationships between weather variables and reproductive output are non-linear, such that critical thresholds exist, below which reproductive output collapses or above which reproduction is significantly increased over average levels. Regardless of the whether the relationship is linear or non-linear, there is compelling evidence that the weather in 1997 and 1998 was not unusual but instead represents conditions that occur fairly commonly, and may indeed change in frequency in the near future. In 1997, Puaiohi had their most successful nesting year within the study period. The breeding season in 1997 was extended, and both fledglings per attempt and number of attempts were substantially higher than the average over all study years. The wet season prior to 1997 (November 1996-March 1997) had high mean monthly rainfall, which carried over into the breeding season when rainfall was higher than in other years, though the actual number of rainy days in the peak season was within the range of other study years (albeit at the high end). However, the opposite happened in 1998, when Puaiohi had much lower than average nest success—fewer young fledged per attempt, pairs attempted to nest fewer times, and the overall production per pair that year was remarkably low. This breeding season and the wet season preceding it exhibited unusual weather opposite to that before and during the 1997 breeding season. In fact, the 1997-1998 wet season (November 1997-March 1998), the driest of any of the studied years, was during one of the strongest El Niño Southern Oscillation (ENSO) events in recent years, with only two others of similar magnitude in the last 60 years (Western Regional Climate Center, 2013). The El Niño then transitioned into a strong La Niña, resulting in a 1998 peak breeding season (April 1-June) which had almost twice the number of rainy days as the next rainiest peak breeding season and was markedly colder than the other years. While rainfall in the prior wet season is similar for 1998 and 2007, the wet season prior to 2007 was warmer than that before 1998. Though both years were dry, the fact that the pre-1998 wet season was both dry and cold may have compounded the effect on subsequent productivity during the breeding season.

Hawaiʻi tends to be drier and drought prone during strong El Niño events and wet during La Niña events, although the effect of the latter is more variable (Chu & Chen 2005, Kolivras & Comrie 2007, Chu et al. 2010). In fact, most major droughts during Hawaii's winter wet season have been preceded by a persistent El Niño event starting from March of the preceding year (Chu 1989). This relationship between drought and El Niño is of particular concern as it is believed that El Niño and La Niña events are more variable and intense over the past several decades, presumably due to the increase in environmental temperatures produced by anthropogenic climate change (Meng et al. 2012, Cobb et al. 2013, DeNezio et al. 2013). If this variability and intensity trend persists, overall yearly precipitation may decrease across Hawaiʻi (Chu et al. 2010), which could be particularly detrimental if it affects the winter precipitation that seems to be essential to a successful Puaiohi breeding season. However, ENSO events are inherently unpredictable, and the potential effects of anthropogenic climate change on ENSO events are as yet unclear.

A second climatic trend, which is believed to be independent of ENSO events, is an apparent negative trend in winter rainfall in Hawaiʻi. This negative trend may be a result of increasing persistence of the trade-wind inversion (TWI; Cao et al. 2007; Giambelluca & Luke 2007), which has increased since 1979. Simulations under future anthropogenic climate change conditions suggest the TWI will continue to become more persistent and lower in height (Cao 2007). Although the connection between TWI changes and climate warming needs further study, the continuation of a more persistent inversion will produce a shift toward a drier climate in Hawaiʻi (Giambelluca & Luke 2007), thereby reducing the amount of precipitation needed to produce adequate conditions for successful Puaiohi nesting.

Given that the prevailing weather conditions of the Alakaʻi Wilderness are predicted to alter with anthropogenic climate change (Benning et al. 2002), it is very important for conservation and management to understand how weather affects the reproductive output of Puaiohi, and all endemic species, as a means of evaluating their chances for long-term survival. A case in point is that nesting attempts of both Hawaiʻi ʻAmakihi (*Hemignathus virens*) and Palila (*Loxioides bailleui*) decreased 96% and 93%, respectively, during the 1992 El Niño drought compared to the preceding non-ENSO year (Lindsey et al. 1997). Similarly, drought conditions dominated 74% of the 2000-2010 period in subalpine Mauna Kea on Hawaiʻi Island and correlated with a 79% decline in Palila abundance from 2003 to 2011 (Banko et al. 2013). While it is less clear how precipitation patterns will change in Puaiohi habitat on Kauaʻi, it seems highly likely that patterns will change, becoming more variable and less stable or predictable (Loope & Giambelluca 1998, Chu et al. 2010).

While the links between Hawaiian birds and ENSO cycles may be less well studied, long term studies in the Galápagos Islands show that several species of Darwin's finches are strongly affected. During El Niño years in the Galápagos rainfall increases and the finches tend to have both larger clutches and more breeding attempts per year, much as Puaiohi do in wet years, whereas during very dry years the finches failed to breed at all (Grant et al. 2000). Breeding success during ENSO years correlated with food supply, such that the wettest years lift the normal constraints on the breeding season, allowing the birds to breed longer and produce more (Grant et al. 2000).

Aside from ENSO events, links between weather and nest success are found in a number of other birds. For instance, annual reproductive success of Lark Buntings (*Calamospiza melanocorys*), Song Sparrows (*Melospiza melodia*), and Wrentits (*Chamaea fasciata*) are positively correlated with annual rainfall levels (Chase et al. 2005, Preston & Rotenberry 2006, Skagen & Yackel Adams 2012). In fact, similar to Snetsinger et al.'s (2005) hypothesis regarding increased predation of Puaiohi on the nest following a drought during the previous wet season, Song Sparrow nest predation rates were also lower during wetter years (Chase et al. 2005). Woodlarks (*Lullula arborea*), on the other hand, seem to lay larger clutches and fledge more chicks when the weather is drier (Wright et al. 2009). Temperature is also linked to nest success in numerous species (Chase et al. 2005, Weatherhead 2005, Wright et al. 2009, Skagen & Yackel Adams 2012), although the mechanisms and relationships tend to be fairly species specific.

Relationships between weather and nest success are not limited to continental locations. For instance, several endemic Hawaiian bird studies identified weather as a cause of nest failure, including ‘Akohekohe (*Palmeria dolei*) (VanGelder & Smith 2001), ‘Apapane (*Himatione sanguinea*) (Nielson 2000), Maui Parrotbill (*Pseudonestor xanthophrys*) (Simon et al. 2000), ‘Amakihi (*Hemignathus virens*) (Kern & van Riper 1984), Hawai‘i Creeper (*Oreomystis mana*) (VanderWerf 1998), I‘iwi (*Vestiaria coccinea*) (Kuntz 2008) and Hawai‘i ‘Elepaio (*Chasiempis sandwichensis bryani*) (van Riper 1995). However, none of these studies investigated persistent patterns between weather conditions and seasonal nest success.

Overall, it seems clear that rainfall, particularly previous wet season rainfall, may be associated with Puaiohi nest success. While the forecasted increase in dry El Niño years may make the Puaiohi's situation seem dire, the possible increase in moderately wet La Niña years may potentially offset this, provided the rainfall and lower temperatures in these years are not too severe. Given the Puaiohi's relatively long life span, individuals may be able to weather the bad years and capitalize on the good. However, this creates a highly variable breeding scheme that could destabilize an already small and threatened population. As such, it is imperative that we both better understand how variable rainfall, particularly ENSO cycles, affect these birds, as well as understand how rainfall patterns will change under future climate scenarios.

Our findings have several important implications for management. First, determining how weather and nest success relate requires detailed demographic data, indicating the need to both continue collecting such data and expanding data collection to other species. Demographic data are not only important for refining our understanding of relationships, but to develop population models and conduct population viability analyses that are urgently needed for many Hawaiian birds. Second, it is important to discern if weather also relates to nest predators, such as rats, which could inform if on the ground management actions need to be taken during specific times. Finally, if our findings are supported with the addition of further data, then understanding and including these relationships will become crucial to include in any structured decision or management modeling undertaken for Puaiohi.

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Table 2.1. Summary of nesting success, 1996-1998, upper Mohihi study area[a] and 2007-2009, Halepa‘akai study areas.

Year	**# of Nests**	**# of Pairs**	**# young fledged/ attempt**	**# attempts**	**# young fledged/pair /year**	**Breeding season length (days)**
1996	26	12	1.4	2.2	2.8	87
1997	44	14	1.7	3.3	4.9	132
1998	24	22	0.4	1.1	0.4	51
2007	30	14	1.36	2.14	2.71	86
2008	20	13	1.40	1.54	2.15	50
2009	16	11	1.38	1.45	2.00	54

[a] Snetsinger et al (2005)

Table 2.2. Best fit nest success models based on AIC*c* over study period (n=6). For all models number of parameters (k) is 2.

Dependent Variable	Explanatory Variable	Relationship	r^2	AIC*c*	ΔAIC*c*	w_i
Number of young fledged per nest attempt	Average number of days with rain in peak breeding season	-	0.720	16.603	0	0.268
	Average monthly maximum temperature during full breeding season	+	0.665	17.679	1.076	0.157
	Average monthly maximum temperature during peak breeding season	+	0.661	17.75	1.147	0.151
	Average total monthly rainfall during previous wet season	+	0.639	18.142	1.539	0.124
	Average monthly minimum temperature in the previous wet season	+	0.592	18.830	2.227	0.088
	Average mean temperature in the full breeding season	+	0.591	18.889	2.286	0.086
Number of nest attempts per breeding season	Average total monthly rainfall during full breeding season	+	0.579	25.804	0	0.289
	Average total monthly rainfall during previous wet season	+	0.575	25.859	0.055	0.281
	Average monthly maximum temperature during full breeding season	+	0.326	28.626	2.822	0.070

Number of young fledged per pair per year	Average total monthly rainfall during previous wet season	+	0.706	31.141	0.000	0.552
	Average monthly maximum temperature during full breeding season	+	0.429	35.123	3.982	0.075
Length of breeding season	Average total monthly rainfall during full breeding season	+	0.691	68.490	0.000	0.597
	Average total monthly rainfall during previous wet season	+	0.443	72.033	3.543	0.102

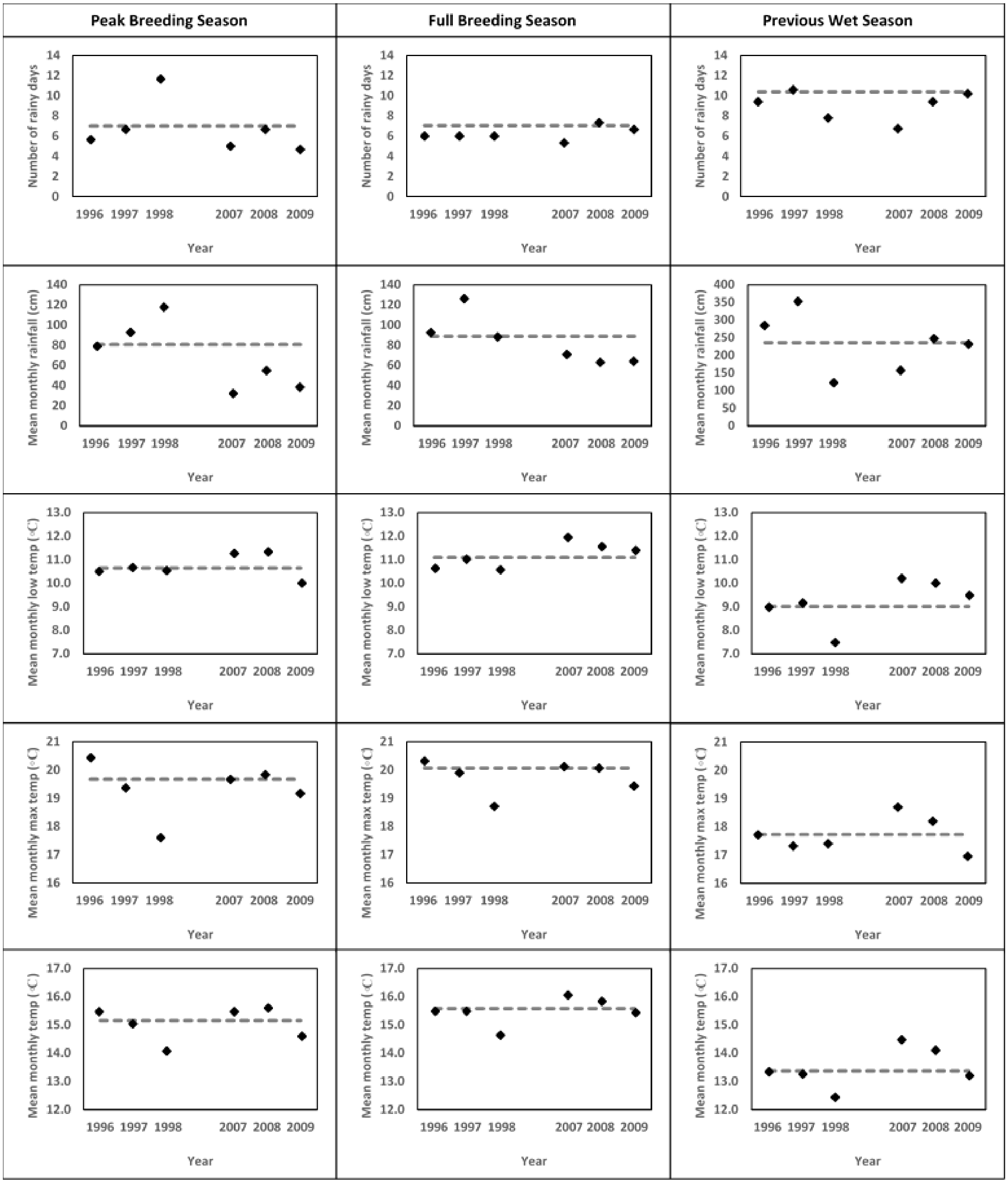

Figure 2.1. Seasonal weather element values by year. Dashed lines represent average historic mean values (1965-1989).

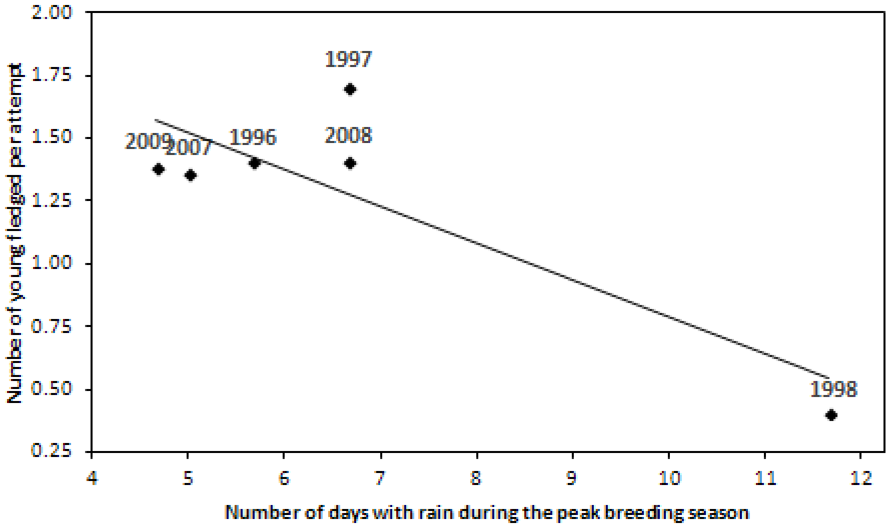

Figure 2.2. Young fledged vs. breeding season rainy days.

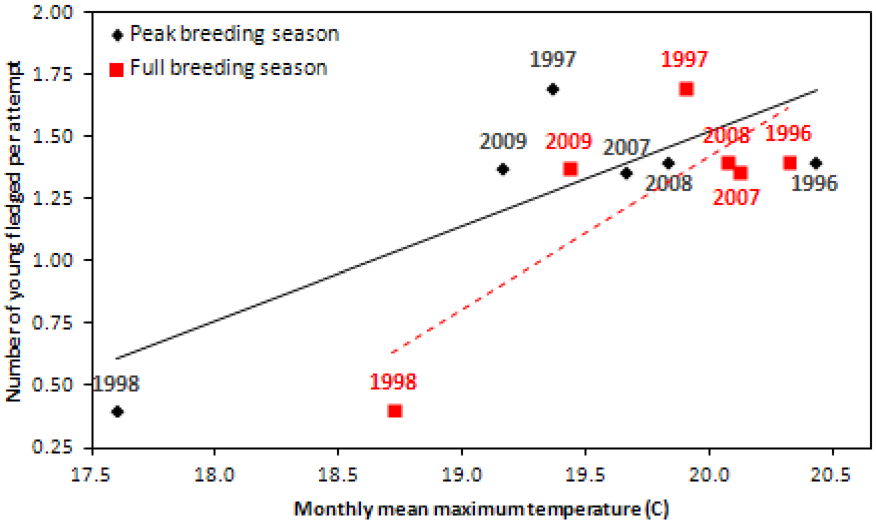

Figure 2.3. Young fledged vs. breeding season temperature.

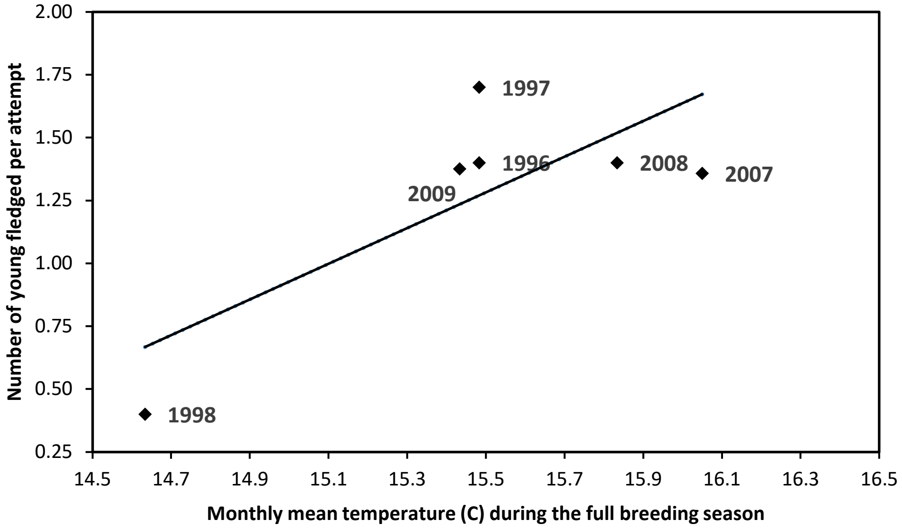

Figure 2.4. Young fledged vs. full breeding season mean temperature.

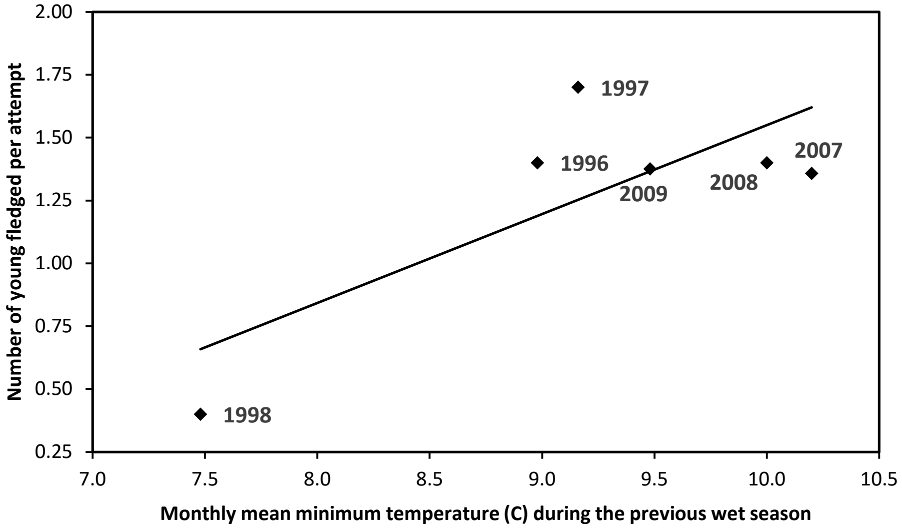

Figure 2.5. Young fledged vs. previous wet season mean minimum temperature.

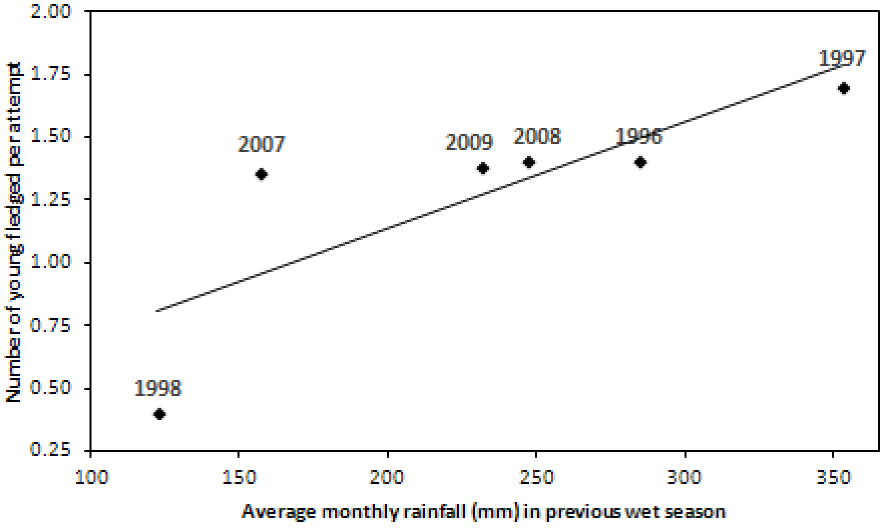

Figure 2.6. Young fledged vs. previous wet season rainfall.

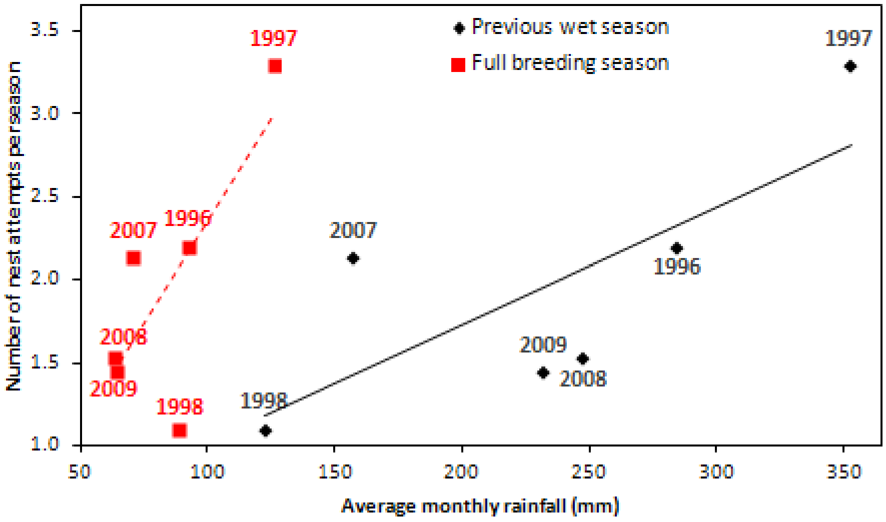

Figure 2.7. Nest attempts vs. seasonal rainfall.

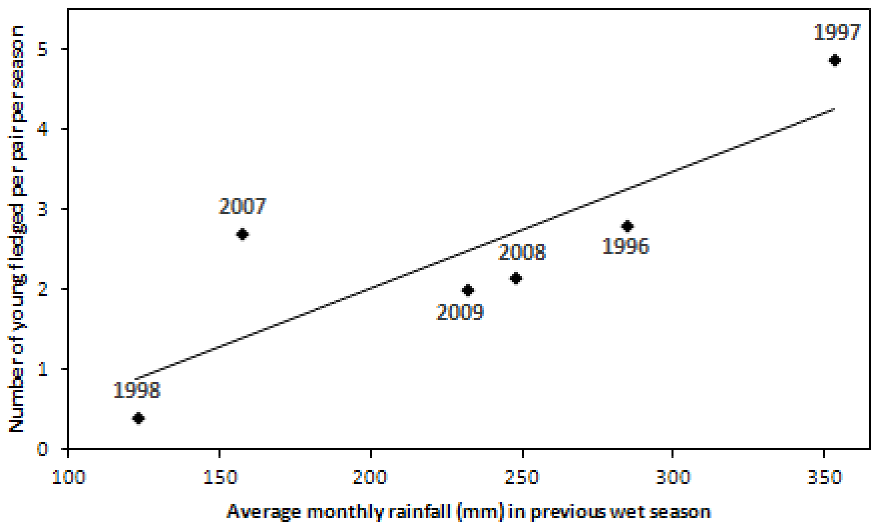

Figure 2.8. Young per pair vs. previous wet season rainfall.

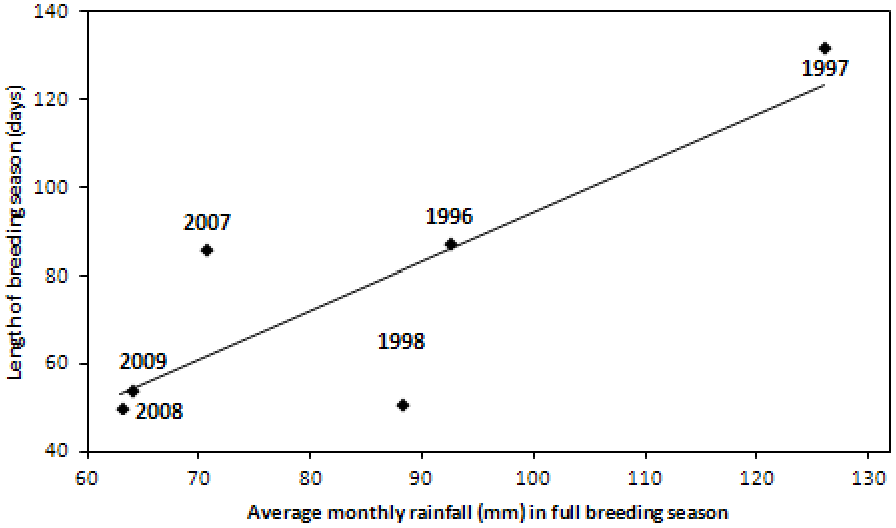

Figure 2.9. Length of season vs. breeding season rainfall.

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CHAPTER 3

USING POPULATION VIABILITY ANALYSIS TO EVALUATE MANAGEMENT ACTIVITIES FOR AN ENDANGERED HAWAIIAN ENDEMIC, THE PUAIOHI (*MYADESTES PALMERI*)

Submitted to *Condor*, in review

ABSTRACT—Evolution in the Hawaiian Islands has produced a unique avian assemblage. Unfortunately, many of these bird species are highly endangered or extinct. Despite numerous and increasing threats and great effort aimed at saving endemic birds, we lack basic science necessary for understanding many species of concern. One such species is the critically endangered (IUCN 2012) puaiohi (*Myadestes palmeri*), a historically rare songbird endemic to the island of Kaua‘i and the only remaining native thrush on the island. At present, the puaiohi’s breeding population is estimated to be about 500 birds restricted to the Alaka‘i Wilderness Preserve. We collected demographic data from 2007-2012, and supplemented it with published sources. Using Vortex and RAMAS, we developed stochastic population models to represent puaiohi population dynamics under current and potential management scenarios to determine management’s potential efficacy in aiding species recovery. Management scenarios modeled included rat control, habitat improvement, general survival facilitation, and provision of nest boxes. Both Vortex and RAMAS indicated a decline in abundance with growth rates of -0.267 (r) and 0.803 (λ), respectively, under baseline conditions. Female and juvenile survival appeared to be the most influential parameters, so management should focus on increasing female and juvenile puaiohi survival. Rat control, even at more conservative levels, appeared to be the most effective method of increasing puaiohi abundance. Our results indicate that practical, attainable management activities can increase puaiohi and bring the species back from the brink of extinction. Such findings provide a model for other endangered species conservation efforts.

KEYWORDS—Hawaiian forest birds**,** *Myadestes palmeri*, PVA, RAMAS, small Kauaʻi thrush, Vortex

INTRODUCTION

The Hawaiian Islands are home to a rare and evolutionarily unique, but rapidly disappearing, assemblage of birds (Banko and Banko 2009, Pratt 2009). Once home to 152 land bird species, 110 of these have gone extinct since human arrival (Walther 2016). Thirty-three of its remaining 42 endemic birds are listed as endangered or threatened, making Hawaiʻi home to one of the most endangered avifaunas in the world (American Bird Conservancy 2016, Walther 2016). However, despite these great threats and relatively large management expenditures directed at saving endemic birds, some of the most basic science necessary for understanding species of concern has not been done (Duffy and Krauss 2008). For instance, population models and population viability analyses (PVA) have not been conducted for 66% of Hawaiʻi's endangered avifauna, representing a critical gap in knowledge. This lack of knowledge is problematic, given that population viability is a criteria used for down listing (or de-listing) a species and that the draft recovery plan for Hawaiian forest birds ranked PVA as an action necessary to prevent a significant decline in the population (U.S. Fish and Wildlife Service 2006). In order to accurately assess the viability of these endangered species in the face of a changing climate, invasive species, and human population growth, and to provide the basis for conservation of these critical species, population models and PVA are urgently needed.

