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Chapter 1

NICHE RESTRICTION AND CONSERVATISM IN A NEOTROPICAL PSITTACINE: THE CASE OF THE PUERTO RICAN PARROT

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ABSTRACT

The factors which govern species' distribution and abundance are myriad, and together constitute the ecological niche of a given species. Because abiotic factors are arguably the most profound of the factors influencing niche boundaries and thus, species distributions, substantial changes in either climatic or habitat-related parameters can be