The Endangered puaiohi, or small Kauaʻi thrush, (*Myadestes palmeri*) is one of the critically endangered bird species that has yet to be evaluated in terms of its population dynamics. Endemic to Kauaʻi, the puaiohi is the only remaining avian native frugivore on the island so it may a critical role in the persistence of native plant species and their associated invertebrates. The puaiohi is also one of the last six endemic forest bird species to remain in Kauai's Alakaʻi Swamp (Conant et al. 1998). Although some of these species were rare at the turn of the 20th century (Perkins 1903), most were more common than the puaiohi. In fact, its larger congener, the kāmaʻo, was once the most common forest bird on Kauaʻi (Perkins 1903, Scott et al. 1986), yet the puaiohi has persisted while the kāmaʻo is now extinct.

The puaiohi has experienced range contraction since the 1960s (Scott et al 1986, U.S Fish and Wildlife Service, 2006), as it is no longer found at lower elevations (1,000-1,050 meters) and is currently restricted to a remnant of the Alakaʻi Wilderness Preserve at 1,050 to 1,300 meters. Recent surveys suggest the population is around 500 birds and appears to have remained relatively stable since 1973 (Crampton et al., in press). A number of factors are thought to affect population vulnerability, including drought, hurricanes, mammalian (rat [*Rattus* spp.] and cats [*Felis catus*]) predation at all life stages, disease (particularly infection with avian malaria [*Plasmodium relictum*] and potentially avian pox [*Avipoxvirus* spp.]), and habitat degradation due to feral livestock (pigs and goats) and invasive plants (Kepler and Kepler 1983, Herrmann and Snetsinger 1997, Snetsinger et al. 2005, U.S. Fish and Wildlife Service 2006, Woodworth and Pratt 2009). The puaiohi's preference for nesting along stream banks on fern-covered ledges may limit the availability of suitable nest sites, particularly because invasive plants often cover cliff faces (Snetsinger et al. 2005).

Given the puaiohi's small population size and range, it is essential to gain a better understanding of the conditions which affect its recruitment and survival, as it faces many potential hazards of unknown impact. One useful tool conservation biologists can use to quantify the risk of extinction and to examine the relative benefits of alternative management actions is population viability analysis (PVA; Ellner and Fieberg 2003) which incorporates demographic and environmental variables to forecast population persistence and extinction risk. Although the significance of the actual quantitative model results may be somewhat limited, PVA is useful for testing the relative importance of model parameters via sensitivity analysis, evaluating management strategies, and identifying priorities for maximizing effective species recovery (Beissinger and Westphal 1998, Brook et al. 2000, Cross and Bessinger 2001, Reed et al. 2002). Such model revelations provide conservation biologists with insights into where they need to devote resources in order to develop the best possible parameter estimates and which demographic characteristics of the population are the most efficacious to manage in terms of conserving the population. In addition to providing information on specific demographic factors, PVA can be used to rank management options amongst a suite of possible activities (e.g., Duca et al 2009, Garcia-Ripolles and Lopez-Lopez 2011, Proctor et al 2004). This predictive power allows managers to explore the possible outcomes of a suite of management options without risking potentially ineffectual ones on a species that needs immediate help.

The goal of this research is to inform puaiohi conservation by comparing potential management options, and to use these comparisons to develop best management practices. To address this goal, we modeled puaiohi populations under current and potential future management scenarios to determine their potential efficacy in aiding in the recovery of this rare and ecologically important species. We predicted that extinction probability would decrease and population growth rate increase if predators were controlled, safer nesting alternatives and/or supplemental food were provided, or survival was increased via control of malaria or other methods. Because many of the issues facing puaiohi are the same as those faced by the other Hawaiian forest birds, this research may provide a template for similar approaches for other forest birds of Hawaiʻi.

METHODS

Study Area

The primary data used for calculating parameters were collected from 2005-2011 at four sites in the Alakaʻi Wilderness Perserve: Kawaikōī, Koaie, Mohihi, and Halepaʻakai. The study sites ranged in elevation from 1,123-1,303 m and occurred in the native wet and mesic forests in the Alakaʻi Plateau inhabited by puaiohi. These forests are dominated by ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa*), ōlapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ʻōhiʻa ha (*Syzygium sandwicensis*), kāwaʻu (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), with a diverse understory of native plants including ʻōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) (U.S. Fish & Wildlife Service 2006). These forests are amongst the wettest in the world, with annual rainfall averaging 6.5 m (NCDC 2013).

PVA Software

A variety of software packages are available to analyze population viability, which is why Beissinger and Westphal (1998) encouraged the use of multiple PVAs to verify a model's robustness. Differing results between programs might indicate problems with input data or model structure or assumptions. We conducted our PVAs using Vortex 10 (Lacy and Pollack

2014) and RAMAS Metapop 4.0 (Akçakaya 2005), both of which simulate stochastic demographic and environmental processes. Vortex is an individual-based simulation model that follows the fates of each animal in the simulated population from birth to death, with all events happening according to defined probabilities. RAMAS, on the other hand, is a stage-based matrix projection model that follows entire cohorts through their life cycle based on the population's demographic structure.

Baseline Model Inputs

Within Vortex (Table 3.1) and RAMAS (Table 3.2), we developed baseline models using all available information on puaiohi. Each model was simulated 1,000 times (Owen-Smith 2007), over a time frame of 25 years. Although long term preservation of the species is the ultimate goal, we felt the recovery program is currently driven by urgent short term needs. Furthermore, longer term time spans tend to produce higher extinction probabilities (Akçakaya et al. 1999), propagate errors (Beissinger and Westphal 1998), and produce more uncertain events (Akçakaya 2005). Thus, we chose the relatively short time frame of 25 years because it allowed for exploring and testing the immediate effects of management strategies while minimizing the effects of uncertainties or errors in our parameter estimates. In Vortex, we defined extinction as occurring when only one sex remained. Since RAMAS does not have this option, we defined extinction as when the population dropped below 5, as this was the average population size at which Vortex declared populations extinct due to existence of a male-only population.

In both Vortex and RAMAS, we modeled four cohorts or stages: juvenile females, adult females, juvenile males, and adult males. We developed our demographic input parameters from a variety of sources, including original data, previously published information, and discussion with experts on the species. Because little is known about the genetics, effects or impacts of inbreeding depression on puaiohi, we developed models both with and without inbreeding depression included in Vortex (Table 3.3); for the inbreeding model we used the default heterosis model of 6.29 lethal equivalents, 50% due to recessive lethals. We tested whether inclusion of inbreeding depression mattered using equivalency testing in Minitab (version 17.3.1). Equivalence testing is a statistical tool used to test whether observations from two groups are similar enough to be biologically analagous. In equivalence testing, the null hypothesis is that the difference between two means is greater than a researcher-defined amount, which is referred to as "interval of tolerable difference". We defined the limits at which we considered model output differences to be trivial as ± 0.05 stochastic r (essentially ± 5% annual growth rate) and ± 10 individuals remaining at 100 years. We found inbreeding depression models to be equivalent to non-inbreeding models based upon these defined limits ($p < 0.001$), and therefore did not include the variable in the model. Since a genetic component was not included in Vortex, we also excluded it in RAMAS. In Vortex, we assumed that the effects of environmental variation on reproduction and survival were correlated. Similarly, in RAMAS we assumed that fecundity, survival, and carrying capacity were all correlated within the population, and that the population was exhibiting demographic stochasticity following a normal distribution.

Reproduction

In Vortex, we assumed puaiohi are monogamous (Woodworth and Pratt 2009), and pairs probably persist from year to year, provided mates survive. Individuals of both sexes can breed at a year old. Though one study observed after hatch year birds helping at 8% of nests, suggesting they may have needed to delay reproduction due to some sort of limiting factor

(Snetsinger et al. 1999), helping behavior has not been seen in other studies. Thus, we assumed that, in general, birds would breed at one year old, and would breed each year. Puaiohi always lay two eggs per clutch (Snetsinger et al. 2005), and during the 2007-2009 study period fledged one chick in 30.77% of attempts and two chicks in 69.23% of attempts. Snetsinger et al. (1999) found up to five nest attempts per season, while we never saw more than four true nest attempts per season between 2007 and 2009. As a result, we assumed four nest attempts to be a reasonable maximum [during the 2007-2009 study period the distribution of successful nest attempts was: 0 (13.16%), 1 (42.11%), 2 (36.84%), 3 (5.26%), and 4 (2.63%)]. A puaiohi mist-netted as a hatch-year bird in 1965 survived in captivity until it was 11 years old (Snetsinger et al. 1999). The longest lived captive female died at 16 years old at the Maui Bird Conservation Center (MBCC), but stopped laying eggs at 9. The oldest captive male lived for 13 years and was still able to fertilize eggs the breeding season before he died and other individuals have lived as long as 10 years (S. Belcher, pers comm). As a result, we decided that a maximum life span of 10 years was reasonable. Of 118 eggs laid at the MBCC, 57 hatched males and 61 females (S. Belcher, pers comm), which we used as the basis for a 1:1 sex ratio at birth.

In RAMAS, we also assumed puaiohi to be monogamous, with individual breeding in the adult (>1year) life stage. We calculated that females produced 2.4 young per year, on average, and modelled a 50:50 sex ratio at birth by dividing the young produced equally among males and females. We assumed that the annual standard deviation in young/sex/year produced was 0.4. Since little information is available on how environmental variation affects yearly reproductive output, we looked at both the parameter range (2-2.93 young/year; difference = 0.93) and the standard deviation (1.6030 young/year). If we assumed the standard deviation split evenly between environmental and demographic variability, this would mean 0.8 young/year (0.4

young/year of each sex) variation would be due to environmental variability. At the same time our range of 0.93 young/year would be divided into 0.46 young/sex/year, which is similar to 0.4 calculated from the standard deviation.

Density dependence

Vortex models density dependence in terms of its effect on reproduction as: P(N) = (P(0)-((P(0)-P(K))*((N/K)^B)))*(N/(A+N)); where P(0) is the percentage of adult females breeding at low density; P(K) is the percentage of adult females breeding at carrying capacity; N is initial population size; K is carrying capacity; B is a steepness parameter, which determines the shape of the curve relating the percentage of adult females breeding to population size; and A is the Allee parameter, which accounts for the decrease in the proportion of females breeding at low densities, due to of the increased difficulty of finding a mate at low population densities.. We assumed that puaiohi would be density-dependent, given that it is a territorial bird with limited nesting sites and food sources. During intensive territory mapping from 2007-2009, an average of 90% of the population encountered was breeding. However, by the 2009 census, fecundity appeared to drop off slightly, perhaps due to the population nearing K. Thus, we assumed 90% of the population was breeding at K. Give that a large proportion of the population still seemed to be breeding at K, we assumed that 100% of the population would breed at low density. In the absence of data to the contrary, and given that puaiohi occur in a relatively small remnant habitat area and would presumably be able to find each other through song, we assumed the Allee effect was zero. In order to determine the appropriate steepness parameter, we graphed a series of density dependent population projection plots using steepness parameters from 0.25 to 16. A steepness parameter of 8 looked the most reasonable, although 4 and 16 also seemed plausible. To test the influence of the steepness parameter, we ran three versions of the baseline without inbreeding model, with steepness values of 4, 8, and 16 (Table 3.3), and as with inbreeding, tested for equivalency with Minitab (version 17.3.1), within the self-defined limits of ± 0.05 stochastic r and ± 10 individuals remaining at 100 years. Because all models showed equivalent results ($p < 0.001$), we chose to use a steepness value of 8 in our baseline model. Vortex used the parameters of percent breeding at low density and percent breeding at high density, the Allee parameter and the steepness parameter to automatically calculate the percent of adult females breeding. For the environmental variation in percent breeding, we used default values of 10% in the absence of other data. We do know that except in extreme weather years, fecundity rates, at least, are fairly stable (Fantle-Lepczyk et al. 2016). Finally, we assumed that 100% of males would be in the breeding pool, though all may not find mates due to limited females resulting from higher female mortality (VanderWerf et al. 2014).

In RAMAS, we assumed density dependence would affect all vital rates, and that it would be based on the abundance of all life stages rather than of a certain cohort or sex. RAMAS models four types of density dependence: scramble, contest, ceiling, and Allee effects. The first three are based on declining recruitment or growth rate as density increases, while with Allee effects, recruitment or growth rates decline as density decreases. As in Vortex, we felt the relatively small geographic distribution of the species did not warrant considering Allee effects. In scramble competition, resources are shared equally so each individual receives fewer resources as populations approach carrying capacity, thereby decreasing the per capita growth rate. Contest competition assumes resources are shared unequally, so as carrying capacity is approached, while some individuals obtain adequate resources, more individuals obtain inadequate resources, again decreasing per capita growth rate. Finally, the ceiling model is a simplified version of the contest type in which the population grows exponentially until it reaches the carrying capacity and stabilizes there, unless random fluctuation in model inputs take it below the ceiling. The main difference between ceiling and the other models is that the ceiling type does not assume that the population would recover from low densities, while the others do (Akçakaya 2005). Given that puaiohi are territorial, we did not think resources were equally shared, and thus ruled out scramble competition. In the absence of data suggesting contest completion, we felt the comparatively simpler ceiling model was the most appropriate mechanism for modeling of density dependence in the puaiohi.

Mortality

Using mark-recapture analysis to estimate the annual survival of juvenile and adult puaiohi, VanderWerf et al. (2014) found that adult males survived at a higher rate (71 ± 9% SE) than females (46 ± 12% SE), and indicated that rat predation may be a significant factor in female mortality, a pattern common in other Hawaiian passerines (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011, Mounce et al. 2013). Additionally, VanderWerf et al. (2014) found juvenile survival to be quite low (26 ± 21% SE), which may limit population growth. Recently fledged young tend to remain on the ground for about four days after fledging, making them particularly vulnerable to predation by rats and feral cats. We used these survival estimates in our baseline model in both Vortex (converted to mortalities) and RAMAS, as they represent the only long term estimate of puaiohi survival rates. Given the relatively high mortalities of juveniles and females and the low starting population, we found our model declined rapidly to zero with environmental variations in mortality rate greater than 10%. Furthermore, as with percent breeding, we assumed that in this relatively stable island environment we would not see large annual fluctuations in mortality rates. Thus, we used Vortex's default, relatively modest deviation in mortality rate of 10% for juvenile mortality and 3% for adult mortalities. We used the same 3% (juvenile) and 10% (adult) rates on survival in RAMAS.

Population size and carrying capacity

In the absence of information to the contrary, we assumed puaiohi achieve a stable age distribution. Estimates of population size have varied, from conservatively exceeding 200 (Snetsinger et al. 1999) to around 500 (USFWS 2006, Crampton et al., in press). We used the more recent USFWS estimates in both our Vortex and RAMAS models as they were the most recent and based on the longest-term data set. No attempts have been made to estimate puaiohi carrying capacity in the Alakaʻi Swamp. However, the puaiohi population is strongly linked to streams, and there have been estimates of bird densities along those streams. Specifically, within puaiohi habitat, there are approximately 221 km of streams, about half of had enough cliff face to be suitable for nesting. At peak nesting density in 2009, with nest success declining (perhaps indicating the population was approaching K), we found 27 nesting territories over 6 km of suitable habitat. Assuming two puaiohi per territory, this yields an upper limit of 1,062 birds over the 118 km of suitable habitat. For our estimate of K in both Vortex and RAMAS, we rounded up to 1,100 to include in the population any unpaired or floater birds also utilizing the resources. This may be an overestimate of K, as these numbers are estimated from one of the higher nest density streams, and not all streams are likely to support this number of birds. However, in the interest of testing increases in other demographics of interest, we choose to err on the side of overestimation in order to give our modeled populations some room for increase.

In the absence of better information, we assumed fluctuation in K due to environmental variation to be ±10%.

Software output

In RAMAS, we computed the deterministic λ, probability of extinction within 25 years, and average population size at 25 years for each scenario (henceforth referred to as λ, probability of extinction, and population size). Since RAMAS does not automatically calculate time to extinction, we calculated mean time to extinction for populations that went extinct within 25 years from the output of iterations extinct per time step (henceforth referred to as mean time to extinction). Vortex's standard output provided us with stochastic r, probability of extinction within 25 years, average population size at 25 years, and mean time to extinction for populations that went extinct within 25 years.

Sensitivity Analysis

We performed sensitivity analysis to understand how uncertainty about parameter values affect model outcomes (Akçakaya and Sjögren-Gulve 2000). In both Vortex and RAMAS, we varied one parameter by ±10%, ±25%, and ±50%, while holding all other parameters to baseline values. The parameters examined were starting population, carrying capacity, and juvenile, male, female and combined adult mortalities, number of reproductive attempts per year, and number of young produced per attempt. We used a standard sensitivity index (S_x; Morris and Doak 2002) for sensitivity analysis. Baseline model values were used to compute the standard sensitivity index for each parameter, which was calculated as:

$$S_x = (x_{new} – x_{baseline}) / (P_{new} – P_{baseline}) \qquad \text{eqn. 1}$$

where x is the output value (stochastic r/λ or N extant) and P is the parameter of interest.

Since the model's sensitivity to mortality at all life stages was of particular interest to us, we also wished to evaluate what levels of error in mortality/survival estimates would provide a stable population projection. To this end, we iteratively decreased mortality from -5% to -25%, in order to determine what magnitude of decrease would be necessary to produce $r = 0$ (Vortex) or $\lambda = 1$ (RAMAS). We calculated the values based on our Vortex mortality numbers and used the same numbers in RAMAS (i.e. 1-Vortex mortality = RAMAS survival) in order to facilitate direct comparisons between the two software packages.

Management Models

After assessing the relative influence of each individual input parameter, we used the best available data to develop a suite of potential management scenarios. The four management scenarios developed included rat management, habitat improvement, survival assistance, and the provision of nest boxes (Table 3.4). In order to keep models directly analogous between Vortex and RAMAS, management models were initially populated based on Vortex baseline inputs and translated into the terms used in RAMAS, rather than calculated based on RAMAS baseline inputs (e.g., when we decreased juvenile mortality by 25% in a Vortex model, we populated the analogous RAMAS model with a survival of 1-0.75*juvenile mortality, rather than increase the RAMAS survival by 25%). To reflect the uncertainty in some of our estimations, we developed two levels of each management activity—standard and conservative.

For the optimistic rat management models, we decreased female mortality to that of males, since recent work (VanderWerf et al. 2014) suggests than mortality due to nest predation by rats is the leading driver behind the higher mortality rates in female. We surmised that in a best-case scenario, removal of rats would produce female mortality rates akin to males. In the O‘ahu ‘elepaio, rat control has been shown to increase female survival by 10%-27% (VanderWerf 2009, VanderWerf et al. 2011) which may make our optimistic estimate slightly high. We increased the number of successful attempts/year by 50%, as Snetsinger et al. (2005) found that 50% more nests fledged young with rat control. No experimental data exists to quantify rat predation effect on juvenile mortality. However, we surmised that rat removal would have less impact on juvenile mortality than on adult female mortality, as juveniles are probably subject to a greater range of mortality effects, and they are likely mostly vulnerable to rat predation in just the first days after fledging. As a result, we decreased juvenile mortality by 25%. We presumed the removal of rats would not have much effect on male mortality, since males due not incubate eggs on the nest (when females are presumably most vulnerable to rat predation) nor would rat removal affect the number of young fledged/attempt since if a rat found a nest, it would likely kill both chicks, resulting in a failed attempt. Since rats are known to consume a variety of native fruits and may damage native fruiting plants (Scott et al. 1986, Banko and Banko 2009), we assumed that they may have some effect on carrying capacity of Puaiohi as competitors for preferred food sources. As a result, we increased carrying capacity by 25%.

In our conservative rat management model, we decreased female mortality by only 25% to allow for incomplete rat control as well as the possibility of other causes of female mortality during breeding. We lowered the increase in number of successful attempts per year to 25% more than baseline to allow for any overestimates in Snetsinger et al.’s (2005) experiment, and for other causes of nest failure. Finally, in the absence of data, in our more conservative model we lowered juvenile mortality by 10% and increased carrying capacity by 10%. Again, we assumed rat removal would not affect male mortality or the number fledged per attempt.

In our nest box models, we assumed that we can eventually design a rat proof nest box design that will be readily used by puaiohi. In this event, females and nests would be protected from rat predation, but there would be no effect on juvenile survival as they would have not added protection once they left the nest. Furthermore, assuming nest sites are a limiting factor, providing more nest sites would increase carrying capacity. As a result, in our optimistic nest box model, we decreased female mortality to that of males, and increased the number of successful attempts/year by 50%, as was done in the rat management models. We also increased carrying capacity by 25%. In our conservative nest box models, we decreased female mortality by 25%, increased the number of successful attempts per year by 25%, and increased K by 10%. We assumed no effect on male mortality, the number of young fledged per attempt, or juvenile mortality.

In our survival assistance models, we explored the effect of just increasing puaiohi survival at all post-fledging life stages, with no increases in fecundity or other factors. While puaiohi mortality has likely increased due to several factors of recent origin, including the predatory issues explored in the previous two models, malarial infection is also a concern, though the extent of its impact on the population remains unclear. Avian malaria (*Plasmodium relictum*) was detected in 22.7% of birds tested in 2007-2008 (Atkinson et al. 2014). This high prevalence may indicate that at least some puaiohi survive acute infection and have some tolerance of malaria (Atkinson et al. 2001). There is evidence, albeit based on relatively small sample sizes, that survivorship of puaiohi with chronic malaria is as good as those without malaria (VanderWerf et al. 2014), but presumably some birds succumb to their first bout of malaria. Given the puaiohi's absence from the lower elevation, where malaria is more prevalent, it seems likely that malaria does have some impact on the population, though habitat degradation and weed prevalence likely influences this distributional pattern as well. To attempt to model how eliminating the effects any non-predator related mortality factors, including malaria, might impact the puaiohi population in the absence of any other population effects, we decreased mortality at all life stages (juvenile, adult female, and adult male) by an optimistic 25%. In the more conservative survival assistance model, we decreased all mortality by 10%. In the specific case of malaria, there is some evidence of that infection can cause nestling mortality, thereby reducing fecundity (Lapointe et al. 2016). However, in the interest of keeping these models more general and to differentiate them from the habitat models which follow, we have not incorporated these effects in the survival assistance models.

Our final models looked at potential impacts of habitat improvements on the puaiohi. This could be as the result of supplemental feeding of fruits as was provided to released, captive bred puaiohi. Alternatively habitat could be improved by controlling invasive species that outcompete native food sources, potentially decreasing food availability, particularly during the breeding season. Snetsinger et al. (2005) saw a 37.5% increase in nest attempts per year in wet years over drier years, presumably due at least in part to increased food supply following higher rainfall. Snetsinger et al. further noted a 54.5% increase in the number fledged per attempt in the wet year over the mean number fledged over the three years of study. However, one really dry year brings the mean down and likely over estimates this impact. In light of these findings, we increased the number of successful nesting attempts per year by 37.5% and number of young fledged/attempt by 25% (lower than Snetsinger et al.'s finding due to our concern of overestimation) to reflect the greater food supply by supplementation. We also assumed that increased food supply could slightly increase carrying capacity and slightly decrease juvenile, male, and female mortality, so those parameters were adjusted by 10% accordingly. In our more conservative habitat improvement model, we increased number of attempts per year and young fledged per attempt and carrying capacity by 10% and decreased juvenile, male and female mortality by 10%. In both the optimistic and conservative habitat improvement models, we held all other parameters to baseline values.

To compare between management models within an individual software package, we describe results of stochastic r (Vortex)/ λ (RAMAS), mean population size, probability of extinction, and mean time to extinction in relation to one another. Specifically, we describe similarities and difference between management models as well as trends. We do not test for statistically significant differences among models because the results would be heavily dependent on our choice of how many replicate iterations of each model to use (White et al. 2014). As a result, the model outputs are meant to provide guidance on management approaches that are likely to be successful relative to one another.

Recent work on the utility of PVAs to inform management decisions has suggested using the model output more explicitly to account for likelihood of success when a management action is performed compared to no action (Robinson et al. 2014). Specifically, evaluating the distributions of PVA parameters, such as rate of growth, between a baseline model and a management model allows for determination of success or failure by engaging in a management action. Using the approach of Robinson et al. (2014) we evaluated Vortex model output for r between baseline and management models in order to determine what percent of the time the management models would lead to successful outcomes. From the raw data output by Vortex, we calculated the stochastic intrinsic growth rate (stochastic r) for each population iteration within a management scenario. In instances where the iteration experienced extinction before the end of the 25 year period, we used time to extinction as *t*. If the number of individuals in the iteration hit carrying capacity (K) and oscillated around it, we truncated the time period to just before the population hit K (e.g., *t* = time to first year it exceeds 1,000, which is just below K, as density dependence started to influence the population's growth rate). If a population iteration failed to hit K, or hit K once and then declined, but did not go extinct by end of 25 years, then we used a *t* of 25.

RESULTS

In both Vortex and RAMAS, baseline models yielded declining populations (r = -0.27, λ = 0.80, respectively; Fig. 3.1, Table 3.5). Probability of extinction was high in both Vortex (0.97) and RAMAS (0.86), with nearly all populations going extinct in Vortex. Vortex also produced a shorter mean time to extinction (16.72 vs. 18.64 years) and smaller mean population size (0.32 vs. 3.25 birds).

Sensitivity Analysis

In both Vortex and RAMAS, our models had very little sensitivity to either initial population size or carrying capacity (Fig. 3.4). In fact, varying either of these even ±50% had very little impact on either growth rate or population size. The model was slightly more sensitive to perturbations in fecundity measures, although not nearly as sensitive as it was to mortality/survival measures (Fig. 3.4). In general, juvenile survival was the most influential parameter in terms of both growth rate and population size, particularly for changes in the ±25%

range. However, both growth rate and N are very sensitive to adult survival, with female survival being relatively more influential than that of males at all levels of parameter change.

While our baseline model predicts a rather steeply declining population, scientists have assumed puaiohi populations have been stable for the last 40 years (USFWS 2006). Given the models' sensitivity to mortality, we were concerned that inaccuracies in estimation of mortality may have resulted in the seemingly overly pessimistic predictions of our model. In order to investigate this further, we decreased all mortality measures by 10%, 15%, 17.5%, 20%, 25%. We found that in both RAMAS and Vortex stable growth ($r = 0$, $\lambda = 1$) was achieved with a decrease in mortality between 17.5% and 20% (Fig. 3.2).

Management Models

Overall, in both Vortex and RAMAS, the eight management models indicated increases in growth rate, population size, and time to extinction, and lower probabilities of extinction (Table 3.5) over the baseline model, although these improvements were less pronounced in the conservative versions of the nest box, supplemental feeding and survival assistance models, in which the population still declined fairly rapidly. While our baseline model exhibited negative growth rates, both the conservative and non-conservative rat control, as well as the non-conservative nest box, non-conservative supplemental feeding and non-conservative survival assistance models all exhibited positive growth rates. Although the conservative nest box, conservative supplemental feeding and conservative survival assistance models growth rates remained negative, they were still an improvement over baseline. For probability of extinction, the baseline model had a higher probability of extinction than all other models, with only the conservative supplemental feeding management model showing much risk of extinction.

Population size was also markedly larger in management scenarios as compared to the baseline model, even in those scenarios exhibiting a negative growth rate. Finally, of models with iterations that went extinct, there were notable, if modest increases in mean time to extinction between baseline vs. management models.

Of the eight management models, rat control resulted in the largest growth rates, increased population sizes, and zero risk of extinction (Table 3.5). The nest box model had smaller growth rates, but resulted in a higher population size, again with no risk of extinction. Survival assistance, habitat improvement, and conservative rat control resulted in positive growth rates, increased population size, and longer time to extinction, though of smaller magnitude than rat control and nest box provision models (Fig. 3.1). Conversely, the conservative nest box, conservative survival assistance, and conservative habitat improvement models produced greater times to extinction, growth rates, and final population sizes than baseline models, although they did not result in positive growth rates.

Evaluating the management model outcomes relative to the baseline model showed a variety of responses in terms of either success or failure. In particular both rat control models demonstrated nearly 100% success in increasing growth rates to at least the target value (Fig. 3.3, Table 3.6). However, for the other three types of management actions, only the standard versions of the models showed great success when compared to their conservative counterparts. Furthermore, even if our baseline is pessimistic and the puaiohi population is in fact stable, all four standard models and the conservative rat control model still exhibit considerable improvement over current conditions.

DISCUSSION

Although Vortex and RAMAS have different model structures, qualitatively and practically, there is little difference in the end results of baseline and management models between the two programs. These consistencies suggest that our results are robust to software assumptions and the two modeling frameworks need not be discussed separately. Baseline models indicated negative growth trends and a very high probability of extinction in the next 25 years. Because the population has been considered stable historically, it is possible that inaccuracies in parameter estimation may be contributing to our overly pessimistic population predictions. Given the model’s sensitivity to estimates in survival, and the difficulty in obtaining these estimates, we suggest that this inaccuracy is the most likely cause. In fact, mortality errors of -17.5% to -20% would result in annual juvenile survival of 36%-38%, female survival of 55%-57%, and male survival of 76%-77%. These estimates, which are well within the 95% confidence limits of survival estimates (VanderWerf et al. 2014), would lead to stable population growth rates. However, even though relatively small errors in survival estimates may affect our baseline models, it should be noted that two other members of the Alaka‘i bird community, the ‘akeke'e and ‘akikiki, are currently undergoing severe population declines (Hammond et al. 2015, Paxton et al. 2016), suggesting that our results cannot be discounted. Moreover it is possible that since many of our inputs were calculated from recently collected data, what we are witnessing in the models is an early indicator of an imminent rapid decline in the real population.

Regardless of whether the puaiohi population is stable or declining, it’s precariously small, and therefore, highly susceptible to any of the threats it currently faces as well as stochastic events. Hence, it is imperative that the population is increased and that we strive to increase habitat quality to support greater numbers of this endemic bird. Our management scenario results indicate that a variety of real world, attainable management activities have the potential to increase puaiohi numbers and bring the species back from the brink of extinction. Both Vortex and RAMAS models confirm our hypotheses that controlling predators, providing safer nesting alternatives, and supplementing food will increase puaiohi population growth rate and size. Specifically, rat control, even at conservative levels, appeared to be the most effective method of increasing puaiohi abundance, as did the provisioning of predator-proof nest boxes. Sensitivity analysis indicates that whichever management action is chosen should incorporate increasing female and juvenile survival.

Caveats and Future Research

The mortality estimates used in our study are based on seven years of data, with somewhat limited re-sight data. It is possible that some emigration is being erroneously attributed to mortality, as it can be difficult to distinguish between the two in mark-recapture studies (Ergon and Gardner 2013). Given that our models are quite sensitive to changes in mortality estimates, and seem to be presenting a more pessimistic view than puaiohi managers see in the field, further study to refine mortality estimates would be helpful.

In addition, reproductive estimates used in this study are based only on three years data and there can be variation in annual reproductive output, particularly associated with fluctuation in local weather patterns (Snetsinger et al. 2007, Fantle-Lepczyk et al. 2016). Our data set was not long enough to know whether these years were average background rate years, or if they represented the relatively rarer boom and bust years exhibited in very wet or very dry years, respectively. A longer study of annual reproductive output could help refine population analyses.

Further information on both current and future carrying capacity would also help improve model performance. At present little is known regarding how many puaiohi can be supported in their remaining habitat. Given the puaiohi's rather particular nest site preference for the ledges of narrow stream cuts, nest site availability may limit population size (Woodworth et al. 2009, VanderWerf 2013). Furthermore, daisy fleabane (*Erigeron annuus*), a relatively new invasive plant, grows well on steep rock walls, and may cover and eliminate formerly suitable nest sites (Woodworth et al. 2009), thereby decreasing an already limited resource. Other recent plant introductions, such as blackberry (*Rubus argutus*), Australian tree fern (*Cyathea cooperi*), and strawberry guava (*Psidium cattleianum*) have significantly altered areas currently and recently occupied by puaiohi (Crampton et al., in press), and may change the Alakai's future carrying capacity, as they have the potential to convert the forest canopy, understory and cliffs to novel habitats likely to be unsuitable to the species. At present, the puaiohi's native range is being taken over by Kāhili ginger (*Hedychium gardnerianum*), a well-known invasive plant which blankets native forests and displaces native vegetation (Minden et al. 2010). While ginger is a fruiting plant, unlike natives such as ʻolapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ʻōhiʻa ha (*Syzygium sandwicensis*) and kanawao (*Broussaisia argute*), its peak October-December fruiting period is not contemporaneous with the puaiohi nesting period (Medeiros 2004), and puaiohi don't appear to eat it (Pejchar, unpubl data).

Inbreeding depression is another demographic aspect which we were unable to adequately model in this study, due to lack of data. We found that using default values in Vortex did not significantly affect our models, but it is unclear whether these default values are appropriate for this bird. Puaiohi, along with the rest of Kauai's endangered birds, persist in numbers so low that lack of genetic diversity may pose potential problems, and population size may fall below the minimum viable population size recommended for long term maintenance of genetic diversity (USFWS 2006). In fact, while the puaiohi has been considered rare even historically (Perkins 1903), it does seem to have suffered a significant range contraction over the intervening years. Though the birds currently only occupy wet montane forest at 1,050 to 1,300 m (Snetsinger et al 1999), they have historically occupied lower mesic forests (Perkins 1903) and subfossil evidence of the species has been found in sinkholes and caves at sea level (Burney et al 2001, James and Olson 1991). Clearly, understanding the levels of genetic diversity still extant in the population could have ramifications for maintenance of the species. Recently, a captive breeding program for puaiohi was discontinued due observed effects of inbreeding. Thus, managers are making important decisions based on a perceived loss of genetic diversity, and it would be useful to confirm the level left to be conserved in the wild population.

The effect on puaiohi of catastrophes, particularly hurricanes and drought, is also unclear. Presumably, their preference for nesting in narrow stream corridors offers them some protection from the high winds associated with hurricanes (VanderWerf 2013). Indeed, while five other species disappeared from the Alaka‘i following Hurricanes ‘Iwa (1982) and ‘Iniki (1992) (Conant et al. 1998), the puaiohi persisted. However, the species was likely extirpated from at least two areas at the edges of its range following these two storms (VanderWerf 2013). Furthermore, in at least one drought year, puaiohi experienced exceptionally low reproductive output, likely due to limited food availability (Snetsinger et al. 2005). However, we only have data from a single drought year. Thus, while future hurricanes and droughts will likely affect the remaining puaiohi population, their precise effects remain unclear, and as such, were not incorporated into our model. Further examination of how these catastrophes may affect puaiohi populations is warranted.

Our lack of understanding of these processes may be further compounded by the unpredictability of future climate conditions, which will likely affect the long term accuracy of our models' predictions. Climate change has the potential to influence puaiohi numbers in several ways. Hawai‘i tends to be drier and drought-prone during strong El Niño events and wet during La Niña events, although the effect of the latter is more variable (Chu et al. 2010, Chu & Chen 2005, Kolivras & Comrie 2007). This relationship between drought and El Niño is of particular concern as evidence suggests that El Niño and La Niña events have been more variable and intense over the past several decades, presumably due to the increase in environmental temperatures produced by anthropogenic climate change (Cobb et al. 2013, DeNezio et al. 2013, Meng et al. 2012). If this trend in variability and intensity persists, overall yearly precipitation may decrease across Hawai‘i (Chu et al. 2010), resulting in more years of low annual reproduction than puaiohi can tolerate (Fantle-Lepczyk et al. 2016). In addition, climate change scenarios often predict an increase in hurricanes (Murakami et al 2013). Thus, understanding and modeling the effects of hurricanes on puaiohi may become even more important to accurately predicting their future persistence.

Furthermore, climate change may affect rates of malarial transmission. This makes understanding the impacts of malaria on puaiohi pressing, if we are judge the import of allocating resources to decreasing the prevalence of malaria in puaiohi habitat or to facilitating malarial resistance in the birds. The incidence of malaria is expected to increase with global climate change as warming temperatures allow the disease's mosquito vector to penetrate into the current malaria transitional zone (altitudes >1,400m). Thus, mosquito vectors will likely expand their distribution to higher elevations, thereby increasing infection rates (Benning et al. 2002). Furthermore, declines in high magnitude precipitation events which flush mosquito larvae from streams, may increase mosquito breeding habitat, and thus adult disease vectors (Atkinson et al. 2014) within the puaiohi's habitat.

While longer data sets and more support for some of our model assumptions would certainly increase our model confidence, it seems unlikely they would qualitatively affect our conclusions. Furthermore, the utility of PVA is less in the actual numbers it provides than as a means of comparing relative extinction risks, either between subpopulations of a species or between alternative management actions (Lindenmayer and Possingham 1996, Brook et al. 2000, Morris and Doak 2002). As with many forest bird species in Hawaii, gathering additional data is time consuming and expensive given the species' often inaccessible locations and very small population sizes. Thus, while gaining more information would be useful, given the limited resources that can be dedicated to this species, we feel this study provides useful, actionable management recommendations with can help increase the puaiohi population.

Management Recommendations

It seems clear that rat control within prime puaiohi nesting habitat is critical for the species' long term survival. Snetsinger et al (2007) previously demonstrated that intensive rat removal had significant positive impact on puaiohi recruitment. Even at levels of impact below what Snetsinger achieved, rat control appears to be quite effective at increasing puaiohi numbers (Fig. 3.1). This has been shown to be true for the O‘ahu ‘elepaio, (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011). Though rat control poses costs, technology exists to implement an effective rat control program. This effort might also act as an umbrella technique, whereby it would benefit not only the puaiohi, but the other few remaining endemic birds of the Alaka‘i.

Providing predator-proof nest boxes also has potential to positively affect puaiohi. This technique would not only increase female survival and reproductive output, but also increase the number of available nesting sites, a potential limiting factor for the species at present. Researchers have experimented with different nest box designs (Pitt et al. 2011), but have yet to find a design readily accepted by puaiohi. Research into effective nest box designs continues, however, providing some hope of an additional effective management option soon.

Other management activities exist that could increase puaiohi populations and growth rates. Supplemental feeding, akin to the papaya and scramble eggs provided to recently released captive birds, may help increase carrying capacity and reproductive output (Newton 1998, Gonzalez et al. 2006, Houston et al. 2007, Schoech et al. 2008), though this is likely similar in its labor intensiveness to rat removal, with smaller pay offs. Removal of invasive plants to promote the return of native vegetation, and thereby, native food sources also has some potential for positive growth rates and number increases. In addition, this action would benefit a large number of native plant species, as well as other endemic birds. Finally, steps can be taken to improve overall puaiohi survival. One of the most likely means to do so would be the management of malaria. While puaiohi do not seem to as susceptible to malaria as some Hawaiian endemic birds, evidence of the disease has been found in the species (Atkinson et al. 2014, Atkinson et al. 2001, VanderWerf et al. 2014), and it likely does have an impact on overall species survival. Though more research is necessary to fully understand the impact of malaria on puaiohi, removal of pigs may decrease to prevalence of suitable mosquito habitat, and thereby malaria, would likely be of some aid to sustaining populations. Pig removal would also limit the damage to native plants and the weed spread, thereby increasing habitat quality. Because many of the issues facing puaiohi are the same as those faced by the other Hawaiian forest birds, this, and all of the recommended management activities could have a substantial and valuable positive impact on the other few remaining endemic birds of the Alakaʻi.

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Table 3.1. Vortex parameter inputs for the baseline puaiohi population model.

Parameter	Value
Species Description	
Inbreeding Depression	
Lethal Equivalent	6.29
% due to Recessive Lethals	50%
EV Concordance of Repro and Survival?	Yes
Reproductive System	
Reproductive System	monogamous, probably long term
Age of 1st Offspring Females	1
Age of 1st Offspring Males	1
Max Age of Repro	10
Max # Broods/Year	4
Max # Progeny/Brood	2
Sex Ratio at birth in % Males	1 to 1
Density Dependent Reproduction	yes
% Breeding at Low Density	100%
% Breeding at K	90%
Allee Parameter	0
Steepness Parameter	8
Reproductive Rates	
% Adult Females Breeding	Will be automatically calc'd from % Breedings, A, and B
EV (SD) in % Breeding	10
Distribution of Broods each Year	0--13.16%; 1--42.11%; 2--36.84%; 3--5.26%; 4--2.63%
# Offspring/Female/brood (exact distribution of brood size)	1--30.77%; 2--69.23%
Mortality Rates	
Mortality of Females as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.54
SD in Mort after Age 1	3

Mortality of Males as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.29
SD in Mort after Age 1	3
Mate Monopolization	
% Males in Breeding Pool	100%
Initial Population Size	
Stable Age Distribution?	Yes
Initial Population Size	500
Carrying Capacity	
K	1100
SD in K due to EV	10

Table 3.2. RAMAS parameter inputs for the baseline puaiohi population model.

Parameter/variable	Value
Replications	1000
Duration	25 years
Density Dependence	
Affects:	all vital rates
Based on Abundance of Which Stages?	all stages
Density Dependence Type	ceiling
Stages	
Stage structure details	4: Female Juvenile, Female Adult, Male Juvenile, Male Adult only adult life stages breed
Sex Structure	
Model includes:	males and females, in separate stages
Number of Stages for Females	2
Mating System	monogamous
Stage Matrix	
Female Adult→Female Juvenile	1.20
Female Juvenile→Female Adult	0.23
Female Adult→Female Adult	0.46
Female Adult→Male Juvenile	1.20
Male Juvenile→Male Adult	0.23
Male Adult→Male Adult	0.71
Standard Deviation Matrix	
Female Adult→Female Juvenile	0.40
Female Juvenile→Female Adult	0.10
Female Adult→Female Adult	0.03
Female Adult→Male Juvenile	0.40
Male Juvenile→Male Adult	0.10
Male Adult→Male Adult	0.03
Populations	
Initial Abundance	500, equally divided into 4 stages
Carrying Capacity	1100
SD of Carrying Capacity	110
Stochasticity	
Stochasticity type and distribution	demographic stochasticity; normal

Extinction threshold	below 5 individuals
Within-population correlation	fecundity, survival and carrying capacity are all correlated

Table 3.3. Baseline candidate model results. The model in bold, Baseline without inbreeding, was chosen as the baseline for all model scenario comparisons. Equivalency testing of model output (stochastic r and N extant) shows models with and without inbreeding depression to be equivalent, so we chose to exclude inbreeding depression. The Baseline without inbreeding model, with a steepness value of 8, was equivalent to models with steepness 4 or steepness 16. As a result, we chose to use a steepness value of 8 in our baseline model.

Model	Prob of Extinct	PE SE	Stoch r mean	Stoch r SE	Stoch r SD	N in all pops mean	N SE	N SD	TE median	TE mean	TE SE	TE SD
Baseline w. inbreeding	0.981	0.004	-0.269	0.002	0.196	0.20	0.02	0.75	17.00	16.64	0.11	3.37
Baseline wo. inbreeding	**0.974**	**0.005**	**-0.267**	**0.002**	**0.201**	**0.32**	**0.04**	**1.24**	**17.00**	**16.72**	**0.11**	**3.53**
Baseline wo. inbreeding, steep4	0.966	0.006	-0.264	0.002	0.199	0.35	0.03	1.07	17.00	16.92	0.11	3.48
Baseline wo. inbreeding, steep16	0.973	0.005	-0.268	0.002	0.199	0.28	0.03	1.06	17.00	16.69	0.11	3.52

Table 3.4. Parameter input for management models.

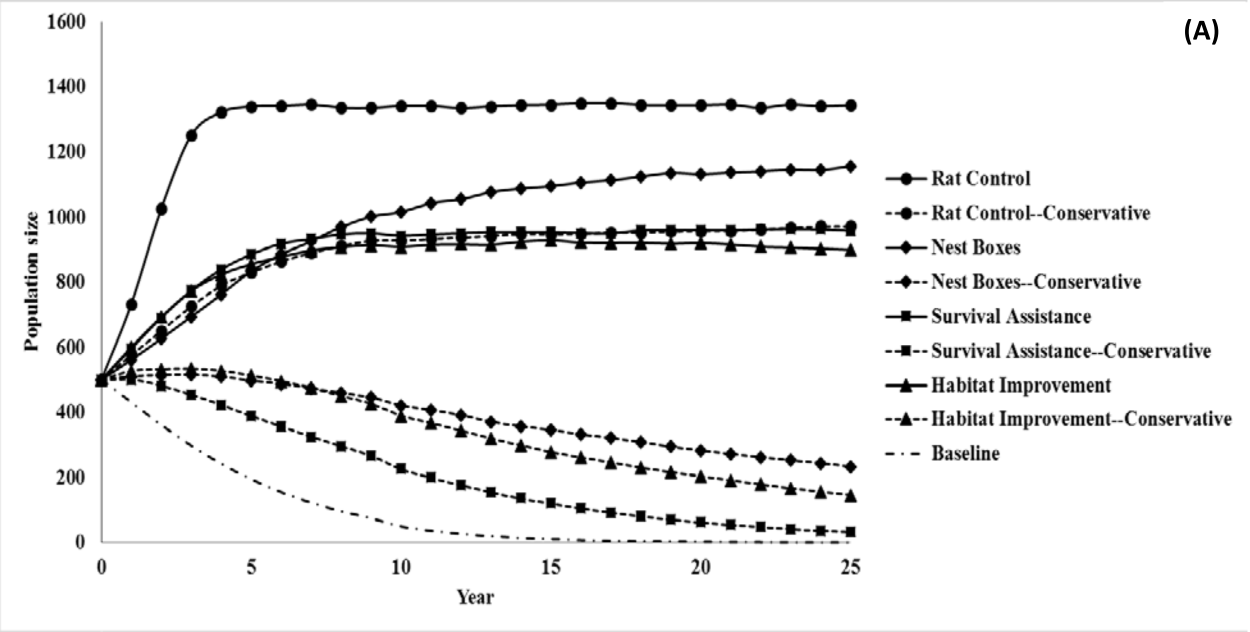
	Vortex						RAMAS				
Model	K	Juv mort	Female mort	Male mortality	Fecundity (successful attempts/ year)	Fecundity (fledged/ successful attempt)	K	Juv surv	Female surv	Male surv	Fecundity/ year
Baseline	1100	0.77	0.54	0.29	1.42	1--30.77%; 2--69.23%	1100	0.23	0.46	0.71	2.40
Rat control	1375	0.58	0.29	0.29	2.13	1--30.77%; 2--69.23%	1375	0.42	0.71	0.71	3.60
Rat control-conservative	1210	0.69	0.41	0.29	1.78	1--30.77%; 2--69.23%	1210	0.31	0.59	0.71	3.01
Nest boxes	1375	0.77	0.29	0.29	2.13	1--30.77%; 2--69.23%	1375	0.23	0.71	0.71	3.60
Nest boxes-conservative	1210	0.77	0.41	0.29	1.78	1--30.77%; 2--69.23%	1210	0.23	0.59	0.71	3.01
Survival assistance	1100	0.58	0.41	0.22	1.42	1--30.77%; 2--69.23%	1100	0.42	0.59	0.78	2.40
Survival assistance-conservative	1100	0.69	0.49	0.26	1.42	1--30.77%; 2--69.23%	1100	0.31	0.51	0.74	2.40
Habitat improvement	1210	0.69	0.49	0.26	1.95	1--13.46%; 2--86.54%	1210	0.31	0.51	0.74	3.64
Habitat improvement-conservative	1210	0.69	0.49	0.26	1.56	1--23.85%; 2--76.15%	1210	0.31	0.51	0.74	2.75

Table 3.5. Population viability model results from Vortex and RAMAS modeling software. Probability of extinction and population size are within 25 years, and mean time to extinction is for all iterations that went extinct within 25 years.

	Vortex						RAMAS					
Model	Stoch r	Prob of extinct	Mean N	N SD	Mean TE	TE SD	λ	Prob of extinct	Mean pop N	N SD	Mean TE	TE SD
Baseline	-0.267	0.97	0.32	1.24	16.72	3.53	0.803	0.86	3.25	8.11	18.65	3.45
Rat control	0.297	0.00	1344.15	124.80	0.00	0.00	1.294	0.00	1367.79	142.47	0.00	0.00
Rat control-conservative	0.075	0.00	972.21	207.36	0.00	0.00	1.038	0.00	735.89	392.43	0.00	0.00
Nest boxes	0.082	0.00	1156.68	205.34	0.00	0.00	1.090	0.00	1131.08	357.58	0.00	0.00
Nest boxes-conservative	-0.048	0.01	234.96	221.30	23.00	2.33	0.952	0.05	182.34	228.85	22.34	2.54
Survival assistance	0.075	0.00	958.02	117.02	0.00	0.00	1.064	0.00	845.23	300.36	0.00	0.00
Survival assistance-conservative	-0.126	0.16	33.01	38.57	22.12	2.46	0.916	0.14	78.08	113.80	21.76	2.60
Habitat improvement	0.059	0.00	899.18	245.71	0.00	0.00	1.048	0.00	811.45	387.16	0.00	0.00
Habitat improvement-conservative	-0.067	0.02	144.95	146.54	22.80	2.46	0.957	0.03	215.12	243.61	22.76	1.79

Table 3.6. Management model outcomes. Percentages represent the proportion of 1,000 iterations that resulted in one of three possible outcomes (Success, Not Needed, or Failure, see Robinson et al. (2015) for details). Also included is the probability that λ rose above stochastic r = 1 when starting below the target (management worked when needed, calculated as *Success*/*Success* + *Fail)*.

	Success	Management Not Needed	Failure	Management Worked
Rat control	100%	0%	0%	100%
Rat control-conservative	98.3%	0%	1.7%	98%
Nest box	99.1%	0%	0.9%	99%
Nest box-conservative	11.9%	0%	88.1%	12%
Survival assistance	100%	0%	0%	100%
Survival assistance-conservative	0.2%	0%	99.8%	0%
Habitat improvement	96.6	0%	3.4%	97%
Habitat improvement-conservative	4%	0%	96%	4%



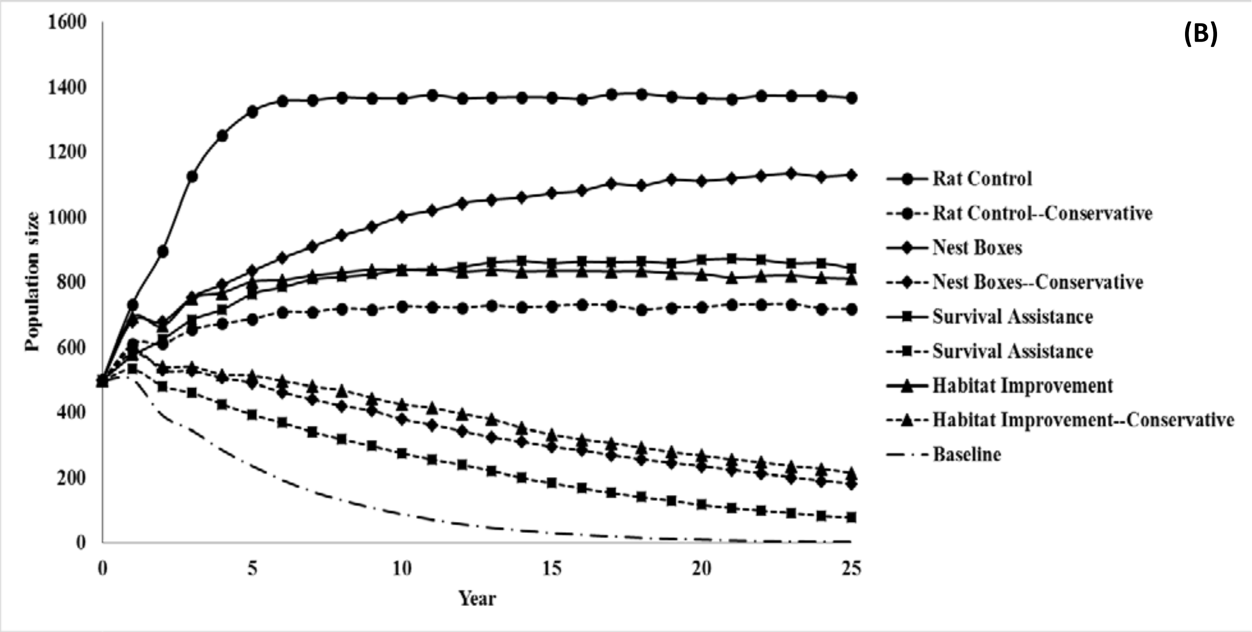


Figure 3.1. Population trajectories of baseline and management models in Vortex (A) and RAMAS (B).

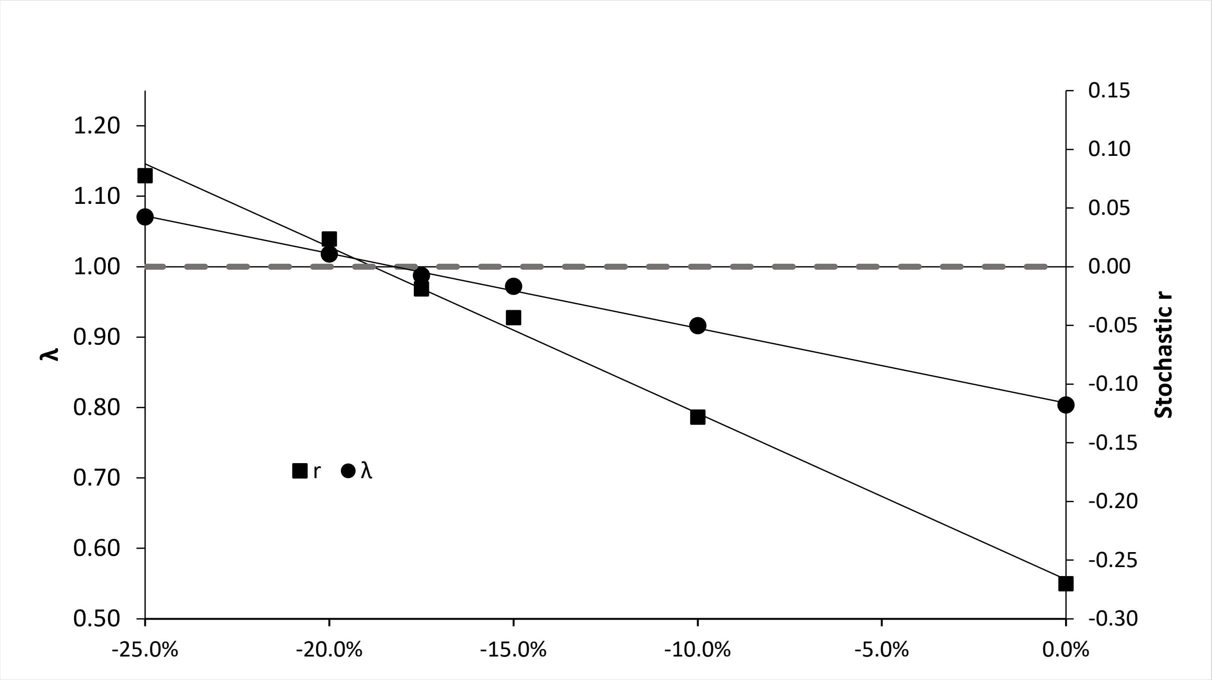


Figure 3.2. Evaluation of varying mortality to achieve a stable growth rate in Vortex (stochastic r) and RAMAS (λ).

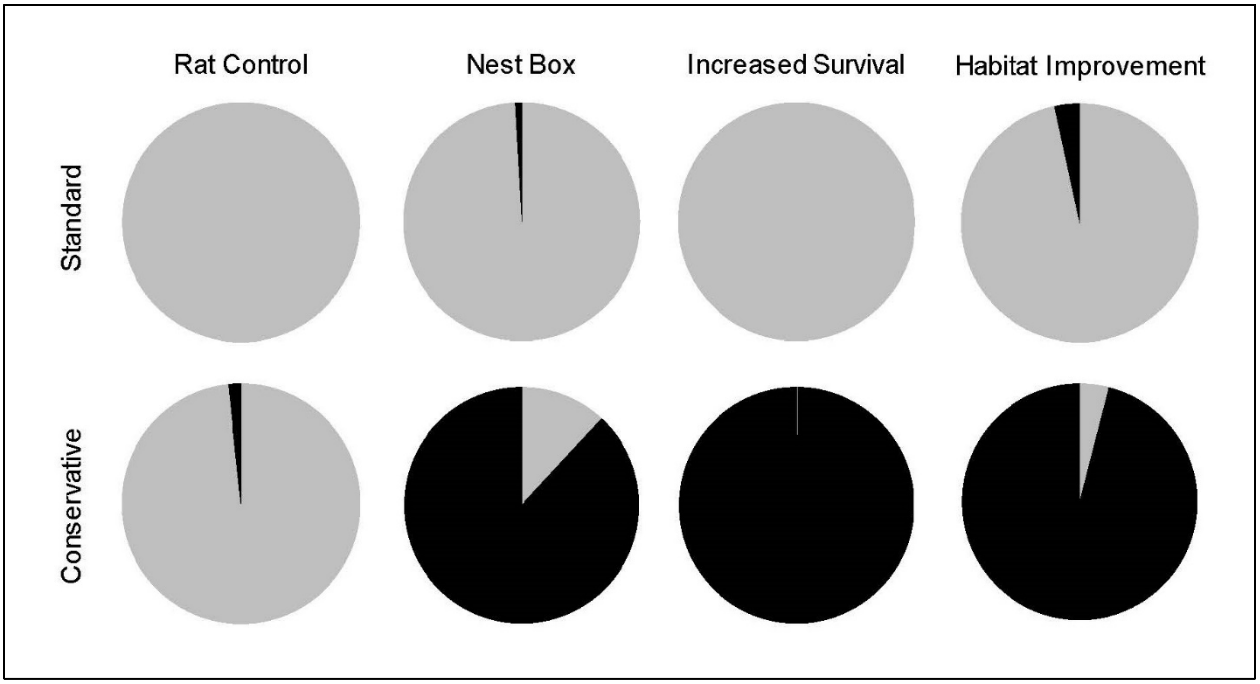


Figure 3.3. Evaluation of management outcome. The pie charts indicate the number iteration in which management was either successful (growth rate was increased from below the target value to at least the target value, gray areas), or failed (growth rate remained below the target after management, black). See Robinson et al. (2015) for details.

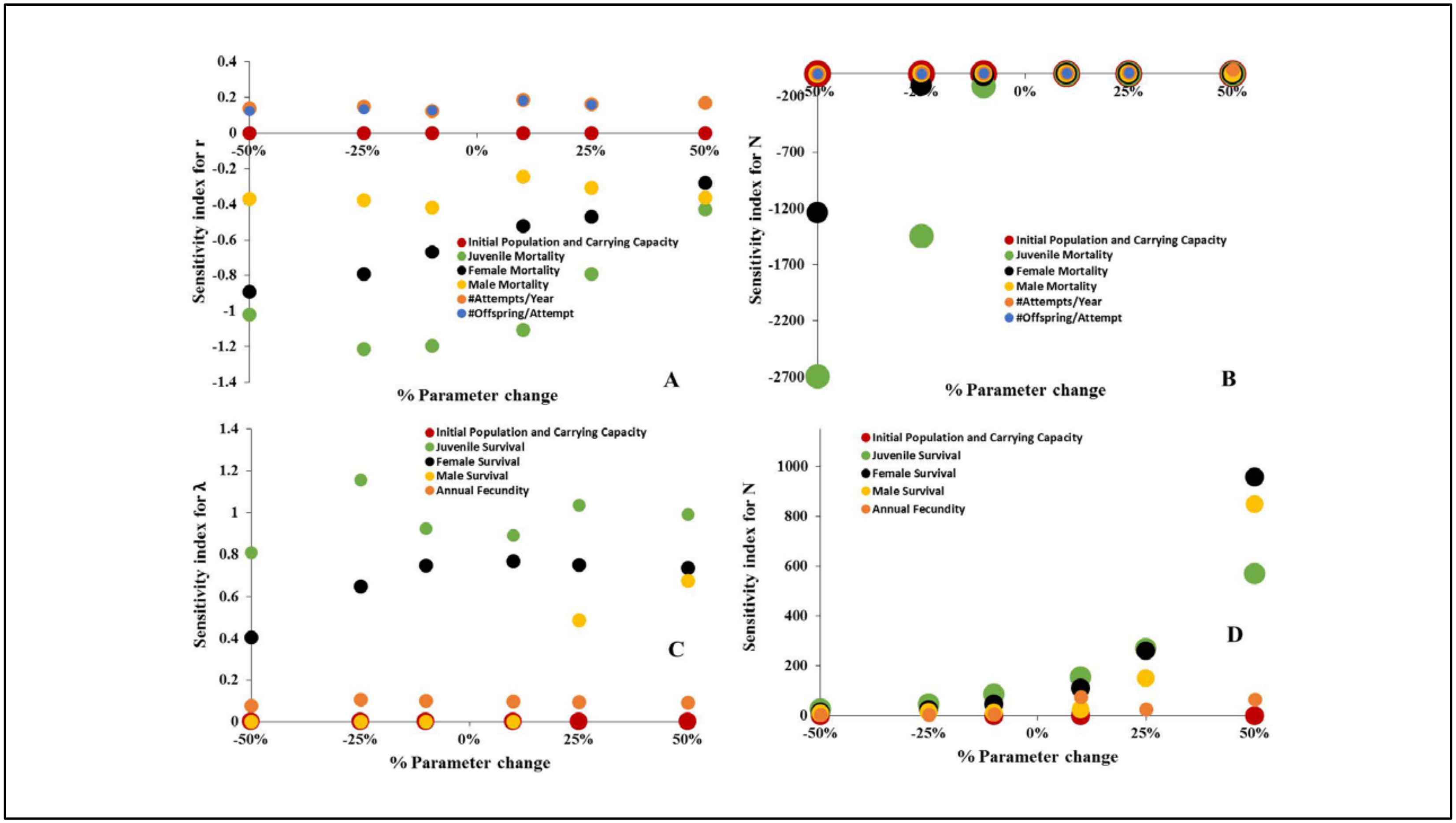


Figure 4. Sensitivity index (SI) on growth rate and final population size in Vortex (A, C) and RAMAS (B, D). Increased distance from X axis (sensitivity index of 0) indicates more sensitivity.

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CHAPTER 4

AN ANALYSIS OF TRANSLOCATION REGIMES FOR THE ENDANGERED PUAIOHI

ABSTRACT—The ongoing and often synergistic effects of habitat loss, invasive species, and climate change pose challenges for species conservation and management as widespread species become greatly reduced, sometimes to a single small population. To address this problem, conservation biologists must consider using approaches such as translocation to create new populations, reducing the probability of extinction by splitting a population into two or more populations in geographically distinct locales. The puaiohi (*Myadestes palmeri*), an endangered Hawaiian forest bird, has a small population size (~500 birds) and restricted range (~40 km^2; Crampton et al., in review). One of the recovery plan involves translocating birds to higher elevation Hawaiian Islands (U.S. Fish and Wildlife Service 2006). To evaluate various translocation scenarios, we built upon previously developed population viability analysis models and considered how translocation regimes (initial population, number supplemented per event, supplementation interval, and length of supplementation) would affect both the original and new population. We considered two different sources of birds to translocate: a declining wild population and a theoretically stable population. Furthermore, we modeled the puaiohi release population under three different conditions: a theoretically stable population, a predator-controlled environment, and a habitat improved in terms of resource availability. Our results indicated that while translocation does offer hope of increasing puaiohi population and decreasing extinction risk, success will depend on the conditions at the release site. Furthermore,

re-establishment of the puaiohi captive breeding program may be necessary to provide enough birds to translocate, as the current wild population may not be productive enough to sustain the levels of harvest necessary to successfully establish a new population.

KEYWORDS—Hawaiian forest birds**,** *Myadestes palmeri*, PVA, small Kaua‘i thrush, Vortex

INTRODUCTION

The ongoing extinction crisis poses challenges for species conservation and management as biologists are forced to negotiate both long-standing problems, such as habitat loss and invasive species, and more recent problems like climate change. Species that were once widespread have been greatly reduced, sometimes resulting in only a single small population remaining. For instance, California condor (*Gymnogyps californianus*) and whooping crane (*Grus americana*) were each reduced to single small populations as a result of overexploitation, pollution and habitat loss (Meretsky et al. 2000, Meine and Archibald 1996). When species exist as only a single population they face a wide variety of challenges, including increased likelihood of extirpation due to stochastic events and inbreeding depression (Lacy 2000, Gilpin and Soulé 1986, Shaffer 1981). Because of the ongoing and often synergistic effects of habitat loss, invasive species, and climate change, managers need to consider more invasive and labor intensive approaches to bring species back from the brink of extinction. One such approach is to create new populations via reintroduction into habitat from which the species was extirpated and/or translocation into novel but biologically appropriate geographic areas (Griffith et al. 1998). The goal of these approaches is the creation of additional populations, thereby reducing the probability of extinction by spreading the risk.

While novel and emergent conservation approaches are relevant throughout the world, nowhere are they more needed than the Hawaiian Islands, home to the largest number of threatened and endangered species in the United States (Wilcove et al. 1998), with one of the most imperiled avifaunas in the world (Scott et al. 2001, Pratt et al. 2009). Amongst the various single population species left in Hawaii, one in urgent need of reduction in risk of extinction is the puaiohi (*Myadestes palmeri*). Endemic to Kaua‘i, the Puaiohi is the only remaining species in the thrush family, Turdidae, and the only remaining native frugivore on the island. The puaiohi has a population of ~500 and is currently restricted to a remnant of the Alaka‘i Wilderness Preserve at 1,050 to 1,300 meters, where 75% of its breeding population occurs in just 10 km^2 of forest (U.S. Fish & Wildlife Service 2006).

Puaiohi face a number of issues that affect their population vulnerability, including drought, hurricanes, invasive predators (e.g., rats [*Rattus* spp.] and cats [*Felis catus*]), disease (particularly infection with avian malaria ([*Plasmodium relictum*])and habitat degradation due to feral livestock (pigs and goats) and invasive plants (Kepler & Kepler 1983, Snetsinger et al. 2005, U.S. Fish & Wildlife Service 2006, Woodworth & Pratt 2009). However, recent work suggests that traditional conservation efforts to control introduced predators, remove invasive species and restore native forest may be insufficient to protect many Hawaiian forest birds, including the puaiohi, from further decline as climate change warms habitats previously devoid of avian malaria (Benning et al. 2002). Though infection with malaria may not affect puaiohi survival as negatively as it does other species (VanderWerf et al. 2014), given the puaiohi’s absence from malarial-infected lower elevations, malaria is likely to have at least some impact on the population. Thus, unless conservation managers are willing to explore novel, long-term solution to managing the species, they risk species’ risk range collapse and extinction (Fortini et al. 2015).

Concerns about puaiohi’s limited range and small population led to the establishment of a captive-bred population in 1996. From 1999 to 2012, 222 birds were released into the Alakaʻi (Switzer et al. 2013). However, due to the relatively low recruitment and survival of released birds in later years of the program and signs of congenital abnormalities in captive bred chicks, the program was discontinued and the last of the captive flock was released in 2016 (DLNR 2016, VanderWerf et al. 2014, Switzer et al. 2013).

While continued monitoring and managing of puaiohi within their current range remains a primary concern, one of the current recovery objectives for the puaiohi is to investigate the feasibility of translocating birds to higher elevation Hawaiian Islands such as Maui and Hawaiʻi (Hawaiʻi Forest Bird Conservation Forum, Sept. 24-25, 2015). Translocation has become of increasing interest because as the climate warms and the malaria threat increases and invasive species negatively impact both the species and the habitat upon which they rely, the persistence of puaiohi in their remaining forest becomes more precarious. Furthermore, given the limitation of nest sites and perhaps other resources within current puaiohi habitat, some speculate that puaiohi are at their carrying capacity (Snetsinger et al. 2005). In addition, as evidenced after the 1982 and 1992 hurricanes ʻIwa and ʻIniki, in which five of the six endangered species in the Alakaʻi Swamp went extinct, small populations on Kauaʻi are extremely vulnerable to hurricanes (Conant et al. 1998). One way to increase carrying capacity and reduce the dangers of catastrophic events would be to establish one or more additional populations that are geographically separated from the remaining one, as was accomplished with the Nihoa millerbird

(*Acrocephalus familiaris kingi*; Freifeld et al. 2016) and Seychelles warbler (*Acrocephalus sechellensis*; Komdeur 1997).

To evaluate future conservation approaches for the species, we modeled potential outcomes of translocating puaiohi to establish another population and identified sustainable levels of effort and support necessary to successfully create the new population, while minimizing effects on the current population. Previous modeling efforts in Hawaii (Conant and Morin 2001) have led to the successful translocation of the Nihoa millerbird from Nihoa to Laysan, an atoll from which millerbirds have been absent for approximately 100 years (Ely and Clapp 1973). As with millerbirds, the objective of our modeling efforts is to evaluate whether translocation offers a feasible tool for recovering puaiohi, and if so, identify how probability of success can be maximized.

METHODS

We calculated model parameters from data collected from 2005-2011 at four sites (Kawaikōī, Koaie, Mohihi, and Halepaʻakai) in the Alakaʻi Wilderness Preserve on the island of Kauaʻi, Hawaiʻi. These sites ranged in elevation from 1,123-1,303 m above sea level in native wet and mesic forests dominated by ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa*), ōlapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ʻōhiʻa ha (*Syzygium sandwicensis*), kāwaʻu (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), with a diverse understory of native plants including ʻōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) (U.S. Fish & Wildlife Service 2006).

To evaluate translocation scenarios, we constructed population viability analysis (PVA) models using Vortex 10 (Lacy and Pollack 2014), which simulates stochastic demographic and environmental processes. Within Vortex we built upon previously developed models (Fantle-Lepczyk et al., in review) using all available information on puaiohi (Table 4.1). In addition to running a baseline control model in which no translocation occurred, we considered how translocation regimes (initial population, number supplemented per event, supplementation interval, and length of supplementation) affected both the original and the new populations. We considered three different sources of birds to translocate: a declining wild population (Fantle-Lepczyk et al. in review), a theoretically stable wild population, and a captive-bred source with no impact on the wild population. We considered the two different wild source population dynamics because although baseline models predict a population declining to extinction, scientists have assumed puaiohi populations have been stable for the last 40 years (USFWS 2006). Modeling under both conditions allowed us to examine the possible range of dynamics currently affecting the wild population.

We also modeled the translocated population under three different release conditions: the same as the wild, theoretically stable population, a predator-controlled environment, and a habitat improved in terms of resource availability. Each model was simulated 1,000 times (Owen-Smith 2007) over a relatively short time frame of 25 years. Although long-term preservation of the species is the goal, we recognized that the recovery program is currently driven by urgent short-term needs. Furthermore, longer time spans tend to produce higher extinction probabilities (Akçakaya et al. 1999), propagate errors (Beissinger and Westphal 1998), and more uncertain events (Akçakaya 2005). Thus, we chose a relatively short time frame of 25 years because it allowed for exploring and testing the immediate effects of management strategies while minimizing the effects of uncertainties or errors in our parameter estimates. We defined extinction as occurring when only one sex remained. Vortex's standard output provided us with stochastic r, probability of extinction, average population size at 25 years, and mean time to extinction.

We modeled four cohorts or stages: juvenile females, adult females, juvenile males, and adult males. We developed our demographic input parameters from a variety of sources, including original data, previously published information, and discussion with experts on the species. Because little is known about the genetics and impacts of inbreeding depression on puaiohi, we chose not to incorporate this parameter into our models. Previous studies (Fantle-Lepczyk et al., in review) found inbreeding depression models to be equivalent to non-inbreeding models based upon these defined limits ($p < 0.001$), so we do not believe this will effect model outcome. We assumed that the effects of environmental variation on reproduction and survival were correlated.

Reproduction

We assumed puaiohi are monogamous (Woodworth and Pratt 2009), and pairs persist from year to year, provided mates survive. Individuals of both sexes can breed at a year old. One study observed after hatch year birds helping at 8% of nests, suggesting they needed to delay reproduction due to some sort of limiting factor (Snetsinger et al. 1999), but this behavior has not been seen in other studies. Puaiohi always lay two eggs per clutch (Snetsinger et al. 2005), and during the 2007-2009 study period fledged one chick in 30.77% of successful attempts and two chicks in 69.23% of successful attempts. Snetsinger et al. (1999) reported up to five nest attempts per season, while we never saw more than four true nest attempts per season between 2007 and 2009. As a result, we assumed four nest attempts to be a reasonable maximum [during the 2007-2009 study period the distribution of successful nest attempts was: 0

(13.16%), 1 (42.11%), 2 (36.84%), 3 (5.26%), and 4 (2.63%)]. A puaiohi mist-netted as a hatch-year bird in 1965 survived until it was 11 years old (Snetsinger et al. 1999). The longest-lived captive female died at 16 years old at the Maui Bird Conservation Center (MBCC), but stopped laying eggs at 9. The oldest captive male lived for 13 years and was still able to fertilize eggs in the breeding season before he died and other individuals have lived as long as 10 years (S. Belcher, pers comm). As a result, we decided to use a maximum life span of 10 years. Of 118 eggs laid at the MBCC, 57 hatched males and 61 females (S. Belcher, pers comm), which we used as the basis for a 1:1 sex ratio at birth.

Density Dependence

Vortex models density dependence in terms of its effect on reproduction as: $P(N) = (P(0)-((P(0)-P(K))*((N/K)^B)))*(N/(A+N))$; where $P(0)$ is the percentage of adult females breeding at low density; $P(K)$ is the percentage of adult females breeding at carrying capacity; N is initial population size; K is carrying capacity; B is a steepness parameter, which determines the shape of the curve relating the percentage of adult females breeding to population size; and A is the Allee parameter, which accounts for the decrease in the proportion of females breeding at low densities, due to of the increased difficulty of finding a mate at low population densities. We assumed that puaiohi would be density-dependent, given that it is a territorial bird with limited nesting sites and food sources. During intensive territory mapping from 2007-2009, an average of 90% of the population encountered was breeding. However, by the 2009 census, fecundity appeared to drop off slightly, perhaps due to the population nearing K. Thus, we assumed that at K, 90% of the population was breeding. Give that a large proportion of the population still seemed to be breeding at K, we assumed that 100% of the population would breed at low density. In the absence of data to the contrary, and given that puaiohi occur in a relatively small remnant habitat area and would presumably be able to find each other through song, we assumed the Allee effect was zero. Previous models (Fantle-Lepczyk et al., in review) showed equivalent results ($p < 0.001$) between iterations with steepness values of 4, 8, and 16, so we used 8 in our baseline model.

Vortex used the parameters of percent breeding at low density and percent breeding at high density, the Allee parameter and the steepness parameter to automatically calculate the percent of adult females breeding. For the effect of environmental variation on percent breeding, we used default values in the absence of other data. We do know that except in years of extreme weather, fecundity rates, at least, are fairly stable (Fantle-Lepczyk et al. 2016). Although hurricanes have caused serious damage to its habitat and been implicated in the extinction of forest bird species that share the puaiohi's habitat, the well-sheltered ravines in which puaiohi prefer to nest probably offer adequate protection from storms (Conant et al. 1998, Snetsinger et al. 1999). Finally, we assumed that 100% of males would be in the breeding pool, though not all may not find mates due to a skewed sex ratio resulting from higher female mortality.

Mortality

Using mark recapture analysis to estimate the annual survival of juvenile and adult puaiohi, VanderWerf et al. (2014) found that adult males survived at a higher rate (71 ± 9%) than females (46 ± 12%), and suggested that rat predation may be a significant factor in female mortality, a pattern common in other Hawaiian passerines (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011, Mounce et al. 2013). Additionally, they found juvenile survival to be quite low (26 ± 21%), which may limit population growth. Recently fledged young tend to remain on the ground for about four days after fledging, making them particularly vulnerable to predation by rats and feral cats. We used these survival estimates in our baseline model, converted to mortalities, as they represent the only long-term estimate of puaiohi survival rates. Given the relatively high mortalities of juveniles and females and the low starting population, initial results showed that our model would not tolerate deviations in mortality rate due to environmental variation greater than 10%. Furthermore, as with percent breeding, we felt that in this relatively stable island environment we would not see large annual fluctuations in mortality rates. Thus, we used Vortex's default, relatively modest deviation in mortality rate of 10% for juvenile mortality and 3% for adult mortalities.

Population Size and Carrying Capacity

In the absence of information to the contrary, we assumed puaiohi achieve a stable age distribution. Estimates of population size have varied, from conservatively exceeding 200 (Snetsinger et al. 1999) to around 500 (USFWS 2006). We used the USFWS estimates because they were the most current and based on the longest data set. No attempts have been made to estimate puaiohi carrying capacity in the Alakaʻi Wilderness Area; however, the puaiohi population is strongly linked to streams, and we have estimated bird densities along those streams. Within puaiohi habitat, approximately 236 km of streams exist of which about half suitable for nesting. At peak nesting density in 2009, with nest success declining (perhaps indicating the population was approaching K), we found 27 nesting territories over 6 km of suitable habitat. Assuming two puaiohi per territory, this yields an upper limit of 1,062 birds over the 118 km of suitable habitat. For our estimate of K, we rounded up to 1,100 to include in the population any unpaired or floater birds also utilizing the resources. This may be an overestimate of K, as these numbers are estimated from one of the higher nest density streams, and not all streams are likely to support this number of birds. However, in the interest of testing increases in other demographics of interest, we choose to err on the side of overestimation in order to give our modeled populations some room for increase. In the absence of better information, we assumed fluctuation in K due to environmental variation to be ±10. In the absence of any specific information on potential release sites, and in order to minimize the number of factors varied between original and translocated populations, we assumed that K would be the same for both populations.

Harvest and Supplementation

To determine sustainable translocation regimes and their impacts on the existing puaiohi population, we modeled all combinations of variations of the initial starting population of the translocated population, the number of birds supplemented at each supplementation interval, length of supplementation interval, and the length of supplementation (n = 36, Table 4.2). For evaluation purposes we calculated two additional measures from the latter three measures: number of supplements and total number of birds supplemented. We set up our models to harvest from the source population and translocate to the new population, with 90% survival due to translocation, as previous releases of captive bred puaiohi found a 91% 30-day post-release survival (Tweed et al. 2006) for primarily juvenile birds. We choose to translocate only juvenile birds, as these exhibited the highest survival and integration into the existing population in previous releases of captive-bred puaiohi (Tweed et al. 2006, VanderWerf et al 2014).

Translocated Population Demographics

We considered three different sets of conditions upon release, in which we assumed the release site would be an improvement over current conditions, which produce, at best, a small and stable, though potentially declining population. The first of these three conditions reflects a stable population, as modeled in the wild theoretically stable population. We also modeled release in a predator-controlled area in which survival and nest success increase due to release from predator impacts. Finally, we modeled release into an area with comparatively improved habitat, in which increased food sources and nesting sites, and some degree of predator control would allow for increase in both survival and reproductive output.

In our models with stable mortality at the release sites, we explored the effect of releasing puaiohi into an area managed to increase puaiohi survival at all life stages, with no increases in fecundity or other factors. To model how eliminating the effects of malaria, predation or any other mortality event might impact the puaiohi population, in the absence of any other population effects, we decreased previously estimated mortality at all life stages (VanderWerf et al. 2014) by 18%, to a level at which they would provide a stable population projection.

In our predator-controlled release condition models, we assumed that predators would be controlled or removed from the release site. While puaiohi are potentially preyed upon by several species, rats are its major predator (Snetsinger et al. 2005), and mortality due to nest predation by rats is presumed to be the leading driver behind higher mortality rates seen in female puaiohi (VanderWerf et al. 2014). To reflect this difference in mortality, we decreased our estimates of female mortality by 25%, from 54% to 41%. For the O‘ahu ‘elepaio, rat control has been shown to increase female survival by 10%-27%, which may make our estimate slightly high (VanderWerf 2009, VanderWerf et al. 2011). However, male puaiohi have an estimated annual survival rate of 29% (VanderWerf et al. 2014), so if nest predation is truly the major differential between male and female survival, removal of nest predators may in fact decrease female mortality substantially more than we have estimated. Snetsinger et al. (2005) found that 50% more nests fledged young when rats were controlled. To allow for any overestimates in Snetsinger et al.'s (2005) experiment and other causes of nest failure, we increased the number of successful attempts per year to 25% more than baseline. No experimental data exist to quantify rat predation effect on juvenile mortality. However, we surmised that rat removal would have less impact on juvenile mortality than on adult female mortality, as juveniles are probably subject to a greater range of mortality effects, and they are likely mostly vulnerable to rat predation in the first days after fledging. Thus, we decreased juvenile mortality by 10%. We presumed the removal of rats would have little effect on male mortality, since males do not incubate eggs on the nest (when females are presumably most vulnerable to rat predation). Furthermore, rat removal should not affect the number of young fledged/attempt because if a rat found a nest it would likely kill both chicks, resulting in a failed attempt.

Our final release scenario looked at potential impacts of habitat improvements on the puaiohi. Under this scenario, we assumed that the release site would be managed such that invasive species, which may displace native food sources and potentially decrease food availability, particularly during the breeding season, would be controlled. Furthermore, we presumed that abundant native and usable food sources would exist. Snetsinger et al. (2005) saw an increase of 37.5% in annual nest attempts for wet years over drier years. Presumably this increase in nesting attempts was due at least in part to increased food supply. Snetsinger et al. further noted a 54.5% increase in the number fledged per attempt in the wet year compared to the mean number fledged over the entire three years of study. However, one very dry year reduces the mean, likely resulting in over estimations of this impact (Fantle-Lepczyk et al. 2016). Considering these findings, we increased the number of successful nesting attempts per year by 37.5% and number of young fledged/attempt by 10% (lower than Snetsinger et al.'s finding due to our concern of overestimation) to reflect the greater food supply. We also assumed that increased food supply could slightly decrease juvenile, male, and female mortality, so those parameters were adjusted by 10% accordingly.

Defining Scenario Outcomes

We made an *a priori* decision that a newly established translocation scenario would be considered minimally successful if the new population attained at least 250 birds by 25 years, had less than a 5% probability of extinction, and a growth rate (stochastic r) greater than 0. A sustainably successful scenario would create a new population of 500 or more birds with a 0% probability of extinction and growth rate (stochastic r) greater than 0.10, a level of potential population increase that should allow some buffering for bad years. We tabulated how many scenarios achieved either level of success for each of the three output parameters of interest (stochastic r, probability of extinction, and final population size). For the original source population, we also tabulated how many harvests of birds to be translocated failed over all 1,000 iterations of each scenario, due to the unavailability of juvenile birds to move. We defined failed harvest attempts over 10% as an unacceptable rate of failure, because at that point too few birds would be available to translocate to maximize the chances of creating a new population.

We tested the impact of harvest (for translocation to new population) on the original population via equivalency testing in Minitab (version 17.3.1). We defined the limits at which we thought model output difference to be trivial, and thus harvest to have minimal impact as ±

0.05 stochastic r (essentially ± 5% annual growth rate), ± 0.05 probability of extinction, and ± 10 individuals or ± 10% of baseline individuals (whichever was greater) remaining at 25 years. Under the scenarios with a declining original population, we also considered time to extinction, as most iterations within these went extinct, with ± 3 years considered trivial.

Statistical Analysis

All statistical analyses aside from equivalency tests were performed in Systat 13. To evaluate the effects of initial population size, number supplemented per event, supplementation interval, length of supplementation, and release conditions on the growth rate, probability of extinction and populations size at 25 years on both the new population created via translocation and the original population, we used ANOVA with Bonferroni pairwise comparisons. We used linear regressions to evaluate how number of times supplemented and number of individuals supplemented effected growth rate, probability of extinction and populations size at 25 years of both populations. We considered a $p \leq 0.05$ as our cutoff for significance.

RESULTS

Nearly all translocation scenarios resulted in a positive growth rate for the new population, with only approximately 40% meeting the minimal criteria for probability of extinction and 30% for population size at 25 years (Table 4.3). Only 9% met the sustainable criteria for all three output measures. Amongst these models, the majority (7 of 10) were under improved habitat release conditions, and the remaining three under predator control release conditions (Table 4.4). While sustainable models were evenly split between initial populations of 10 and 20 individuals, most models required 10 years of supplementation (9 of 10), 20 individuals supplemented per translocation event (8 of 10), and yearly supplementation (7 of 10). All sustainable models required translocating ≥110 birds, which represented the most bird-intensive scenarios modeled. Of the top six models, the same three translocation protocols appear twice, under both habitat improvement and predator control release conditions.

Comparisons amongst different levels in the initial population size, number supplemented per event, supplementation interval, and length of supplementation indicated that all but one resulted in significant differences in stochastic r, probability of extinction, and population size at 25 years (Table 4.5). For stochastic r, growth rates depended on initial supplementation parameter value, except that supplementation of 5 or10 individuals per event were equivalent and resulted in lower growth rates than supplementing 20 individuals. For all other parameters, as the number of individuals and length of supplementation increased or supplementation interval decreased, the growth rate increased. For probability of extinction, supplementation of 10 or 20 individuals per event did not differ significantly, though supplementing 5 individuals resulted in a significantly higher extinction probability. In addition, supplementing every year or every other year did not yield significant differences in probability of extinction, while supplementing only every 5 years did produce a significantly higher probability of extinction.

For initial population size and number of years supplemented, as number of individuals and length of supplementation increased, the probability of extinction decreased. For population size, initial population size had no significant impact on population size at 25 years. However, a significant difference existed in the population size at 25 years, based on supplementing for 5 versus 10 years. Supplementation of 20 birds per supplementation event yielded a significantly higher final population size than supplementing 5 or 10 birds per event, as did supplementing every year or every other years versus every five years.

Both number of times and total number of individuals supplemented were significantly related to growth rate, probability of extinction, and population after 25 years (Table 4.5); as supplementations increased, growth rate and final population size increased and probability of extinction decreased. Amongst the three types of release conditions, habitat improvement yielded the highest growth rate and greatest population size after 25 years and lowest (though not significantly different from predator removal) probability of extinctions. In all cases, the stable mortality scenarios yielded the lowest growth rates and population sizes, and significantly higher probabilities of extinction.

While several scenarios successfully established translocated populations, these scenarios had varying effects on the original donor population, with the greatest impact on the declining wild population. Though all models were equivalent to the declining baseline model in terms of probability of extinction ($p > 0.97$) and population size at 25 year ($n < 0.4$ individual), this was likely due the extremely high probability of extinction and low population sizes exhibited by all of these models. However, 28% of translocation models did not exhibit growth rates and 22% did not have a mean time to extinctions equivalent to baseline (Table 4.6a). All sustainably successful translocation scenarios (Table 4.4) exhibited significantly lower growth rates and shorter mean times to extinction in a harvested original population than in a non-harvested one. Furthermore, during harvest for translocation, occasionally too few juveniles existed to harvest (Table 4.7). In 44% of our translocation scenarios, 10% or more all translocations attempted across all scenario iterations resulted in an inability to harvest sufficient juveniles for translocation, which exceeds the level above which we deemed failure to harvest unacceptable. Furthermore, all but two of the models in which harvest lasted 10 years exhibited failure rates over 10%.

In our theoretically stable population, all models were equivalent in terms of growth rate and probability of extinction (Table 4.6b). However, translocation regimes did have an impact on the donor population size at 25 years for 36% of scenarios. Again, all sustainably successful translocation scenarios (Table 4.4) were amongst the non-equivalent models. We were unable to test time to extinction since the vast majority of scenarios, and iterations within scenarios, did not go extinct.

The translocation scenarios did not differ in the growth rate, probability of extinction, population size at 25 years, and time to extinction of the original declining baseline population, based on the initial number of individuals harvested for translocation (Table 4.8). The number of individuals harvested per event did not significantly impact probability of, or time to extinction, but did affect growth rate and population size at 25 years. Specifically, harvesting 20 individuals resulted in a significantly lower growth rate than did harvesting 5 individuals, and a significantly smaller population size at 25 years than did harvesting 5 or 10 individuals. Harvesting every year resulted in a significantly lower growth rate and shorter time to extinction than did harvesting every other or every five years. Harvesting every year also produced a significantly higher probability of extinction and lower population size at 25 years than harvesting every five years. Harvesting for five years led to a significantly lower growth rate, higher probability of extinction, smaller population size after 25 years, and shorter time to extinction than did harvesting for 10 years. As both total number of times harvested and total number of individuals harvested increased, growth rate, population size after 25 years and time to extinction decreased, and probability of extinction increased.

If the original population is assumed to be stable, initial population still had no significant impact on probability of extinction, growth rate, population size or time to extinction (Table 4.9).

Total number of individuals harvested exhibits the same patterns. However, while the number harvested is the same for growth rate and probability of extinction, when the population is theoretically stable, only harvesting 5 individuals per event is significantly different than harvesting 20. Harvest interval has the same effect on growth rate under with baseline condition, but if the population is stable, it has no significant impact on probability of extinction. Only harvesting every year produces a significantly lower population size at 25 years than did harvesting every other or every fifth year. Finally, the number of years harvested did not significantly affect growth rate, probability of extinction, or population size in the theoretically stable population.

DISCUSSION

Of the 108 possible models for our translocated population, only 32 met our overall criteria for success, and only ten were sustainably successful. Amongst these ten, seven occurred under habitat improvement release conditions and three under predator-controlled release conditions. Notably, none of our sustainably successful models occurred under stable mortality release conditions.

In general, initial population size did not have a major effect on translocation outcome, but as more individuals were supplemented per event, supplemented more frequently or supplemented over ten rather than five years, establishing a new population was more likely to be successful. In terms of release conditions, better results were generally achieved under habitat improvement conditions, followed by predator controlled conditions. The stable mortality models were uniformly less successful than the other two release conditions.

Unfortunately, the models providing sustainable translocation success for a new population had the greatest impacts on the source population. Regardless of whether we modeled the existing source population based on available data or as a theoretically stable population, the seven sustainably successful translocation regimes were all among the models that were not equivalent to baseline condition (n = 10, 13 respectively). These seven models negatively impacted the source population such that growth rates, population size at 25 years, or mean time to extinction was no longer comparable to a population that sustained no harvest for translocation. Furthermore, as supplementation levels increased and occurred over a longer time frame, an increasing percentage of translocations failed due to lack of juveniles to harvest in the data-driven declining baseline models.

Given that the more successful a translocation regime was at establishing a new population, the more detrimental it was to original population, it may not be possible to build a new population of puaiohi from the existing wild flock. Although the wild flock has been presumed stable in recent years (U.S. Fish & Wildlife Service 2006), recent models based on best available data indicate that it may in fact be declining (Fantle-Lepczyk et al. 2016). Given the profound difference in effects of harvest based on source population, understanding more accurately the actual dynamics of the wild population is of great importance prior to any translocation project that involves regular removal of individuals.

Whether or not the original population is declining, one alternative that would decrease the impact on the wild population and allow for higher rates of supplementation is to re-initiate a captive breeding program for the puaiohi. Under the original captive breeding program, the entire captive population was derived from 15 eggs (of 19 collected), and annually produced an average of almost 16 releasable birds per year (Switzer et al. 2013). Given that the removal of up to 20 juveniles for establishing and initial translocated population did not have an overall significant effect on the source populations in our models, it seems safe to assume that harvesting a like number of eggs for captive rearing would have a similarly small impact. Furthermore, as the average of 16 birds formerly released annually via the captive breeding program is comparable to many of our sustainably successful models, captive breeding may offer a reliable and sufficient source of birds to ensure translocation success. Previous reintroductions were perceived to have met with limited success due to lack of genetic diversity, understanding of puaiohi life history and demographics, and ecosystem restoration (Switzer et al. 2013), lessons learned from the original program could produce a more robust captive breeding program.

Though our results have implications for puaiohi conservation, several caveats must be recognized. First, though we have tried to provide realistic estimates of puaiohi demographics under a suite of release conditions, these estimates are not based upon real locations. Success of a translocation program is dependent upon identifying available locations that approximate the conditions modeled in our improved habitat or predator-controlled release conditions. Should puaiohi be translocated, one of the higher elevation Hawaiian Islands, such as Maui or Hawaiʻi, will likely be considered (Hawaiʻi Forest Bird Conservation Forum, Sept. 24-25, 2015). Although agency consultation would utilize a structured decision framework to select an appropriate location, Maui seems the most likely candidate as its native thrush, the ʻāmaui (*Myadestes woahensis*) is extinct, while the congeneric ōmaʻo (*Myadestes obscurus*) is still extant in appropriate puaiohi habitat on the island of Hawaiʻi. A second caveat is that PVAs are often criticized for their dependence on the large amounts of quality data necessary to provide accurate output (Hamilton & Moller 1995; Taylor 1995; Groom & Pascual 1998; Ludwig 1999, Ellner et al. 2002). Although we have used the best available data to populate our models, this study faces the same limitations. However, the utility of PVA is less in the actual numbers it provides, but rather as a means of comparing options through considering relative extinction risks, either between subpopulations of a species or between alternative management actions (Lindenmayer & Possingham 1996, Brook et al. 2000, Morris & Doak 2002, Akçakaya & Sjögren-Gulve 2000).

Our results suggest that tradeoffs exist in establishing a second puaiohi population. If a harvesting approach is used to successfully establish a second population, it is likely to negatively impact the existing wild population. Alternatively, the re-establishment of a captive breeding program may offer a way to both preserve the wild population and allow for a sufficient supply of birds for supplementing a new population. Ultimately, however, the success of the reintroduction program is dependent upon ecosystem restoration, both in the source and translocation habitats. As novel, and perhaps more drastic, management techniques are considered, active management and restoration of puaiohi habitat must also continue to occur to preserve this rare species for future generations.

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Table 4.1. Vortex parameter inputs for the baseline puaiohi population model.

Parameter	Value
Species Description	
Inbreeding Depression	
Lethal Equivalent	6.29
% due to Recessive Lethals	50%
EV Concordance of Repro and Survival?	Yes
Reproductive System	
Reproductive System	monogamous, probably long term
Age of 1st Offspring Females	1
Age of 1st Offspring Males	1
Max Age of Repro	10
Max # Broods/Year	4
Max # Progeny/Brood	2
Sex Ratio at birth in % Males	1 to 1
Density Dependent Reproduction	yes
% Breeding at Low Density	100%
% Breeding at K	90%
Allee Parameter	0
Steepness Parameter	8
Reproductive Rates	
% Adult Females Breeding	Will be automatically calc'd from % Breedings, A, and B
EV (SD) in % Breeding	10
Distribution of Broods each Year	0--13.16%; 1--42.11%; 2--36.84%; 3--5.26%; 4--2.63%
# Offspring/Female/brood (exact distribution of brood size)	1--30.77%; 2--69.23%
Mortality Rates	
Mortality of Females as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.54
SD in Mort after Age 1	3

Mortality of Males as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.29
SD in Mort after Age 1	3
Mate Monopolization	
% Males in Breeding Pool	100%
Initial Population Size	
Stable Age Distribution?	Yes
Initial Population Size	500
Carrying Capacity	
K	1100
SD in K due to EV	10

Table 4.2. Suite of possible input parameters used in translocation regimes.

Source Population	Initial pop	No. supplement	Supplement interval	No. years supplement	Release conditions
Wild--declining baseline	10	5	q 1 yr	5	Stable mortality
Wild--stable baseline	20	10	q 2 yr	10	Predator removal
Captive-bred		20	q 5 yr		Improved habitat

Table 4.3. Tabulation of minimally and sustainably successful regimes for establishing a translocated population.

Output parameter	Number minimally successful	Number sustainably successful	Total successful
Growth rate (stochastic r)	80 (74.1%)	26 (24.1%)	106 (98.1%)
Probability of extinction	33 (30.6%)	17 (15.7%)	50 (42.3%)
Population size at 25 years	21 (19.4%)	11 (10.2%)	32 (29.6%)
Meets all three criteria	22 (20.4%)	10 (9.3%)	32 (29.6%)

Table 4.4. Optimally successful supplementation regimes for establishing a translocated population.

Initial pop	No. supplement	Supplement interval	No. years supplement	Release conditions	No. times supplement	Total no. supplement	Stoch r	SD (r)	PE	N at 25 years	SD (N at 25 years)
10	20	q2yr	10	HI	5	110	0.17	0.36	0	662	289
20	20	q1yr	10	HI	10	220	0.14	0.23	0	647	299
10	20	q1yr	10	HI	10	210	0.17	0.28	0	629	301
10	20	q2yr	10	PC	5	110	0.16	0.36	0	540	287
20	20	q1yr	10	PC	10	220	0.13	0.22	0	538	292
10	20	q1yr	10	PC	10	210	0.15	0.27	0	516	282
20	20	q1yr	5	HI	5	120	0.12	0.23	0.004	501	320
20	10	q1yr	10	HI	10	120	0.12	0.20	0.002	494	310
20	20	q2yr	10	HI	5	120	0.12	0.23	0.002	483	318
10	10	q1yr	10	HI	10	110	0.14	0.23	0.002	451	304

Table 4.5. Translocated population supplementation regime ANOVA results. Values below F-statistic are least square means ± SE. Different superscripts denote significant differences between groups based on Bonferroni post-hoc pairwise comparisons.

	Growth rate (stochastic r)	Probability of extinction	Population size
Initial pop	$F_{1,106} = 5.31$, $p = 0.023$	$F_{1,106} = 5.92$, $p = 0.017$	$F_{1,106} = 1.05$, $p = 0.308$
10	0.08 ± 0.01^{a}	0.13 ± 0.02^{a}	177.65 ± 20.76^{a}
20	0.06 ± 0.01^{b}	0.08 ± 0.02^{b}	207.71 ± 20.76^{a}
No. supplement	$F_{2,105} = 14.24$, $p < 0.001$	$F_{2,105} = 11.31$, $p < 0.001$	$F_{2,105} = 12.76$, $p < 0.001$
5	0.05 ± 0.01^{a}	0.17 ± 0.02^{a}	122.02 ± 23.02^{a}
10	0.07 ± 0.01^{a}	0.10 ± 0.02^{b}	173.04 ± 23.02^{a}
20	0.1 ± 0.01^{b}	0.04 ± 0.02^{b}	282.97 ± 23.02^{b}
Supplement interval	$F_{2,105} = 23.33$, $p < 0.001$	$F_{2,105} = 27.56$, $p < 0.001$	$F_{2,105} = 16.71$, $p < 0.001$
q 1 yr	0.10 ± 0.01^{a}	0.03 ± 0.02^{a}	278.41 ± 22.36^{a}
q 2 yr	0.08 ± 0.01^{b}	0.07 ± 0.02^{a}	203.11 ± 22.36^{a}
q 5 yr	0.04 ± 0.01^{c}	0.20 ± 0.02^{b}	96.52 ± 22.36^{b}
No. years supplement	$F_{1,106} = 8.59$, $p = 0.004$	$F_{1,106} = 12.52$, $p < 0.001$	$F_{1,106} = 6.67$, $p = 0.011$
5	0.06 ± 0.01^{a}	0.15 ± 0.02^{a}	155.73 ± 20.23^{a}
10	0.08 ± 0.01^{b}	0.07 ± 0.02^{b}	229.63 ± 20.23^{b}
No. times supplement	$F_{1,106} = 56.36$, $p < 0.001$	$F_{1,106} = 52.33$, $p < 0.001$	$F_{1,106} = 44.77$, $p < 0.001$
r^2	0.35	0.33	0.29
slope	0.01	-0.02	28.29

Total no. supplement	$F_{1,106} = 94.96$, $p < 0.001$	$F_{1,106} = 57.78$, $p < 0.001$	$F_{1,106} = 123.30$, $p < 0.001$
r^2	0.47	0.35	0.54
slope	0.0006	-0.002	2.35
Release conditions	$F_{2,105} = 24.31$, $p < 0.001$	$F_{2,105} = 7.41$, $p < 0.001$	$F_{2,105} = 25.61$, $p < 0.001$
Stable mortality	0.04 ± 0.01^{a}	0.16 ± 0.02^{a}	84.1 ± 21.05^{a}
Predator removal	0.08 ± 0.01^{b}	0.08 ± 0.02^{b}	196.97 ± 21.05^{b}
Improved habitat	0.10 ± 0.01^{c}	0.07 ± 0.02^{b}	296.97 ± 21.05^{c}

Table 4.6a. Equivalency tests for the original population under data-driven declining conditions.

Initial pop	No. suppl	Suppl. interval	No. years suppl	Growth rate (stoch r)	SD (r)	p-value	Mean TE	TE SD	p-value
Baseline				-0.267	0.179		16.7	3.5	
10	5	q1yr	10	-0.304	0.207	$p = 0.074$	13.2	3.7	$p = 0.999$
20	5	q1yr	10	-0.308	0.211	$p = 0.144$	13.2	3.5	$p = 0.999$
10	20	q1yr	5	-0.308	0.226	$p = 0.164$	14.4	3.9	$p < 0.001$
20	20	q1yr	5	-0.311	0.224	$p = 0.240$	14.2	3.8	$p = 0.001$
10	20	q2yr	10	-0.322	0.223	$p = 0.702$	13.2	3.5	$p = 0.999$
20	20	q2yr	10	-0.325	0.221	$p = 0.810$	13.2	3.3	$p = 0.999$
10	10	q1yr	10	-0.328	0.216	$p = 0.884$	11.9	3.2	$p = 1.000$
20	10	q1yr	10	-0.331	0.216	$p = 0.937$	11.8	3.0	$p = 1.000$
10	20	q1yr	10	-0.354	0.211	$p = 1.000$	10.6	2.6	$p = 1.000$
20	20	q1yr	10	-0.357	0.203	$p = 1.000$	10.1	2.3	$p = 1.000$

Table 4.6b. Equivalency tests for the original population under theoretical stable conditions.

Initial pop	No. suppl	Suppl. interval	No. years suppl	Population size at 25 years	SD (N at 25 years)	p-value
Baseline--stable				492.29	256.23	
20	10	q2yr	5	461.29	262.3	p = 0.051
10	10	q1yr	5	453.15	261.94	p = 0.173
20	20	q2yr	5	450.26	266.96	p = 0.247
20	10	q1yr	5	448.86	262.58	p = 0.285
20	5	q1yr	10	447.81	270.33	p = 0.320
10	20	q1yr	5	437.8	256.29	p = 0.653
20	20	q2yr	10	432.54	266.43	p = 0.799
10	20	q2yr	10	431.55	269.2	p = 0.819
20	20	q1yr	5	429.82	269.32	p = 0.856
10	10	q1yr	10	421.49	259.55	p = 0.964
20	10	q1yr	10	409.89	266.44	p = 0.997
10	20	q1yr	10	329.03	259.36	p = 1.000
20	20	q1yr	10	328.07	260.02	p = 1.000

Table 4.7. Total number of harvests attempted and failed per 1000 scenario iterations.

Initial pop	Number harvested	Harvest interval	No. years harvested	Total failed	Total attempted	% failed
20	20	q1yr	10	86237	200000	43.12%
10	20	q1yr	10	84094	200000	42.05%
20	20	q5yr	10	15832	40000	39.58%
10	20	q5yr	10	15363	40000	38.41%
20	20	q2yr	10	27977	100000	27.98%
10	20	q2yr	10	27458	100000	27.46%
20	10	q1yr	10	25942	100000	25.94%
10	10	q1yr	10	25115	100000	25.12%
10	10	q5yr	10	4959	20000	24.80%
20	10	q5yr	10	4788	20000	23.94%
10	5	q5yr	10	1634	10000	16.34%
20	5	q5yr	10	1625	10000	16.25%
20	5	q1yr	10	7422	50000	14.84%
20	10	q2yr	10	7397	50000	14.79%
10	5	q1yr	10	7388	50000	14.78%
10	10	q2yr	10	6673	50000	13.35%

Table 4.8. Declining source population harvest regime ANOVA results. Values below F-statistic are least square means ± SE. Different superscripts denote significant differences between groups based on Bonferroni post-hoc pairwise comparisons.

	Growth rate (stochastic r)	Probability of extinction	Population size	Time to extinction
Initial pop	$F_{1,34} = 0.01, p = 0.924$	$F_{1,34} = 0.11, p = 0.746$	$F_{1,34} = 0.02, p = 0.896$	$F_{1,34} = 0.01, p = 0.937$
10	-0.29 ± 0.01^{a}	0.98 ± 0.002^{a}	0.20 ± 0.02^{a}	14.82 ± 0.39^{a}
20	-0.29 ± 0.01^{a}	0.98 ± 0.002^{a}	0.19 ± 0.02^{a}	14.78 ± 0.39^{a}
No. harvest	$F_{2,33} = 4.88, p = 0.014$	$F_{2,33} = 2.16, p = 0.131$	$F_{2,33} = 3.39, p = 0.046$	$F_{2,33} = 2.39, p = 0.107$
5	-0.28 ± 0.01^{a}	0.98 ± 0.003^{a}	0.23 ± 0.03^{a}	15.44 ± 0.46^{a}
10	-0.29 ± 0.01^{ab}	0.98 ± 0.003^{a}	0.23 ± 0.03^{a}	14.92 ± 0.46^{a}
20	-0.31 ± 0.01^{b}	0.99 ± 0.003^{a}	0.14 ± 0.03^{b}	14.04 ± 0.46^{a}
Harvest interval	$F_{2,33} = 8.53, p = 0.001$	$F_{2,33} = 7.68, p = 0.002$	$F_{2,33} = 5.69, p = 0.007$	$F_{2,33} = 9.00, p = 0.001$
q 1 yr	-0.31 ± 0.01^{a}	0.99 ± 0.002^{a}	0.13 ± 0.03^{a}	13.51 ± 0.39^{a}
q 2 yr	-0.29 ± 0.01^{b}	0.98 ± 0.002^{ab}	0.21 ± 0.03^{ab}	15.07 ± 0.39^{b}
q 5 yr	-0.28 ± 0.01^{b}	0.98 ± 0.002^{b}	0.25 ± 0.03^{b}	15.83 ± 0.39^{b}
No. years harvest	$F_{1,34} = 8.59, p = 0.001$	$F_{1,34} = 22.00, p < 0.001$	$F_{1,34} = 30.59, p < 0.001$	$F_{1,34} = 18.69, p < 0.001$
5	-0.28 ± 0.004^{a}	0.98 ± 0.002^{a}	0.26 ± 0.02^{a}	15.77 ± 0.32^{a}
10	-0.31 ± 0.004^{b}	0.99 ± 0.002^{b}	0.13 ± 0.02^{b}	13.83 ± 0.32^{b}
No. times harvest	$F_{1,34} = 63.77, p < 0.001$	$F_{1,34} = 49.04, p < 0.001$	$F_{1,34} = 51.54, p < 0.001$	$F_{1,34} = 157.17, p < 0.001$
r^2	0.65	0.59	0.6	0.82
slope	-0.01	0.0001	-0.03	-0.03
Total no. harvest	$F_{1,34} = 323.30, p < 0.001$	$F_{1,34} = 54.08, p < 0.001$	$F_{1,34} = 57.70, p < 0.001$	$F_{1,34} = 101.92, p < 0.001$
r^2	0.9	0.61	0.63	0.75
slope	-0.0004	0.002	-0.002	-0.48

Table 4.9. Stable source population harvest regime ANOVA results. Values below F-statistic are least square means ± SE. Different superscripts denote significant differences between groups based on Bonferroni post-hoc pairwise comparisons.

		Growth rate (stochastic r)	Probability of extinction	Population size at 25 years
Initial pop		$F_{1,34} = 0.01$, $p = 0.906$	$F_{1,34} = 0.02$, $p = 0.877$	$F_{1,34} = 0.28$, $p = 0.602$
	10	-0.01 ± 0.001^{a}	0.002 ± 0.001^{a}	460.16 ± 9.07^{a}
	20	-0.01 ± 0.001^{a}	0.002 ± 0.001a	453.41 ± 9.07^{a}
No. harvest		$F_{2,33} = 5.36$, $p = 0.009$	$F_{2,33} = 2.22$, $p = 0.125$	$F_{2,33} = 5.59$, $p = 0.008$
	5	-0.003 ± 0.002^{a}	0.001 ± 0.001^{a}	476.08 ± 9.79^{a}
	10	-0.006 ± 0.002^{ab}	0.001 ± 0.001^{a}	463.15 ± 9.79^{ab}
	20	-0.011 ± 0.002^{b}	0.004 ± 0.001^{a}	431.13 ± 9.79^{b}
Harvest interval		$F_{2,33} = 8.17$, $p = 0.001$	$F_{2,33} = 2.57$, $p = 0.092$	$F_{2,33} = 9.54$, $p < 0.001$
	q 1 yr	-0.01 ± 0.002^{a}	0.004 ± 0.001^{a}	425.98 ± 9.02^{a}
	q 2 yr	-0.01 ± 0.002^{b}	0.001 ± 0.001^{a}	464.21 ± 9.02^{b}
	q 5 yr	-0.003 ± 0.002^{b}	0.0003 ± 0.001^{a}	480.17 ± 9.02^{b}
No. years harvest		$F_{1,34} = 3.97$, $p = 0.054$	$F_{1,34} = 3.76$, $p = 0.061$	$F_{1,34} = 3.88$, $p = 0.057$
	5	-0.005 ± 0.002^{a}	0.0002 ± 0.001^{a}	468.81 ± 8.63^{a}
	10	-0.01 ± 0.002^{a}	0.003 ± 0.001^{a}	444.77 ± 8.63^{a}
No. times harvest		$F_{1,34} = 34.49$, $p < 0.001$	$F_{1,34} = 13.72$, $p < 0.001$	$F_{1,34} = 38.70$, $p < 0.001$
	r^2	0.50	0.29	0.53
	slope	-0.002	0.001	-9.37
Total no. harvest		$F_{1,34} = 451.90$, $p < 0.001$	$F_{1,34} = 58.05$, $p < 0.001$	$F_{1,34} = 503.14$, $p < 0.001$
	r^2	0.93	0.63	0.94
	slope	-0.0001	0.0001	-0.77

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CHAPTER 5

IDENTIFYING COST-EFFICIENT MANAGEMENT OPTIONS FOR THE CRITICALLY ENDANGERED PUAIOHI

ABSTRACT—Conservation faces a consistent challenge of how best to protect, conserve, and manage an increasing number of species with limited budgets. This challenge necessitates the identification of cost-effective management strategies and approaches to explore potential management activities before committing significant funds and time. Based on currently planned or proposed interventions for the endangered Hawaiian endemic puaiohi, we constructed population viability analysis (PVA) models and estimated financial costs for proposed management activities. Specifically, we modeled ten scenarios (rat control at identified puaiohi nests; habitat-wide rat suppression; habitat-wide rat eradication; habitat restoration; supplemental feeding; provision of nest boxes; habitat restoration coupled with rat control, suppression, or eradication; and translocation of a second population to improved habitat), considered several different options for achieving the management objective, and calculated total and per capita costs of that option over a 25-year period. All ten models indicated substantial increases in growth rate, population size, time to extinction, and lower probabilities of extinction compared to the baseline model. Each option yielded markedly different per capita and total costs, with the least expensive being translocation from the wild population (total cost = \$409,568; per capita costs = \$974) and the most expensive being habitat restoration and rat eradication with bait stations (total cost of \$262,398,485 and supplemental feeding at a per capita cost of \$206,803). Notably even the supplemental feeding option was better than the per capita cost of the baseline model for current expenditures, which would cost $11,658,349/puaiohi extant after 25 years. We found no relationship between either total cost or per capita cost in relation to probability of extinction, growth rate, or population size after 25 years. Of the 25 cost comparisons, 17 would benefit more species than puaiohi, five would benefit only puaiohi, and three would primarily benefit puaiohi with some positive effects for other endemic species as well. We concluded that a suite of cost-effective management does exists that could bring the endangered puaiohi back from the threat of extinction.

KEYWORDS—economic analysis, Hawaiian forest birds, *Myadestes palmeri*, population viability analysis, small Kaua‘i thrush, Vortex

INTRODUCTION

Our planet is in the midst of an on-going and increasing extinction crisis. Every year, the list of endangered species grows (Rutledge et al. 2001; IUCN Red List, 2016). However, the budgets dedicated to conserving these species are not keeping pace with the increase in those that need intervention (Center for Biological Diversity 2015). As a result, conservation researchers and managers are charged with protecting and recovering an increasing number of species while per species budgets decrease. Identification of cost-effective management strategies must occur to explore potential management activities before committing significant resources and time.

One tool that conservation biologists can use to quantify the risk of extinction and to examine the relative benefits of alternative management actions is population viability analysis (PVA; Ellner and Fieberg 2003) which incorporates demographic and environmental variables to forecast population persistence and extinction risk. PVA can be used to rank management options amongst a suite of possible activities (e.g., Duca et al. 2009, Garcia-Ripolles and Lopez-Lopez 2011, Proctor et al. 2004). Its predictive power allows managers to explore possible outcomes for a suite of options and identify the potentially ineffectual ones. The use of PVAs, which are integrated with decision support tools will assist conservation biologists that face limited resources. Integrating these two approaches facilitates the evaluation and comparison of various conservation strategies (Clark et al. 1991, Drechsler and Burgman, 2004) before investing in implementing them. For instance, incorporating realistic economic costs can aid in determining how the conservation benefit of different conservation actions or management options for a given financial expenditure (Noon and McKelvey 1996, Possingham et al. 2001, Yokomizo et al. 2003, Haight et al. 2004, Yokomizo et al. 2004, 2007).

While valuable, the integration of PVAs and economic assessments has been quite limited (e.g., Larson et al. 2003, Tisdell et al. 2005). Such rarity is particularly disconcerting since funding available for conserving many threatened and endangered species is very limited. By failing to integrate economic considerations into PVA modeling efforts may result in decisions to implement management plans, which divert resources away from more cost-efficient conservation actions (Baxter et al. 2006). Given the large numbers of threatened and endangered species in places like Hawai‘i, this inefficient use of resources is particularly problematic (Baillie et al. 2004), as optimizing conservation spending requires tightly focused research agendas having benefits or results clearly linked to costs (Duffy and Kraus 2008).

Nowhere is the need for cost-effective management more urgent than in the Hawaiian Islands. An island archipelago in which the taxa evolved in relative isolation, its species have been devastated by the arrival of humans (Pratt 2009, Banko and Banko 2009). The rats, pigs, goats, cats, mosquitos and hosts of plants and insects introduced to Hawai‘i have indelibly altered its unique ecosystems. Once home to 152 land bird species, 110 of these have gone extinct since human arrival (Walther 2016). Thirty-three of its remaining 42 endemic birds are listed as endangered or threatened, making Hawaiʻi home to one of the most endangered avifaunas in the world (American Bird Conservancy 2016, Walther 2016). Though 1/3 of the United States' endangered species live in Hawaiʻi, as of 2004 the state's entire annual budget for managing endangered species was only $30,592,692, or 4.1% of total expenditures on nationally listed birds (Leonard 2008). Little has been done to change this situation in the intervening 12 years. For instance, the most recent budget (2009) dedicated primarily to management and research on the puaiohi (*Myadestes palmeri*), a critically endangered forest bird endemic to the island of Kauaʻi, was about $225,069 (adjusted to 2016 dollars). Since then, two additional species which share its habitat, the ʻakikiki (Kauaʻi creeper; *Oreomystis bairdi*) and ʻakekeʻe (Kauaʻi ʻākepa; *Loxops caeruleirostris*), have seen precipitous declines (Paxton et al. 2016), and management funds for the puaiohi have become convoluted with those needed by these and other species.

Endemic to Kauaʻi, the puaiohi is the only remaining avian native frugivore on the island, thus it may play a critical role in the persistence of native plant species and their associated invertebrates (Liba Pejchar, pers comm). The puaiohi has experienced range contraction since the 1960s (Scott et al 1986, U.S Fish and Wildlife Service, 2006), is no longer found at lower elevations (1,000-1,050 meters), and is currently restricted to a remnant of the Alakaʻi Wilderness Preserve at 1,050 to 1,300 meters. Recent surveys suggest the population is around 500 birds and appears to have remained relatively stable since 1973 (Crampton et al., in review). A number of factors are thought to affect population vulnerability, including: drought; hurricanes; mammalian (rat [*Rattus* spp.] and cats [*Felis catus*]) predation at all life stages;

disease (e.g., avian malaria (*Plasmodium relictum*) and potentially avian pox (*Avipoxvirus* spp.); habitat degradation due to feral pigs and goats and invasive plants; and limited availability of suitable nest sites, particularly because invasive plants often cover cliff faces (Kepler and Kepler 1983, Herrmann and Snetsinger 1997, Snetsinger et al. 2005, U.S. Fish & Wildlife Service 2006, Woodworth & Pratt 2009).

The puaiohi was added to the United States Federal Endangered Species List on March 11, 1967 (U.S. Fish & Wildlife Service 2006), and included in the Kaua‘i Forest Bird Recovery Plan (US Fish & Wildlife Service 1983). Since 1995, research on determining puaiohi population size and status and assessing the influence of food availability, habitat structure and composition, predation, and introduced disease on survival and reproductive success (and ultimately abundance) have been carried out by the United States Geological Society (1995-2000) and the Kaua‘i Forest Birds Recovery project (2001-present; Kaua‘i Forest Bird Recovery Project, 2016). Concurrently, the puaiohi has been actively managed in hopes of increasing the population to sustainable levels. Early studies showed that placing poison bait stations around active puaiohi nests reduced rat predation on nests and increased nest success (Snetsinger et al. 2005). Mangers have recently begun controlling rats via 100 Goodnature A24 self-resetting rat traps distributed across 50 ha of remote forest. In addition, several types of nest boxes have been installed in puaiohi nesting habitat to increase nest site availability, decrease nest predation, and expand puaiohi range (VanderWerf 2013). However, thus far only a few pairs have successfully used them, and a preferred rat-resistant design has not yet been identified. KFBRP continues to investigate the feasibility of using artificial nest boxes. Several NGOs control invasive alien plants in the Alaka‘i Wilderness Preserve, and in 2010 a 810 ha unit was fenced with ungulate proof fencing and ungulates are being eradicated, with plans to fence three more adjacent units and protect an additional 1,215 ha in core puaiohi area (VanderWerf 2013).

Concerns about puaiohi's limited range and small population led to the establishment of a captive-bred population in 1996. From 1999 to 2012, 222 birds were released into the Alakaʻi (Switzer et al. 2013). However, due to the relatively low recruitment and survival of released birds and signs of congenital abnormalities in captive bred chicks, the program was discontinued and the last of the captive flock was released in 2016 (Department of Land and Natural Resources 2016, VanderWerf et al. 2014, Switzer et al. 2013).

The goal of this research is to compare the cost-effectiveness of potential management options to identify the management practices which offer the greatest likelihood of maintaining the species. To address this goal, we modeled puaiohi populations under current and potential future management scenarios to determine their potential efficacy in aiding in the recovery of this species, and developed budget estimates for each proposed management activity. We assumed that the best conservation strategy maximized population persistence and final population size while minimizing financial costs. Because many of the issues facing puaiohi are the same as those faced by the other Hawaiian forest birds, this research can provide a template for similar approaches for other forest birds of Hawaiʻi.

METHODS

Species data used in this study were collected from 2005-2011 at four sites (Kawaikōī, Koaie, Mohihi, and Halepaʻakai) in the Alakaʻi Wilderness Preserve on the island of Kauaʻi, Hawaiʻi. These sites ranged in elevation from 1,123 to 1,303 m above sea level in native wet and mesic forests dominated by ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa*), ōlapa

(*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ‘ōhi‘a ha (*Syzygium sandwicensis*), kāwa‘u (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), with a diverse understory of native plants including ‘ōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) (U.S. Fish & Wildlife Service 2006).

Based on currently planned or proposed puaiohi interventions, we constructed population viability analysis (PVA) models in Vortex 10 (Lacy and Pollack 2014), software which simulates stochastic demographic and environmental processes. We also estimated financial costs for each scenario based on published information and communication with experts in the field. In addition to the baseline, we modeled ten scenarios: rat control at identified puaiohi nests; habitat-wide rat suppression; habitat-wide rat eradication; habitat restoration; supplemental feeding; provision of nest boxes; habitat restoration coupled with rat control, suppression, or eradication; and translocation of a second population to improved habitat. For each management scenario, we considered several different options for achieving the management objective.

Within Vortex, we built upon a previously developed baseline model (Fantle-Lepczyk et al., in review) using all available information on puaiohi (Table 5.1). For all models, we assumed the area being managed covers most of the puaiohi range, and we used an initial population of 500 individuals (Crampton et al., in review). Each model was simulated 1,000 times over a relatively short time frame of 25 years (Fantle-Lepczyk et al., in review). We defined extinction as occurring when only one sex remained. Vortex’s standard output provided us with stochastic r, probability of extinction within 25 years, average population size at 25 years, and mean time to extinction.

Management Scenarios and Costs

While the ten management scenarios varied in many attributes, several commonalities existed across them in terms of estimating costs. Specifically, we used a pay rate of $17.50/hr/person ($14.00 pay rate plus 25% benefits), based on the current base pay rate for Kauaʻi Forest Bird Recovery Project (KFPRP) field personnel. Each helicopter flight costs $600 and can hold about 272 kg. All financial costs are estimated in 2016 USD dollars.

We developed a hypothetical predator-proof fenced area for all habitat-wide rat removal scenarios (Fig. 5.1). Currently, predator-proof fencing in the Alakaʻi is beyond the reach of technology as fencing in wet areas with drainages is not yet reliable. Inclusion of culverts over drainages holds promise, and fencing the Alakaʻi could eventually be a possibility. Inclusion of this option here assumes that technology will soon improve sufficiently so that fencing puaiohi habitat will be possible, and will not be significantly more expensive that the current design. As the culverts are not particularly expensive, this seems a reasonable assumption.

To estimate fencing costs, we used ArcGIS to designate a core area of puaiohi habitat which contained most medium to high density occupied streams within the altitudinal zone of >1,050 m (Crampton et al., in review). This 30,324 m long fence encloses about 3898 ha and has about 114 km of streams. All scenarios including ungulate fencing are based on a configuration of already built or planned fence sections, along with future additional units to approximate the same core puaiohi habitat area used in trapping and baiting scenarios. At present, The Nature Conservancy (TNC) has already fenced a 539 ha (10,970 m perimeter length) unit at Halehāhā and has already planned but not implemented units at Drinking Glass, Koaie, and Mohihi (Fig. 5.1). In addition to this, we have estimated additional units at Kawaikōī and in the Southwest, which all together comprise a multi-celled 4,032 ha area enclosed by 44,522 m of fence.

Rat management

We modeled rat management at three different scales: local control at nests; habitat-wide ongoing suppression, and permanent eradication, investigating each using three to four different options for achieving each objective (Table 5.2). Controlling rats at nests would entail the identification of most puaiohi nests in core puaiohi territory. Once found, managers would put four traps at each nest (Snetsinger et al. 2009). Traps would be set one month before first breeding until after last known breeding (VanderWerf et al. 2011). From 2007-2009, the earliest puaiohi nest found by KFBRP was March 20, and the last estimated fledge date was August 10. Since newly fledged young might be on the ground for a week or so more after fledging (Snetsinger 1999), trapping would occur from mid-February to mid-August. Based on stable age distribution from Vortex PVA, in a population of 500, the average number of females in the breeding population over the course of the 25 years modeled would be 267, which means that we would need to protect 267 nests per year, on average.

In previous attempts to identify puaiohi territories, 6 km of stream were surveyed ~2.5 times over a ten-day period, and we assumed finding nests would take about a similar amount of time. Thus, ~1.5 km of stream can be surveyed for nests/person/day. Our designated core puaiohi habitat area contains about 114 km of streams, which would take 76 person-days/nest search. We assumed all streams would be surveyed three times to find all/most nests, resulting in 226 total person-days to find nests annually.

We considered two options for rat control, Goodnature self-resetting A24 rat and stoat traps vs. bait stations stocked with diphacinone poison baits (Table 5.2). A24 traps are self-resetting kill traps that require a monthly lure check and semiannual lure and gas cartridge replacement. The A24 traps are currently being used with puaiohi on a smaller scale by the KFBRP, and many other conservation agencies throughout the world. Each trap costs $157.97 with strike counter (digital strike counters record kill tally), plus $27.59 per year for gas cartridge and lure supplies. We assumed that each trap would need to be replaced every 10 years.

Our second option for rat control at nests would consist of Protecta Heavy Duty Rat Bait Stations (Bell Labs; VanderWerf et al. 2011; $21.84/station), baited with Ramik Block Rodenticide (0.005% diphacinone; VanderWerf et al. 2011 and Snetsinger et al. 2009; $28.27/64 baits on Amazon), the only bait currently approved for use in Hawaiʻi (Table 5.2). Stations would initially need 0.45 kg of bait, then checked and re-baited weekly with up to 0.45 kg additional (VanderWerf et al. 2011, Young et al. 2013). Average bait replacement at Kaʻena Point in drier habitat on Oahu was 3.69 g/day/station (Young et al. 2013), so we estimated each station would use about 1.28 kg, at $15.52/kg, over the six months of baiting. Traps last at least 10 years on Oʻahu (Tyler Bogardus, pers comm), so we assumed they would be replaced every 10 years.

To set out traps and bait stations, we assumed effort would be similar to KFBRP's previous experiences putting up nest boxes, with six people put up about 30 nest boxes in two days (i.e., 2.5 boxes/person/day). Thus, at 267 territories it would require 106.8 person-days to deploy all traps initially. We assumed traps and bait stations would stay out between seasons, so we would only need to do this at project onset and when traps/stations are replaced every 10 years.

To maintain traps and bait stations, we assumed time invested would be similar to that KFBRP has previously invested in nest monitoring, in which a crew of two people monitored ~8 active nests/day. Thus, it would take a crew of two people 66.75 person-days, to maintain 287 traps or stations. However, A24 traps and bait stations require different recheck intervals, with A24 traps maintained monthly and bait stations maintained weekly.

Given the remote location of puaiohi habitat and the need to helicopter in supplies to the high elevation habitat, we also considered these costs. Since each A24 trap weights 0.395 kg, each lure 0.07 kg and each gas cartridge 0.065 kg, the total freight weight in trap replacement years would be 710.22 kg for 287 traps, and would require three helicopter trips/year. When only lure and gas cartridges are replaced, the total weight would be 288.36 kg, resulting in two trips. Bait stations weigh 0.73 kg each with bait sold by the ounce. Each station uses 1.28 kg in a six-month season, so the total weight for 287 stations in station replacement years is 2146.96 kg, resulting in eight helicopter trips. When only bait is replaced, total weight is 3024.44 lbs, which would require six helicopter loads.

We also explored wide-scale rat suppression over the core puaiohi habitat, using four options: Goodnature traps in a grid, Goodnature traps as a “fence” around streams, bait stations, and aerial broadcast of rodenticide (Table 5.2). With no barriers to rat reintroduction, we assumed that suppression efforts would be necessary at a static rate of effort throughout the entire 25 years of study. For the Goodnature A24 traps in a grid formation scenario, we followed the manufacturer recommended trap density of every 50 m on trap lines set 100 m apart. Overlaying this grid on our mapped core puaiohi habitat results in 7,795 traps necessary to fill the 38.98 km^2. Based on previous experience, we estimated that one person can set out 20 A24s in one day or check 25 A24s on a standard grid in a day. Thus, it would take 389.75 person-days to set out all the traps, and 311.8 person-days to check all traps. Traps would need to be checked and maintained monthly, and replaced every 10 years. Total weight in trap replacement years would be 5183.67 kg, requiring 19 helicopter trips and 2104.65 kg in the intervening years, requiring eight trips.

An alternative for running A24 traps in a grid would be to set them in lines along streams in core puaiohi habitat (Table 5.2). Traps would be placed every 50 m along each side of the 114 km of streams within the core puaiohi habitat area. At a rate of 40 traps/km of stream, this would result in 4,560 traps needed to cover the area. Given the closer density of trap lines, we assumed a worker could set out about 28 traps/day and check about 40 traps/day. Thus, we would need 161.47 person-days to set out all traps and 114 person-days to check them. As before, traps would need to be maintained monthly and replaced every ten years. Total weight in trap replacement years is 3032.40 kg, which would require 12 helicopter trips in replacement years, and in non-replacement years, the 1231.20 kg freight weight would require five helicopter trips/year.

Another option we considered for core habitat-wide rat suppression was a grid of bait stations with rodenticide (Table 5.2). In previous studies, bait stations were laid every 25 m (Young et al. 2013), which, when overlaid on our core puaiohi habitat area, would result in the need for 62,350 bait stations. At this station density, we assumed one person could set out about 31 bait stations/day and check about 45 bait stations/day. Thus, 2,034.92 person-days would be required to set them out and 1,385.56 person-days to maintain them. Stations need to be checked and maintained weekly and replaced every 10 years. Assuming that each station would use 2.06 kg of bait in a year, total weight in station replacement years would be 173970.11 kg, requiring

640 helicopter trips/year. Total weight when only bait is replaced is 128716.11 kg, which would necessitate 473 helicopter trips/year.

The final core-wide rat suppression option we considered was aerial broadcast of rodenticide (Table 5.2). If aerial broadcast is approved in the future, it may only be within ungulate fenced areas to prevent rodenticide uptake by feral pigs, goats, and deer that will later be consumed by humans. Current contracted costs for the State's Halehāhā ungulate fence project (and estimated for the Drinking Glass and Koaiʻe units) is ~$164/meter (Lucas Behnke, pers comm), and current budgets allow about ~$2.25/m for maintenance of existing and under-construction fences (Lucas Behnke, pers comm). Since the Halehāhā unit is already built, we have not included its costs in the 33,552 m of fencing additionally needed to cover our area, but we have considered it in the 44,522 m of fence to be maintained. The result is a cost of $5,502,528 to complete the fencing and $100,174.50 annually for maintenance.

The mean all-inclusive price for implementation of aerial broadcast for projects >500 ha was $412.17/ha (Holmes et al. 2015). We only used projects of >500 ha in our estimate because economies of scale appear to exist, with smaller projects being much more variable in price/ha. Aerial application of rodenticide to the 4,032 ha in our designated core puaiohi habitat would cost $ $1,661,869.44. We assumed that it would be necessary to drop rodenticide every year due to rebound and lack of a barrier to recursion.

We also considered the scenario of rat eradication over our designated core puaiohi range. The key difference between the two scenarios is that for eradication, while all control efforts would be the same in scale, we included the costs of a predator-proof fence. Another predator-proof fencing project on Kauaʻi, the Upper Limahuli/Manoa fence project is about 5,600 m of fence, with an estimated mid-range cost of $3,060,711 (Lindsay Young, pers comm), which equates to \$546.56/m for materials and labor. The perimeter of our mapped fence would be 30,324 m long, resulting in a cost of \$16,573,885.44. Maintenance for the Limahuli fence will be at least \$14,000/year or about \$2.50/m. Extrapolating this out to our fence results in a cost of \$75,810/year for upkeep. The main advantage of a predator-proof fence would be that rats would eventually be removed from within the fence, and rat management would not be necessary in perpetuity, as would be the case with suppression. According to the Database of Island Invasive Species Eradications (2016), the average length of rat eradications on all islands >1 km^2 with start and end dates available was 1.47 years. Since all project lengths were in whole year increments, and we wanted to err on the side of caution because complete eradication is essential, we assumed eradication efforts would take two years. We considered Goodnature A24 traps, bait stations, and aerial broadcast as modeled for suppression as sufficient means to eradicate rats in our core puaiohi area. However, we did not include the Goodnature A24 traps along streams as an option in this case, as we deemed it a less than efficient way to permanently remove rats from the area.

We assumed that rat eradication would have the most positive affect on puaiohi populations, followed by rat suppression, with local rat management having the least positive effects (Table 5.3). For habitat-wide rat eradication we modified our population model by decreasing female mortality to that of males, as recent work (VanderWerf et al. 2014) suggests mortality due to nest predation by rats is the leading driver behind the higher mortality rates in female. We surmised that in a best-case scenario, removal of rats would produce female mortality rates akin to those of males. We increased the number of successful attempts/year by 50%, as Snetsinger et al. (2005) found 50% more nests fledged young with rat control.

No experimental data exist to quantify rat predation effect on juvenile mortality. However, we surmised that rat eradication would have less impact on juvenile mortality than on adult female mortality, as juveniles are probably subject to a greater range of mortality effects, and are likely mostly vulnerable to rat predation just in the first days after fledging. Thus, we decreased juvenile mortality by 25%. We presumed rat eradication would have little effect on male mortality since males do not incubate eggs on the nest (when females are presumably most vulnerable to rat predation) nor would it affect the number of young fledged/attempt since if a rat found a nest, it would likely kill both chicks, resulting in a failed attempt. Since rats are known to consume a variety of native fruits (Banko and Banko 2009, Shiels and Drake 2011, Shiels et al. 2013), we assumed they may have some effect on carrying capacity (K) of puaiohi as competitors for preferred food sources. Thus, we increased K by 25%.

While habitat-wide suppression of rats should affect puaiohi population in a manner similar to eradication, we assumed it would be slightly less effective due to incomplete and impermanent removal of rats. To reflect this, we decreased female puaiohi mortality by only 40%. We lowered the increase in number of successful attempts per year to 40% more than baseline to allow for any overestimates in Snetsinger et al.'s (2005) experiment, and for other causes of nest failure. Finally, in the absence of data, we lowered juvenile mortality by 20% and increased K by 20%. For local-scale rat control at nests, we assumed that incomplete rat control due to further decreased removal pressure and missed nests would occur. In the O'ahu 'elepaio, rat control has been shown to increase female survival by 10%-27% (VanderWerf 2009, VanderWerf et al. 2011). Thus, we decreased female puaiohi mortality by only 20%, roughly the midpoint of the 'elepaio's numbers, and lowered the increase in number of successful attempts per year to 20% more than baseline. Finally, we lowered juvenile mortality by 10% and increased K by 10%. For all rat management scenarios, we assumed rat removal would not affect male mortality, or the number fledged per attempt.

Restoration of existing habitat

Our habitat restoration models estimated potential impacts of habitat improvements on puaiohi by controlling invasive plant species that outcompete native food sources, potentially decreasing food availability, particularly during the breeding season (Table 5.2). In the Alakaʻi, common invasive plant species include kāhili ginger (*Hedychium gardnerianum*), daisy fleabane (*Erigeron annuus*), blackberry (*Rubus argutus*), Australian tree fern (*Cyathea cooperi*), and strawberry guava (*Psidium cattleianum*). While some of these species, such as ginger, blackberry and strawberry guava are fruiting plants, little is known about their utility as puaiohi food sources. Strawberry guava fruits are likely too big to be consumed by the birds, and, unlike the native fruits puaiohi have historically depended on, ginger's October-December fruiting period is not contemporaneous with the species' nesting period (Medeiros 2004), and puaiohi do not appear to eat it (Pejchar, unpubl data).

Ginger, fleabane, *Rubus* and other herbaceous invasives are generally controlled by ground treatment, which can vary dramatically across the Alakaʻi (Katie Cassel, pers comm). Australian tree fern is often controlled via aerial treatment, and at high densities, strawberry guava can be controlled via biocontrol. However, in the Alakaʻi , guava densities are likely too low to make this efficacious. Removal of pigs can also diminish spread of guava.

In areas of low weed density (i.e. the deep Alakaʻi, such as at Drinking Glass, Halepaʻakai, Halehāhā, and Koaie; Fig. 5.1), ground treatment costs about $159.37/ha (Katie Cassel, pers comm). With 2,618 ha of low density weeds, weeding costs $417,230.66/treatment and would need to be occur again in two years, and then at five year intervals thereafter. In areas of medium weed density (Mohihi), weeding costs average $656.61/ha. At 640 ha of medium density weeds, this costs $420,230.40/treatment. In areas of high weed density (Kawaikōī) costs average $1483.31/ha. At 1,304 ha of high density weeds, this costs $1,934,236.24/treatment. In areas of both medium and high density weeds, treatment should occur again a year, then after three years, and after this at five year intervals. The ideal scenario for aerial control of ATF would include remote sensing surveys initially and then every three years, at $2.02/ha, followed by an initial, single year treatment effort of $100,000 and on-going treatment of $30,000/year across the entire range (Lucas Behnke, TNC, pers comm). We have not accounted for the need to outplant or reseed, as generally the wet forests in the Alakaʻi still have sufficient canopy to reseed native plants, especially in the areas of lower weed density, and where follow-up is done to prevent weeds from reinvading (Katie Cassel, pers comm).

We evaluated the restoration action with and without the use of an ungulate fence. In principle, fencing an area and removing ungulates may decrease the required number of weed treatments or increase time between treatments, as pigs spread strawberry guava along trails, and sun-loving weeds such as blackberry and non-native grasses tend to fill in areas that pigs have disturbed. However, within puaiohi habitat, ungulate fencing likely keeps out none of the target invasive plants as they are all spread primarily by birds or wind. Thus, in-fencing probably does not decrease time or money invested in weeding, particularly if moderate amounts of ginger, guava, and ATF within several km outside the fence exists (Katie Cassel, KRCP, pers comm). However, it may still be beneficial to fence areas, even in instances without aerial broadcast, as removal of feral ungulates could still limit disease spread (i.e. feral pig wallows may create habitat for malaria-carrying mosquitos) and prevent habitat destruction (Cabin et al. 2000, Atkinson and LaPointe 2009, Pratt and Jacobi 2009). Therefore, we have included ungulate fencing as an option for habitat restoration.

We used the same estimates for fence construction and upkeep as used in the aerial broadcast rat suppression scenario, and included the costs of removing invasive ungulates from within the fenced area (Table 5.2). We based these calculations on the approximate current cost for removing ungulates within the Halehāhā unit of $520/ha (spread over the course of 4 years; Lucas Behnke, TNC, pers comm). This $520/ha estimate is close to costs on Sarigan in the Commonwealth of the Northern Mariana Islands ($524/ha; Holmes et al 2013), suggesting this is a reasonable estimate. Thus, ungulate removal would cost $1,816,360 for the additional 3,493 ha enclosed. Maintenance/monitoring costs are a significant reduction from the original cost, at ~10% in subsequent years (Lucas Behnke, TNC, pers comm), resulting in upkeep starting at year 5 being $52/ha, or $209,664/year for the entire 4,032 ha.

To estimate the effects of our management scenario, we assumed that the modeled habitat restoration would affect both the number of successful breeding attempts/year and the number fledged/attempt, as well as overall mortality and K (Table 5.3). Snetsinger et al. (2005) saw a 37.5% increase in nest attempts/year in wet years over drier years, presumably due at least in part to increased food supply following higher rainfall. Furthermore, Snetsinger et al. noted a 54.5% increase in the number fledged/attempt in wet years over the mean number fledged over three years of study. However, one very dry year decreases the mean and likely over estimates this impact. Considering these findings, we increased the number of successful nesting attempts/year by 37.5% and number of young fledged/attempt by 25% (lower than Snetsinger et al.'s finding due to our concern of overestimation) to reflect the greater food supply by supplementation. We also assumed that increased food supply could slightly increase K and slightly decrease juvenile, male, and female mortality, so those parameters were each adjusted by 10%.

Restoration and rat control

Because conservation and management efforts are often done in tandem using several approaches, we also modeled the effects of combining habitat restoration and each of our rat management levels and options. We assumed that the combined restoration and rat control efforts would not include ungulate fencing, except where required for aerial broadcast of herbicide. We assumed that costs associated with combing habitat restoration with rat management options would be strictly additive, thus we added our estimated costs of restoring puaiohi habitat to the rat management options at the local scale as well as habitat-wide suppression and eradication (Table 5.2).

We assumed that by combining management techniques the most beneficial parameter value of the two scenarios would be realized, but did not consider any additive benefits (Table 5.3). Thus, when rats are controlled at the local scale and habitat is restored, we assumed that we would see the estimated results of local rat control on female mortality, while number of successful nest attempts/year, number of attempts/year, and K would be that of habitat restoration. Juvenile mortality was the same for both scenarios, so we kept it as such. We reduced female mortality 20%, juvenile mortality by 10%, male mortality by 10%, and increased successful attempts/year by 37.5%, young fledged/attempt by 25%, and K by 10% from baseline. For the combined effect of rat suppression and habitat restoration, we assumed that we would see the predicted results of rat suppression on female mortality, juvenile mortality, successful nest attempts/year, and K. We reduced female mortality by 50%, decreased juvenile mortality by

20%, increased the successful attempts/year by 40%, and increased K by 20%. However, we also predicted that habitat restoration would additionally contribute to the population by increasing young fledged/attempt by 25% and decreasing male mortality by 10%. We predicted the same pattern for combined rat eradication and habitat restoration, with slightly larger values contributed by the rat eradication. We reduced female mortality rates to that of males, decreased juvenile mortality by 25%, increased successful attempts/year by 50%, increased K by 25%, and used the habitat restoration values of +25% young fledged/attempt and -10% male mortality.

Supplemental feeding

The third puaiohi management option we modeled was supplemental feeding of the population, to increase food availability and, thereby increase reproductive output (Table 5.2). We modeled the effects of supplemental feeding for the entire puaiohi population via papaya and scrambled eggs at feeding stations as previously provided to released, captive bred puaihoi. To institute a program of supplemental feeding, we proposed placing a feeding station in each identified puaiohi breeding territory and providing food via the station consisting of a platform feeder mounted on ground pole with a predator baffle resulting in a total cost/station of $114.67. We assumed feeders would need to be replaced every 10 years. Based on the Vortex PVA stable age distribution for supplemental feeding, the average number of females in the breeding population over the course of the 25 years modeled would be 119, so on average we would have about 119 nests to protect annually. Costs of finding territories would be the same as for previous nest-based scenarios, with 226 person-days/nests/year. Placing feeders would be similar to placing traps at nests, with 2.5 feeding stations/person/day, which would result in 47.6 person-days needed to deploy all stations in the first year. Given the perishable nature of the food, we would maintain feeders daily (Bryce Masuda, pers comm). Based on previous management experience a crew of two technicians can monitor about eight active territories in a day (Cali Crampton, pers comm), requiring 29.75 person-days to maintain all stations. We assumed birds would be fed year-round since previous wet season food availability may play a part in subsequent reproductive output (Fantle-Lepczyk et al. 2016).

In captivity, each puaiohi would receive a ring of papaya (0.635 cm thick)/day and 5-10 ml/eggs/day. Papayas are about 17.78 cm long, so each papaya feeds about 28 birds or 14 pairs (feeders), resulting in use of ~8.5 papaya/day at $2.00/papaya. One egg contains about 45 ml and feeds about six birds or three pairs (feeders), resulting in the use of ~39.67 eggs/day at $0.25/egg. We assumed preparation time was one hour/day (0.125 person-days/day). Each feeder weighs 5.56 kg, resulting in 661.22 kg for 119 feeders. Thus, in years when feeders need to be placed or replaced, three helicopter trips would be required to transport materials and supplies. We assumed that food would be carried in small, daily increments due to its perishability.

We assumed that the effects of supplemental feeding would be akin to those found with habitat restoration, though artificially supplementing food would be less beneficial than restoring native habitat (Table 5.3). To reflect this, we increased number of attempts/year, young fledged/attempt, and K by 10%, and decreased juvenile, male, and female mortality by 10%.

Nest box provision

In our nest box model scenarios, we assumed that a rat-proof nest box design will be developed that will be readily used by puaiohi (Table 5.2). Puaiohi have a strong preference for cavity nests, and these nest sites may be a limiting factor, particularly as invasive daisy fleabane covers cliff faces and renders these nest sites less available. Managers have been investigating designs to attract puaiohi, and while use of nest boxes is not yet widespread, it has potential. Currently, the most promising nest box design uses a double walled flower pot construction with insulation between layers, a predator baffle below and a predator shield above, at a cost of $71.75/box. We assumed that each box would be equipped with a sensor, data logger, and trail camera to monitor use at a cost of $209.35/box. We further anticipated that the lifespan of nest boxes is about 10 years and monitoring equipment about 5 years.

Based on the Vortex PVA stable age distribution for nest boxes, the average number of females would be 119 in the breeding population over the course of the 25 years modeled, so we assumed we would provide 119 nest box and monitoring set ups each year. Finding territories each year would be the same as previous territory-based scenarios, with 226 person-days needed to find territories along the 114 km of streams within the puaiohi core habitat area. We based estimates for the cost of nest boxes and monitoring equipment on previous attempts to supply nest boxes to puaiohi. In the past, eight people took one day to build 30 nest boxes (Cali Crampton, pers comm), meaning one person can assemble 3.75 boxes/day. Thus, 31.73 person-days are required to assemble 119 nest boxes. For monitoring equipment, it took ~$2,500 (17.86 person-days) in labor to assemble 45 sensor/camera units (Cali Crampton, pers comm), or about 0.40 person-days/monitoring unit. Thus, it would take about 47.6 person-days to assemble 119 nest boxes. Furthermore, previous experience has shown that six people can put up about 30 nest boxes in two days, so about 2.5 boxes/person/day, resulting in 47.6 person-days to put out 119 nest boxes (Cali Crampton, pers comm).

We assumed deploying camera monitoring equipment would take a similar amount of time and that maintaining nest boxes would take about as long as it does to put them out. Thus, it would take 47.6 person-days to put out 119 nest boxes. Nest boxes would need to be monitored/maintained monthly to replace batteries and/or memory cards on the monitoring equipment. Total cargo weight in years when both cameras and boxes are replaced is 578.50 kg, requiring three helicopter trips, while total weight in years when monitoring equipment is replaced is 117.00 kg, requiring one helicopter trip in those years. No helicopter trips are needed in other years.

If a successful nest box design is found, females and nests would be protected from rat predation with no effect on juvenile survival as they would have no added protection once they left the nest (Table 5.3). Furthermore, assuming nest sites are a limiting factor, providing more nest sites would increase K. Thus, we decreased female mortality by 25%, increased the number of successful attempts/year by 25%, and increased K by 10%. We assumed no effect on male mortality, the number of young fledged/attempt, or juvenile mortality.

Translocation to improved habitat on a higher island

In our final management scenario, we considered the outcomes of translocating puaiohi, both from the wild population and a captive-reared source with little to no impact on the wild population (Table 5.2). Previous modeling attempts have identified optimal translocation regimes to maximize the probability of success in establishing a new population (Fantle-Lepczyk et al. in review). We assumed translocation would be to one of the higher elevation Hawaiian Islands, such as Maui or Hawaiʻi (Hawaiʻi Forest Bird Conservation Forum, Sept. 24-25, 2015). Maui is the most likely candidate as its native thrush, the ʻāmaui (*Myadestes woahensis*) is extinct, while the congeneric ōmaʻo (*Myadestes obscurus*) is still extant in apparently appropriate puaiohi habitat on the island of Hawaiʻi.

We based our translocation model on the optimal regime identified by previous research (Fantle-Lepczyk et al., in prep). This regime consisted of an initial translocation of ten birds, followed by supplementation of 20 birds every other year for 10 years (Table 5.3). We modeled this both by harvesting translocated birds directly from the existing population or by collecting eggs and hatching and rearing the resulting nestlings until releasable. Presumably, given the high re-nesting rate of puaiohi, the removal of eggs early in incubation would have little impact on the population overall (Snetsinger et al. 2005). We assumed we would need to catch 25% more birds or harvest 25% more eggs to allow for unfit birds, infertile eggs, and nestling mortality. We assumed birds would be released into an area with comparatively improved habitat, in which increased food sources and nesting sites, and some degree of predator control would allow for improvements in both survival and reproductive output, as compared to their current habitat.

Translocation from the wild population

In terms of translocating birds from the existing wild population, previous mist netting efforts have shown that a field crew of two generally catches zero to two birds on a given day. Thus, we assumed that on average, they could catch one bird a day, resulting in the need for two people for 13 days to catch the 10 birds required in the first year and, and two people for 25 days for the subsequent five supplementation intervals. After capture, we assumed that all birds would be held in quarantine for one month after the last birds are trapped, resulting in about 6 weeks in the first year and 8 weeks in subsequent supplements. To implement this quarantine procedure, a temporary holding facility would be built with separate and divided aviaries for each bird, due to the bird’s solitary and territorial nature, as well as to prevent any potential spread of disease. The aviaries would need to be robust, rodent-proof, and mosquito-proof. The most secure and cost effective aviary would be constructed using pre-fabricated panels and would cost about $30,000 to build for each group of ten birds and should last the lifetime of the translocation project. Thus, we assumed one facility would be built in the first year and an additional facility in the second to accommodate the greater number of birds. Once captured, we would need to test (physical exam, blood test, fecal test) each bird for diseases, parasites, etc., which would cost about $100/bird. Care of these birds would take three fulltime workers 30 person-days each the first year and 40 person days each subsequent translocation event. Feeding would be the same as supplemental feeding (each papaya feeds 28 birds/day and each egg feeds six birds/day), resulting in a total food budget of $61.75 for 13 birds and $158.33 for 25 birds during quarantine. Before release, each bird would be fitted with a Holohil BD-2, 1.2g transmitter, each costing $182 with shipping.

After birds have passed quarantine, they can be flown to the island of release. Commercial airlines will fly the birds as baggage and each flight can take three birds. Thus, it would take four flights the first year and seven flights in subsequent years to move the puaiohi to another island. One-way flights from Lihue to Kahului cost about $125/flight, resulting in total costs of $500 and $875, respectively.

We assumed that birds would be held near enough to the release site so as not to require further transportation, within a temporary facility of the same design as the quarantine facility. Birds would be held here for one month. Effort and costs should be the same as at the quarantine facility. After release, we would offer supplemental food for one month, following the supplemental feeding protocol, resulting in a total food budget of $31.67 for ten birds and $63.33 for 20 birds. We would put out three feeding stations in the first year when 10 birds were released, and five feeding stations in subsequent years, when 20 birds were released. Given that feeders would be relatively close together, we assumed field crews would need one day to place three to five feeders. While acclimating, birds would be fed scrambled eggs and papaya for one month, and feeders would need to be maintained daily. Birds would be monitored daily for one month, weekly for three months, and then monthly for one year. We assumed that this would take a crew of two people 36.5 days each for 10 birds and four people 36.5 days each for 20 birds, resulting in total labor costs of $10,220 and $20,440, respectively. During the first month of monitoring, we assumed feeders could be maintained within this time as well. We assumed that three helicopter trips would be needed to set up aviaries on each island in the first two years, and none in additional years, and that food could be driven/packed in on a weekly or so basis.

Translocation from a captive-reared population

To rear and release 10 juvenile puaiohi in the first year, and 20 in subsequent release years, we assumed we would need to collect 13 eggs (+25% of target to account for infertility/loss if nestlings) from as many different pairs as possible in the first year and 25 eggs for subsequent supplemental intervals. A KFBRP field crew of four would be needed each year for 5 months, resulting in a total labor cost of $61,660. Eggs must be flown down via helicopter to an egg house as they are collected, for hatching and rearing, and eggs will come from 10 nests the initial year and 20 nests in subsequent supplemental years, which means 10 and 20 helicopter trips, respectively, to bring eggs down. Effort and cost of a puaiohi egg house would be similar to current attempts to collect and rear eggs to establish a captive ‘akikiki population, in which facility rental, zoo staff personnel, supplies, etc., was $80,000. This also includes the cost of getting the hatchlings to the rearing facility on another island.

Once hatched, we assumed birds would be reared on Maui in January (~10 months). To rear nestlings to release would take one staff member, food, and aviary space at about $80,000 (modeled after cost for egg house) for a building that could house 10-20 puaiohi and could be run every other year as needed for releases. After rearing to a releasable age, birds would be flown to the release site, requiring one helicopter flight to transport 10 birds and two flights for 20 birds. Before release, birds would be acclimated at the release site in facilities modeled after the quarantine and holding pens in the wild translocation scenario. This would cost $30,000 in the first year, and an additional $30,000 at the next release to scale up from 10 to 20 birds. Birds would stay in the acclimation facilities for a month with two full time staff. Feeding would be at the same rate as with the wild translocation, resulting in a total food budget of $33.67 for 10 birds and $63.33 for 20 birds. Before release, each bird would be affixed with a Holohil BD-2, 1.2g transmitter, each of which cost $182, with shipping. Post release feeding and monitoring would be the same as for the wild translocation. Three helicopter trips would be needed to set up aviaries on each island in the first two years, and none in additional years, and that food could be driven/packed in on a weekly or so basis.

Analysis

For each management option, we calculated the total cost over the 25-year period modeled, using a 1.5% discount rate (10 year US Treasury bond rate). Within a given management option, we calculated total discounted cost by the number of puaiohi extant at 25 years, to give us a per capita cost of management options at 25 years. To evaluate if relationships existed between total cost or per capita cost and either extinction probability, growth rate or population size at 25 years, we conducted a simple linear regression in Systat 13.

RESULTS

The baseline PVA model demonstrated a population in decline with a negative intrinsic rate of increase (r = -0.26; Fig. 5.2, Table 5.4). In nearly all simulations the baseline population went extinct, with a 0.95 probability of extinction. Of the populations that went extinct, the mean time to extinction was 16.6 years and mean population size at 25 years was less than one individual. All ten management models indicated substantial increases in growth rate, population size, time to extinction, and lower probabilities of extinction over the baseline model (Table 5.4). Among the management models, rat eradication and suppression, habitat restoration, and combination models all exhibited positive population growth rates. In addition, rat control exhibited a positive, small growth rate (r = 0.009). The nest box and supplemental feeding models exhibited negative growth rates and were an improvement over the baseline model. In the case of population size, all management scenarios resulted in markedly larger final numbers compared to the baseline model, even in those scenarios exhibiting a negative growth rate (Table 5.4). For models with iterations that went extinct, modest increases in mean time to extinction were found between the management and the baseline models.

While all ten management scenarios resulted in improved conditions for future puaiohi populations, they varied in several notable ways. First, the only management models that demonstrated zero probability of extinction were those that had involved rat management (Table 5.4). All rat management models also yielded positive population growth rates, with the models of rat eradication yielding the greatest rate of increase and the largest population size at the end of 25 years. Of the remaining management options, six situations resulted in negative population growth (supplemental feeding, nest box provision, wild populations used in translocation, and the metapopulation during a wild translocation) and two resulted in positive growth (the translocated populations on a new island). Supplemental feeding, nest box provisioning, and the remaining wild populations used in the translocation models all had markedly smaller final population sizes at 25 years and had a risk of going extinct (Table 5.4). For the two models involving translocating birds, both resulted in increasing populations on a new island, reaching final population sizes that were close to current puiaohi population sizes at the expense of the wild populations on Kauaʻi. The wild population sustaining harvest for translocation (Table 5.4) exhibited a lower growth rate and shorter mean time to extinction than did the baseline wild population. Furthermore, the translocated population had a smaller mean population size and growth rate than did the translocated population sourced from a captive population, as for 27.46% of the translocations attempts, too few juveniles were available for harvest.

Each of the management models yielded markedly different costs to conduct over the 25 year period. Costs ranged over two orders of magnitude difference, with the least expensive being translocation from the wild population at $409,568.06 and the most expensive being habitat restoration and rat eradication with bait stations, at a cost of $262,398,484.88 (Table 5.5). On a per capita basis, the least expensive management option was still translocation from the wild population at a cost of $973.70/puaiohi extant after 25 years, compared to the most expensive, which was supplemental feeding at a cost of $206,803.20/puaiohi. The supplemental feeding option was better than the per capita cost of the baseline model over current expenditures, which would cost $11,658,348.70/ puaiohi extant after 25 years.

In general, within a given level of rat management, Goodnature traps were less expensive than bait stations, especially in longer-term removal operations, and aerial broadcast of rodenticide was only cost-competitive when coupled with a predator-proof fence so that long term control was unnecessary. Overall, each habitat-wide rat management option was more cost-efficient when coupled with a predator-proof fence. These are quite expensive, but they pay for themselves in the long term by limiting intensive rat removal efforts. Furthermore, concentrating Goodnature traps along streams is a more economical method of rat suppression compared to traps in a grid.

We found no relationship between either total cost or per capita cost in relation to probability of extinction ($F_{1,22} = 0.55$; p = 0.47, for total; $F_{1,22} = 0.55$; p = 0.47, for per capita), growth rate ($F_{1,22} = 2.68$; p = 0.12, for total; $F_{1,22} = 0.02$; p = 0.90, for per capita), or population size after 25 years ($F_{1,22} = 3.22$; p = 0.09, for total; $F_{1,22} = 0.004$; p = 0.95, for per capita; Fig. 5.3). Of the 25 cost comparisons 17 of them are ones that would benefit more than puaiohi, five would only benefit puaiohi, and three would primarily benefit puaiohi, but likely have some positive effects for other endemic species, particularly forest birds (Table 5.5).

DISCUSSION

Management intervention demonstrates improvement in the long-term viability of puaiohi compared to current management efforts. While these alternatives indicate improvements, clear winners and losers emerged from a purely demographic point of view. Specifically, management options that used some form of rat management were superior to all other alternatives, resulting in increased future populations and little to no probability of extinction. Translocations also provided a means by which puaiohi could persist into the future at approximately current population size. However, the tradeoff in translocation is that success in translocation (without any concurrent management of the wild population) results in a new population on a different island, while the original wild population would decrease and go extinct. Supplemental feeding and nest box provisioning would still result in a population 25 years in the future, albeit one that is only 20%-25% of the current population, and continuing to decline.

From a cost perspective, management options range from less than half a million dollars to hundreds of millions of dollars over 25 years, demonstrating a markedly wide range in potential expenditures. Likewise, on a per capita basis there was a nearly 200-fold difference in cost per individual puaiohi between the lowest and highest costs expended per bird. The baseline model, when coupled with status quo spending, is by far the least cost-efficient option for puaiohi. When considering the costs of management in conjunction with a given management option, the more optimal management options become clearer.

Supplemental feeding and nest boxes seem to be the least effective options. Supplemental feeding not only results in a negative growth rate or unstable population size and is the least cost-effective due to the labor-intensive nature of daily feeder visits. While nest boxes are cost-efficient in terms of the cost/bird after 25 years, the population's growth rate is still negative and size is small, indicating that this option is unlikely to prevent puaiohi extinction. Translocation may be a very cost-effective method for successfully establishing a new population of puaiohi and thereby reducing probability of extinction. However, translocation alone is not enough, as without intervention the wild population will likely go extinct. Effectively, translocation would just be moving the population to a new island, while letting the species go extinct in the area to which it is endemic. Given how cost-efficient translocation from the wild population is, it remains an important option to consider if management action is also taken on the wild population. The price for captive rearing is not much more than the rat control at nests using the Goodnature traps option. This suggests that if translocation is deemed important for decreasing puaiohi extinction risk, it might be more cost-efficient to control rats in the wild population, thereby producing a stable, slightly larger population that can sustain harvest, rather than investing in captive rearing.

In terms of rat management, every option returns at least stable, if not growing, population outcomes. Among the rat control options, those of smaller scale return the most cost-efficient management outcomes, and, within a scale, Goodnature traps are generally more cost-efficient than bait stations or aerial broadcast. The one exception to this is for habitat-wide rat eradication with predator-proof fencing. In this case, aerial application of rodenticide represents the most cost-efficient of all the rat management models above the local, at-nest scale projects, though the same scenario with a grid of Goodnature traps is nearly as cost-efficient. Habitat restoration, either with or without ungulate fencing, offers an intermediate degree of cost-effectiveness that is not as cost effective as some of the simpler rat management options, and more so than many of the more intensive management options.

The absence of a relationship between either total cost or per capita costs associated with management options and any of our model outcomes of interest (probability of extinction, growth rate, or population size at 25 years) indicates that effective conservation of puaiohi is not achievable simply by spending more money, but by choosing management options that maximize the benefit to the population.

In general, management scenarios with acceptable outcomes fall out into three general categories: those containing rat eradication or suppression (or combinations thereof), which grow to K and stabilize there; habitat restoration or habitat restoration and rat control, which grow to an intermediate size and stabilize there; and rat control which stays stable just at or above the initial population (Fig. 5.2). Overall, decisions as to the most appropriate rat control option will depend upon whether the goal is to increase puaiohi to the greatest possible K, how fast to grow the population, and the available budget.

In addition to financial considerations, management decisions must ultimately consider some externalities, both positive and negative, that we were unable to incorporate into our analysis. Perhaps greatest among these externalities is that we only calculated benefits in terms of puaiohi. For some options, such as supplemental feeding, nest box provision, and translocation, puaiohi are probably the only species that will benefit. Other options, such as the local-scale rat control at nests, will likely be of primary benefit to puaiohi and of some benefit to other native plants and animals that are affected by rat predation. Likewise, while placing Goodnature traps along streams instead of in a habitat-wide grid is cost-efficient for managing the stream-affiliated puaiohi, it will likely be less effective for other species because large areas of habitat would not be protected. However, any of the rat suppression, rat eradication, and habitat restoration options are likely to have benefits that far exceed this, including those to other endangered forest birds, and the many endangered endemic plants and invertebrates impacted by rats. This externality is difficult to quantify, and is likely to have a significant impact on this imperiled endemic ecosystem.

The ecological impacts of any management option should also be considered. Options that require daily maintenance of feeding stations or weekly checking of bait stations range-wide would likely inflect great ecological damage from the trails they would make and the nests they might disturb. Furthermore, while predator-proof fencing may offer an invaluable opportunity in terms of rat eradication, the margins that need to be cleared around it and the canopy that must be trimmed to prevent rodent reinvasion may have major effects on the fragile and imperiled ecosystem.

The limitations of these models also need to be recognized. Although we have used the best available data to populate our models, this study faces these same limitations. PVAs are often criticized for their dependence on the large amounts of data necessary to provide accurate output (Hamilton & Moller 1995; Taylor 1995; Groom & Pascual 1998; Ludwig 1999, Ellner et al. 2002). However, the utility of PVA is as a means of comparing options through considering relative extinction risks, either between subpopulations of a species or between alternative management actions (Lindenmayer & Possingham 1996, Brook et al. 2000, Morris & Doak 2002, Akçakaya & Sjögren-Gulve 2000). The same idea holds for our estimates of costs. While costs of management options are based on the best available information and consultation with experts in the field, financial markets and pricing may fluctuate over time. In some cases, fluctuations in pricing may affect all options similarly (e.g., discount rate), or a group of options similarly. For example, the price of Goodnature A24 traps may decrease as this relatively new technology goes into wider use. Such a situation has already occurred for predator-proof fencing in Hawaiʻi, as managers found less expensive sources for materials and local labor to build them (Lindsay Young, pers comm).

While most successful management models may appear to be expensive and the logistics for implementing them daunting, this must be contextualized within the greater field of conservation biology. The technology is not quite in hand for all methods we propose. For instance, we have not yet erected a predator-proof fence in this type of habitat. However, this would not be the first time that fencing projects were deemed impossible, only to become possible as technology advances or an agency or organization install one. And scale, though often a stumbling block for many projects, becomes less daunting when one sees that eradication on islands like 12,785 hectare Macquarie could successfully eradicate all its rodents.

In terms of costs, our models indicate two options exist which eradicate rats throughout core puaiohi habitat, and restore nearly 40 km^2 of endemic wet forest to its native, predator-free state, for under $21 million over the 25-year project life. By comparison, the red-cockaded woodpecker received $11,666,267 in the eight years between 1996 and 2004 (Leonard 2008), to protect a less imperiled species and ecosystem. Furthermore, the U.S. Bureau of Land Management spent $75.3 million on the wild horse and burro program in 2015 (U.S. Bureau of Land Management 2016), to maintain a non-native species to the detriment of its native ecosystem. Thus, to suggest that we begrudge a much smaller amount of money and less effort to protect a species that exists nowhere else on earth, seems short-sighted and foolish.

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Table 5.1. Vortex parameter inputs for the baseline Puaiohi population model.

Parameter	Value
Species Description	
Inbreeding Depression	
Lethal Equivalent	6.29
% due to Recessive Lethals	50%
EV Concordance of Repro and Survival?	Yes
Reproductive System	
Reproductive System	monogamous, probably long term
Age of 1st Offspring Females	1
Age of 1st Offspring Males	1
Max Age of Repro	10
Max # Broods/Year	4
Max # Progeny/Brood	2
Sex Ratio at birth in % Males	1 to 1
Density Dependent Reproduction	yes
% Breeding at Low Density	100%
% Breeding at K	90%
Allee Parameter	0
Steepness Parameter	8
Reproductive Rates	
% Adult Females Breeding	Will be automatically calc'd from % Breedings, A, and B
EV (SD) in % Breeding	10
Distribution of Broods each Year	0--13.16%; 1--42.11%; 2--36.84%; 3--5.26%; 4--2.63%
# Offspring/Female/brood (exact distribution of brood size)	1--30.77%; 2--69.23%
Mortality Rates	
Mortality of Females as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.54
SD in Mort after Age 1	3

Mortality of Males as %	
Mort from 0 to 1	0.77
SD in Mort from 0 to 1	10
Annual Mort after Age 1	0.29
SD in Mort after Age 1	3
Mate Monopolization	
% Males in Breeding Pool	100%
Initial Population Size	
Stable Age Distribution?	Yes
Initial Population Size	500
Carrying Capacity	
K	1100
SD in K due to EV	10

Table 5.2. Cost inputs for all management options. All costs are annual unless otherwise noted.

Management option	Base Price	Units	# times purchased/year	Total	Comments
Goodnature traps at nests					
Traps	$157.97	1068.00	1	$168,711.96	Years 1, 11, & 21
Gas & lure	$27.59	1068.00	1	$29,466.12	
Labor to find nests	$140.00	226	1	$31,640.00	
Labor to set out traps	$140.00	106.8	1	$14,952.00	Years 1, 11, & 21
Labor to maintain traps	$140.00	66.75	6	$56,070.00	
Helicopter flights to stock supplies	$600.00	1	3	$1,800.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1	2	$1,200.00	All other years
Bait stations at nests					
Stations	$21.84	1068.00	1	$23,325.12	Years 1, 11, & 21;
Bait	$0.44	45.31	1068	$21,375.25	
Labor to find nests	$140.00	226	1	$31,640.00	
Labor to set out stations	$140.00	106.8	1	$14,952.00	Years 1, 11, & 21
Labor to maintain stations	$140.00	66.75	26	$242,970.00	
Helicopter flights to stock supplies	$600.00	1	8	$4,800.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1	6	$3,600.00	All other years
Rat suppression with Goodnature trap grid					
Traps	$157.97	7795.00	1	$1,231,376.15	Years 1, 11, & 21
Gas & lure	$27.59	7795.00	2	$430,128.10	
Labor to set out traps	$140.00	389.75	1	$54,565.00	Years 1, 11, & 21
Labor to maintain traps	$140.00	311.80	12	$523,824.00	
Helicopter flights to stock supplies	$600.00	1	19	$11,400.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1	8	$4,800.00	All other years

Rat suppression with Goodnature traps along streams					
Traps	$157.97	4560.00	1	$720,343.20	Years 1, 11, & 21
Gas & lure	$27.59	4560.00	2	$251,620.80	
Labor to set out traps	$140.00	161.47	1	$22,605.80	Years 1, 11, & 21
Labor to maintain traps	$140.00	114.00	12	$191,520.00	
Helicopter flights to stock supplies	$600.00	1.00	12	$7,200.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1.00	5	$3,000.00	All other years
Rat suppression with bait stations					
Stations	$21.84	62350.00	1	$1,361,724.00	Years 1, 11, & 21
Bait	$0.44	45.31	62350	$1,247,890.14	
Labor to set out stations	$140.00	2034.92	1	$284,888.80	Years 1, 11, & 21
Labor to maintain stations	$140.00	1385.56	52	$10,086,876.80	
Helicopter flights to stock supplies	$600.00	1	640	$384,000.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1	473	$283,800.00	All other years
Rat suppression with aerial broadcast of rodenticide					
Cost/m ungulate fencing	$164.00	33552	1	$5,502,528.00	Year 1
Cost/ha of aerial rodenticide	$412.17	4032	1	$1,661,869.44	
Cost/m ungulate fencing upkeep	$2.25	44522	1	$100,174.50	Years 2-25
Rat eradication with a Goodnature trap grid					
Fencing	$546.56	30324	1	$16,573,885.44	Year 1
Fencing upkeep	$2.50	30324	1	$75,810.00	Years 2-25
Traps	$157.97	7795.00	1	$1,231,376.15	Year 1
Gas & lure	$27.59	7795.00	2	$430,128.10	Years 1-2
Labor to set out traps	$140.00	389.75	1	$54,565.00	Year 1
Labor to maintain traps	$140.00	311.80	12	$523,824.00	Years 1-2
Helicopter flights to stock supplies	$600.00	1	19	$11,400.00	Year 1
Helicopter flights to stock supplies	$600.00	1	8	$4,800.00	Year 2

Rat eradication with bait stations					
Fencing	$546.56	30324	1	$16,573,885.44	Year 1
Fencing upkeep	$2.50	30324	1	$75,810.00	Years 2-25
Stations	$21.84	62350.00	1	$1,361,724.00	Year 1
Bait	$0.44	45.31	62350	$1,247,890.14	Years 1-2
Labor to set out stations	$140.00	2034.92	1	$284,888.80	Year 1
Labor to maintain stations	$140.00	1385.56	52	$10,086,876.80	Year 1-2
Helicopter flights to stock supplies	$600.00	1	640	$384,000.00	Year 1
Helicopter flights to stock supplies	$600.00	1	473	$283,800.00	Year 2
Rat suppression with aerial broadcast of rodenticide					
Cost/m predator proof fencing	$546.56	30324	1	$16,573,885.44	Year 1
Cost/ha of aerial rodenticide	$412.17	3898	1	$1,606,638.66	Years 1-2
Cost/m predator fencing upkeep	$2.50	30324	1	$75,810.00	Years 2-25
Restoration of existing habitat without ungulate fencing					
Price/ha for hand application (low weed density)	$159.37	2618	1	$417,230.66	Years 1, 3, 8, 13, 18, & 23
Price/ha for hand application (med weed density)	$656.61	640	1	$420,230.40	Years 1, 2, 5, 8, 3, 18, & 23
Price/ha for hand application (high weed density)	$1,483.31	1304	1	$1,934,236.24	Years 1, 2, 5, 8, 3, 18, & 24
Price/ha for aerial application (imagery)	$2.02	4032	1	$8,144.64	Years 1, 4, 7, 10, 13, 16, 19, 22, &25
Aerial herbicide treatment for Australian tree ferns	$100,000.00	1	1	$100,000.00	Year 1
Aerial herbicide treatment for Australian tree ferns	$30,000.00	1	1	$30,000.00	Years 2-25
Restoration of existing habitat with ungulate fencing					
Cost/m ungulate fencing	$164.00	33552	1	$5,502,528.00	Year 1
Cost/m ungulate fencing upkeep	$2.25	44522	1	$100,174.50	Years 2-25

Price/ha for hand application (low weed density)	$159.37	2618	1	$417,230.66	Years 1, 3, 8, 13, 18, & 23
Price/ha for hand application (med weed density)	$656.61	640	1	$420,230.40	Years 1, 2, 5, 8, 3, 18, & 23
Price/ha for hand application (high weed density)	$1,483.31	1304	1	$1,934,236.24	Years 1, 2, 5, 8, 3, 18, & 24
Price/ha for aerial application (imagery)	$2.02	4032	1	$8,144.64	Years 1, 4, 7, 10, 13, 16, 19, 22, &25
Aerial herbicide treatment for Australian tree ferns	$100,000.00	1	1	$100,000.00	Year 1
Aerial herbicide treatment for Australian tree ferns	$30,000.00	1	1	$30,000.00	Years 2-25
Supplemental feeding					
Feeding stations	$114.67	119.00	1	$13,645.73	Years 1, 11, & 21
Food: egg	$0.25	39.67	365	$3,619.89	
Food: papaya	$2.00	8.50	365	$6,205.00	
Labor to identify territories	$140.00	226	1	$31,640.00	
Labor to place feeders	$140.00	47.6	1	$6,664.00	Years 1, 11, & 21
Labor to maintain feeders	$140.00	29.75	365	$1,520,225.00	
Helicopter flights to stock supplies	$600.00	1	3	$1,800.00	Years 1, 11, & 21
Nest boxes					
Nest boxes	$71.75	119.00	1	$8,538.25	Years 1, 11, & 21
Monitoring equipment	$209.35	119.00	1	$24,912.65	Years 1, 6, 11, 16, & 21
Labor to identify territories	$140.00	226	1	$31,640.00	
Labor to build nest boxes	$140.00	31.73	1	$4,442.20	Years 1, 11, & 21
Labor to assemble sensor/camera units	$140.00	47.6	1	$6,664.00	Years 1, 6, 11, 16, & 21
Labor to install nest boxes	$140.00	47.6	1	$6,664.00	Years 1, 11, & 21
Labor to maintain boxes	$140.00	47.6	6	$39,984.00	

Helicopter flights to stock supplies	$600.00	1	3	$1,800.00	Years 1, 11, & 21
Helicopter flights to stock supplies	$600.00	1	1	$600.00	Years 6 & 16
Translocation from wild population					
Labor to mist net birds	$140.00	2	13	$3,640.00	Year 1
Labor to mist net birds	$140.00	2	25	$7,000.00	Years 2, 4, 6, 8, & 10
Pre-translocation quarantine facility	$30,000.00	1	1	$30,000.00	Years 1 & 2
Testing of birds	$100.00	13	1	$1,300.00	Year 1
Testing of birds	$100.00	25	1	$2,500.00	Years 2, 4, 6, 8, & 10
Labor for quarantine care	$140.00	30	3	$12,600.00	Year 1
Labor for quarantine care	$140.00	40	3	$16,800.00	Years 2, 4, 6, 8, & 10
Quarantine papaya	$2.00	0.46	42	$39.00	Year 1
Quarantine egg	$0.25	2.17	42	$22.75	Year 1
Quarantine papaya	$2.00	0.89	56	$100.00	Years 2, 4, 6, 8, & 10
Quarantine egg	$0.25	4.17	56	$58.33	Years 2, 4, 6, 8, & 10
Transmitter	$182.00	10	1	$1,820.00	Year 1
Transmitter	$182.00	20	1	$3,640.00	Years 2, 4, 6, 8, & 10
Transport to Maui	$125.00	4	1	$500.00	Year 1
Transport to Maui	$125.00	7	1	$875.00	Years 2, 4, 6, 8, & 10
Post-translocation quarantine facility	$30,000.00	1	1	$30,000.00	Years 1 & 2
Labor for post-translocation care	$140.00	20	3	$8,400.00	Year 1
Labor for post-translocation care	$140.00	20	3	$8,400.00	Years 2, 4, 6, 8, & 10
Post-translocation papaya	$2.00	0.36	28	$20.00	Year 1

Post-translocation egg	$0.25	1.67	28	$11.67	Year 1
Post-translocation papaya	$2.00	0.71	28	$40.00	Years 2, 4, 6, 8, & 10
Post-translocation egg	$0.25	3.33	28	$23.33	Years 2, 4, 6, 8, & 10
Supplemental feeding stations	$114.67	3	1	$344.01	Year 1
Supplemental feeding stations	$114.67	2	1	$229.34	Year 2
Supplemental papaya	$2.00	0.36	28	$20.00	Year 1
Supplemental egg	$0.25	1.67	28	$11.67	Year 1
Supplemental papaya	$2.00	0.71	28	$40.00	Years 2, 4, 6, 8, & 10
Supplemental egg	$0.25	3.33	28	$23.33	Years 2, 4, 6, 8, & 10
Labor for post-release monitoring	$140.00	36.5	2	$10,220.00	Year 1
Labor for post-release monitoring	$140.00	36.5	4	$20,440.00	Years 2, 4, 6, 8, & 10
Heli trips	$600.00	3	1	$1,800.00	Years 1 & 2
Translocation from captive-reared population					
Egg collection--KFBRP personnel	$140.00	110	4	$61,600.00	Year 1
Egg collection--KFBRP personnel	$140.00	110	6	$92,400.00	Years 2, 4, 6, 8, & 10
Helicopter trips to transport eggs to egg house	$600.00	1	10	$6,000.00	Year 1
Helicopter trips to transport eggs to egg house	$600.00	1	20	$12,000.00	Years 2, 4, 6, 8, & 10
Egg house (including zoo personnel, etc) on Kaua‘i	$80,000.00	1	1	$80,000.00	Years 1, 2, 4, 6, 8, & 10
Rearing house on Maui	$80,000.00	1	1	$80,000.00	Years 1, 2, 4, 6, 8, & 10
Heli transport to release site	$600.00	1	1	$600.00	Year 1

Heli transport to release site	$600.00	1	2	$1,200.00	Years 2, 4, 6, 8, & 10
Temporary holding facility	$30,000.00	1	1	$30,000.00	Years 1 & 2
Labor at holding facility	$140.00	20	2	$5,600.00	Years 1, 2, 4, 6, 8, & 10
Holding facility papaya	$2.00	0.36	28	$20.00	Year 1
Holding facility egg	$0.25	1.67	28	$11.67	Year 1
Holding facility papaya	$2.00	0.71	28	$40.00	Years 2, 4, 6, 8, & 10
Holding facility egg	$0.25	3.33	28	$23.33	Years 2, 4, 6, 8, & 10
Transmitter	$182.00	10	1	$1,820.00	Year 1
Transmitter	$182.00	20	1	$3,640.00	Years 2, 4, 6, 8, & 10
Supplemental feeding stations	$114.67	3	1	$344.01	Year 1
Supplemental feeding stations	$114.67	2	1	$229.34	Year 2
Supplemental papaya	$2.00	0.36	28	$20.00	Year 1
Supplemental egg	$0.25	1.67	28	$11.67	Year 1
Supplemental papaya	$2.00	0.71	28	$40.00	Years 2, 4, 6, 8, & 10
Supplemental egg	$0.25	3.33	28	$23.33	Years 2, 4, 6, 8, & 10
Labor for post-release monitoring	$140.00	36.5	2	$10,220.00	Year 1
Labor for post-release monitoring	$140.00	36.5	4	$20,440.00	Year 2
Heli trips	$600.00	3	1	$1,800.00	Years 1 & 2

Table 5.3. Input parameters for Vortex puaiohi management models.

Model	Starting population	K	Juv. mort	Female mort	Male mort	Fecundity (attempts/ year)	Fecundity (fledged/ attempt)
Rat control at nests	500	1210	0.69	0.43	0.29	1.71	1--30.77% 2--69.23%
Rat suppression	500	1320	0.62	0.32	0.29	1.99	1--30.77% 2--69.23%
Rat eradication	500	1375	0.58	0.29	0.29	2.13	1--30.77% 2--69.23%
Restoration of existing habitat	500	1375	0.69	0.49	0.26	1.95	1--13.46% 2--86.54%
Rat control and restoration	500	1375	0.69	0.43	0.26	1.95	1--13.46% 2--86.54%
Rat suppression and restoration	500	1375	0.62	0.32	0.26	1.99	1--13.46% 2--86.54%
Rat eradication and restoration	500	1375	0.58	0.29	0.26	2.13	1--13.46% 2--86.54%
Supplemental feeding	500	1210	0.69	0.49	0.26	1.56	1--23.85% 2--76.15%
Nest box provision	500	1210	0.77	0.41	0.29	1.78	1--30.77% 2--69.23%
Translocation from wild population	490	1100	0.77	0.54	0.29	1.42	1--30.77% 2--69.23%
	10	1100	0.69	0.49	0.26	1.95	1--23.85% 2--76.15%
Translocation from captive population					Captive flock		
	10	1100	0.69	0.49	0.26	1.95	1--23.85% 2--76.15%

Table 5.4. Vortex model results for puaiohi management scenarios.

Model	Population	PE within 25 years	PE SE	Mean stoch r	Stoch r SD	Mean N at 25 years	N SD	Mean TE	TE SD
Baseline	Wild	0.953	0.006	-0.2663	0.2086	0.40	1.36	16.61	3.62
Rat control at nests	Wild	0.000	0.000	0.0091	0.1565	597.19	308.04	0.00	0.00
Rat suppression	Wild	0.000	0.000	0.218	0.1587	1266.75	117.98	0.00	0.00
Rat eradication	Wild	0.000	0.000	0.3019	0.1645	1339.28	126.23	0.00	0.00
Restoration of existing habitat	Wild	0.000	0.000	0.0558	0.1673	976.76	310.56	0.00	0.00
Rat control and restoration	Wild	0.000	0.000	0.0499	0.1567	967.14	309.82	0.00	0.00
Rat suppression and restoration	Wild	0.000	0.000	0.2601	0.1624	1334.14	122.78	0.00	0.00
Rat eradication and restoration	Wild	0.000	0.000	0.3462	0.1734	1348.04	127.76	0.00	0.00
Supplemental feeding	Wild	0.018	0.005	-0.0668	0.1567	156.74	159.01	22.53	2.21
Nest box provision	Wild	0.036	0.006	-0.0832	0.1834	110.98	128.43	22.22	2.04
Translocation from wild population	Wild	0.994	0.002	-0.2898	0.1905	0.05	0.42	9.51	3.49
	Translocated	0.002	0.001	0.1377	0.2937	420.58	308.86	17.00	2.83
	Meta	0.002	0.001	-0.01111	0.1584	420.63	308.91	18.00	2.83
Translocation from captive population	Wild	0.965	0.006	-0.2668	0.2070	0.33	1.21	16.64	3.46
	Translocated	0.002	0.001	0.1455	0.2909	468.36	308.07	19.00	1.41
	Meta	0.002	0.001	-0.0109	0.1725	468.69	308.19	20.00	1.41

Table 5.5. Total and per capita cost of puaiohi management options after 25 years of management, sorted by per capita cost. Total costs calculated at a discount rate of 1.5%. In “Other spp benefit column”: N = no, Y = yes, I = intermediate (of primary benefit to puaiohi, but other species will see some benefit at well).

Management option	Total cost	Net cost/No. birds after 25 years	Other spp benefit
Translocation--Option A: from current population	$409,568	$973.70	N
Translocation from captive population	$1,657,035	$3,535.46	N
Rat control at nests--Goodnature traps	$2,925,465	$4,898.72	I
Rat suppression--Goodnature rats traps along stream w/o fencing	$11,160,789	$8,810.57	I
Rat control--Bait stations with diphacinone	$6,308,574	$10,563.76	I
Nest box provision	$1,674,838	$15,091.35	N
Rat eradication--Aerial broadcast of rodenticide w/ predator proof fence	$20,967,413	$15,655.74	Y
Rat eradication--Goodnature rat traps in grid w/ predator proof fence	$20,973,662	$15,660.40	Y
Restoration of existing habitat-W/o fence	$17,184,580	$17,593.45	Y
Rat suppression--Goodnature rat traps in grid w/o fence	$23,181,183	$18,299.73	Y
Rat control and restoration--Goodnature traps	$20,110,044	$20,793.31	Y
Rat suppression and restoration--Goodnature rats traps along streams w/o fencing	$28,345,369	$21,246.17	Y
Rat control and restoration--Bait stations with diphacinone	$23,493,154	$24,291.37	Y
Restoration of existing habitat--W/ fence	$24,582,672	$25,167.57	Y
Rat eradication and restoration--Aerial broadcast of rodenticide w/ predator proof fence	$38,151,993	$28,301.83	Y
Rat eradication and restoration--Goodnature rat traps in grid w/ predator proof fence	$38,158,242	$28,306.46	Y
Rat suppression and restoration--Goodnature rat traps in grid w/o fence	$40,365,763	$30,256.02	Y
Rat eradication--Bait stations in grid w/ predator proof fence	$42,270,576	$31,562.16	Y
Rat suppression--Aerial broadcast of rodenticide w/ungulate fence	$41,831,381	$33,022.60	Y
Rat eradication and restoration--Bait stations in grid w/ predator proof fence	$59,455,155	$44,104.89	Y

Rat suppression and restoration--Aerial broadcast of rodenticide w/ungulate fence	$59,015,961	$44,235.21	Y
Rat suppression--Bait stations in grid w/o fence	$245,213,905	$193,577.19	Y
Rat suppression and restoration--Bait stations in grid w/o fence	$262,398,485	$196,679.87	Y
Supplemental feeding	$32,414,333	$206,803.20	N
Baseline	$4,663,339	$11,658,348.70	N

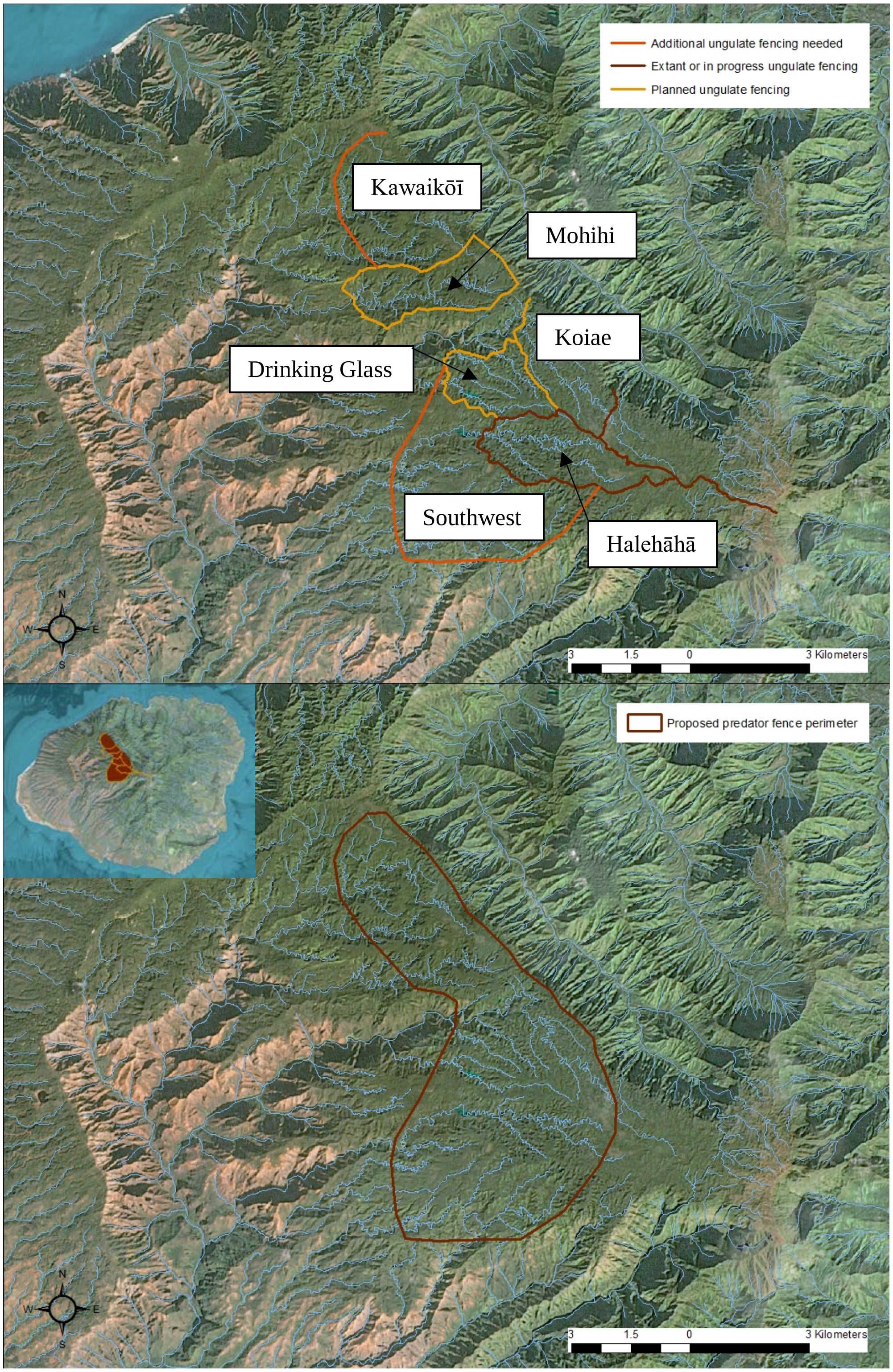

Figure 5.1. Location of existing and proposed ungulate (top panel) and hypothetical predator-proof (bottom panel) fences. Unit names on top panel indicate specific fence sections.

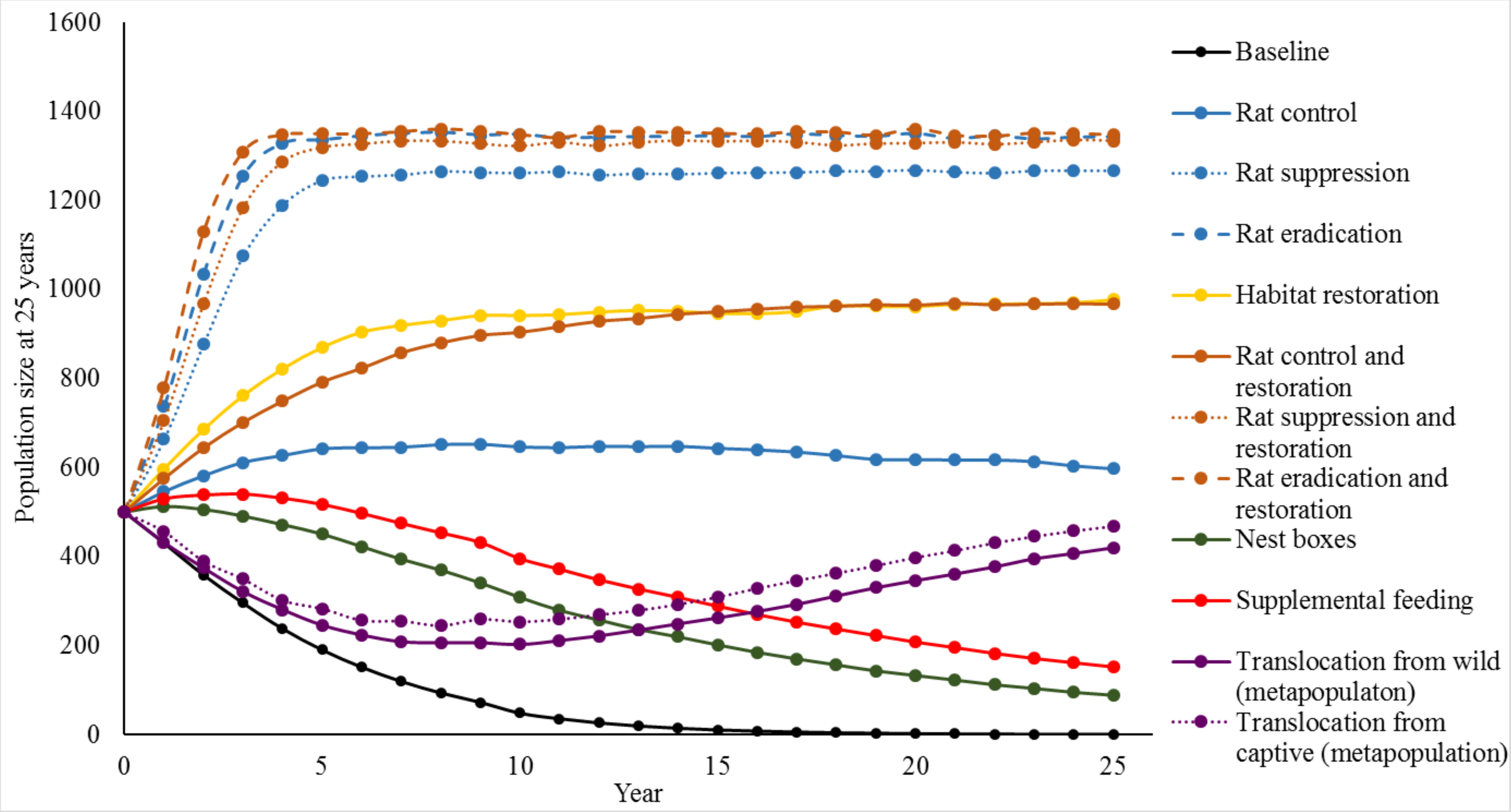

Figure 5.2. Population trajectories of baseline and ten management scenarios.

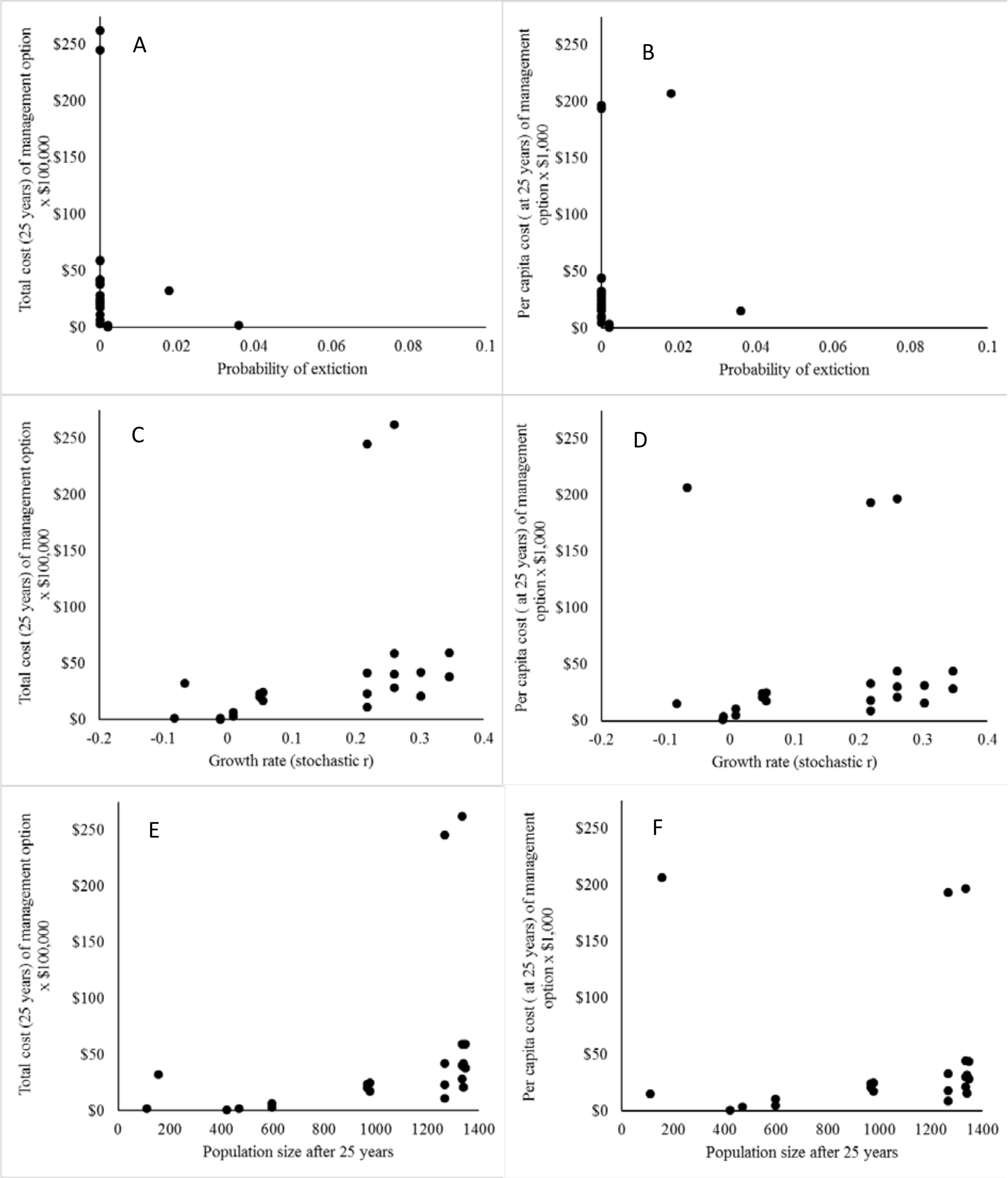

Figure 5.3. Scatterplot of total costs and per capita costs versus management model outputs for probability of extinction (A and B), mean stochastic r (C and D), and population size after 25 years (E and F).

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CHAPTER 6

CONCLUSION

The puaiohi is a bird in crisis. It lives in a habitat greatly reduced from its historic range and faces numerous threats to its long-term persistence. These threats are unlikely to disappear any time soon, and indeed, are likely to increase in the future. However, the puaiohi has managed to persist when other species around it have gone extinct. Now, before it is too late, evaluating the species' viability and the management actions needed is essential to ensure their continued persistence. To begin addressing this gap, I modeled puaiohi populations under current and potential future management scenarios and determined alternatives for species recovery. As such, this work can directly inform conservation by providing information on aspects of puaiohi biology that are poorly understood, as well as a method for understanding both the demographic and cost impacts of management options prior to investing time and resources in them.

One factor which may have great influence on puaiohi is climate change, as illustrated in Chapter 2. The puaiohi demonstrates correlations between its reproductive output and measures of rainfall, both within its breeding season and in the wet season preceding it. Total rainfall in the previous wet season was strongly and positively correlated with breeding attempts/season, number of young fledged/attempt, and total number of young fledged/season. Mean rainfall during the breeding season was positively correlated with reproductive effort (attempts/season and length of breeding season) and with total reproductive output, though some evidence exists that too many rainy days during the peak breeding season was associated with fewer young fledged per nesting attempt. Given that the prevailing weather conditions of the Alakaʻi

Wilderness are predicted to experience anthropogenic climate change, conservation and management must understand how weather affects the reproductive output of puaiohi, and other endemic species, as a means of evaluating their chances for long-term survival. In the puaiohi's case, the forecast increase in dry El Niño years may have a profound impact on the species' reproductive potential, while at the same time, the possible increase in moderately wet La Niña years may compensate for the dry years. Given the puaiohi's relatively long life span, individuals may be able to weather the bad years and capitalize on the good, if the bad years happen infrequently and rainfall and lower temperatures in the good years are not too severe. The risk remains, however, that this creates a highly variable breeding scheme that could destabilize a population already at risk due to its small size.

While mitigating climate change is beyond the scope of current management for the species, many management approaches exist that provide mechanisms to achieve long-term viability for the puaiohi. To investigate which of these is most demographically effective, in Chapter 3, I modeled management scenarios including rat control, habitat improvement, general survival facilitation, and provision of nest boxes within a population viability framework. Although baseline models showed a worrisome decline in abundance and predicted extinction of the species within the next 25 years, several management scenarios served to halt this decline, and in some cases, even increase population size. In particular, rat control, even at more modest levels, was the most effective method of increasing puaiohi abundance. As female and juvenile survival rates were the most influential parameters, management should focus on increasing female and juvenile puaiohi survival to maximize our ability to protect this species.

While *in situ* conservation is generally a more desirable means of protecting the species, in some cases it is necessary to take a more interventionist approach, such as translocating individuals to create new populations and thereby reducing the probability of extinction. In Chapter 4, I compared different translocation approaches directed at creating new puaiohi populations on another island. By exploring a suite of translocation regimes, two different sources of birds available for translocation, and three different release conditions, I concluded that though translocation does offer hope of increasing puaiohi population size and decreasing extinction risk, success will depend on the conditions established at the release site. Furthermore, re-establishment of the puaiohi captive breeding program may be necessary to provide enough birds to translocate, as the current wild population may not be productive enough to sustain the levels of harvest necessary to successfully establish a new population.

While my previous work has identified viable and attainable means of protecting the puaiohi, no management action would be complete without an assessment of its financial costs. In Chapter 5, I expanded upon our previous management scenarios by developing real world management options that have the potential to be implemented in the field. Specifically, I modeled different options within ten scenarios: rat control at identified puaiohi nests; habitat-wide rat suppression; habitat-wide rat eradication; habitat restoration; supplemental feeding; provision of nest boxes; habitat restoration coupled with rat control, suppression, or eradication; and translocation of a second population to improved habitat. While each of the ten management models resulted in increases in growth rate, population size, time to extinction, and lower probabilities of extinction, they yielded markedly different per capita and total costs over the lifespan of the project. The least expensive option was translocation from the wild population, with the most expensive being habitat restoration and rat eradication with bait stations (total cost) and supplemental feeding (per capita cost). The costs of the management actions were unrelated to the outcomes of the population models, indicating that the success of a management option was not tied to its cost. Notably, about two thirds of the management options considered would produce benefits to additional species beyond the puaiohi, indicating even greater possible benefits. Ultimately, the most cost-effective management options all included some form of rat management, which appears critical for changing the future direction of the puaiohi population from one of decline to one of improvement.

While this dissertation has answered many important questions about puaiohi, it has also highlighted areas in which additional work would be valuable. We must better understand how climate change, particularly ENSO cycles, affect these birds, as well as understand how rainfall patterns will change under future climate scenarios. Further understanding of basic demographics, taken over longer time periods, would help refine understanding of the species' biology and where best to invest our resources. The puaiohi's native habitat is undergoing constant and unrelenting alteration as invasive, non-native plants and animals further invade the Alakaʻi Wilderness area. Understanding how these invasive species alter food resources and nesting habitat will be crucial to determining best management practices. Finally, while translocation appears to be an important option for increasing species numbers and creating an additional population, thereby decreasing extinction risk, its success hinges upon the existence of a new habitat in which mortality is reduced and reproductive output increased. Before this technique can be pursued, it is imperative that a location be identified or created.

Though all the efforts mentioned would aid in our understanding of puaiohi and their demographics, research should not be initiated solely to answer these questions. In fact, I believe that the time for research without action, on this or any other Hawaiian forest bird, has passed. Rather, I would suggest that best identified conservation practices be implemented immediately, but that it be done in an adaptive management framework, such that while we are actively protecting the species, we are continually gathering data to help refine and redirect our understanding of these best management practices by reducing uncertainty.

Viewed in total, the results of this dissertation indicate that while puaiohi face a number of negative environmental impacts, hope exists. Using the best available data and real world scenarios suggests that we have a real opportunity to affect change for the better. Although any option will take time and money, current work on removing invasive species in New Zealand and Australia, the recent translocation of millerbirds to the Northwest Hawaiian Islands, and Island Conservation's great success at removing invasive species from islands around the world, indicates that restoration is possible.

The findings presented here are important not just for the puaiohi, but for other endangered forest birds of Hawai‘i as well. While we are missing some important demographic information concerning the puaiohi, it is one of the better studied Hawaiian forest birds, and as such, can serve as a model organisms for other birds in the community. While the project focused solely on this one species, it should be noted that research and management on most of the endangered forest birds in Hawai‘i are similarly underfunded and lacking in data-supported management decisions. The methods and procedures developed here could be applied to many other Hawaiian species. For instance, rats pose one of the greatest threats to native species in insular environments and the modeling efforts shown here demonstrate that controlling this invasive species would have marked impacts on species' recovery.

Ultimately, conserving Hawaii's avifauna, and in fact all its endemic species, does require additional research but management is primarily a matter of resources and will. As I have demonstrated in this dissertation, a future for puaiohi exists, and by extension, for the many other species that call Hawai‘i home. We can no longer claim ignorance of the root of these problems and how to solve them. Whether this is our moral imperative, or simply the right thing to do, it is our responsibility and our privilege to end the extinction crises in Hawaiʻi and preserve the legacy of this ecological treasure for future generations.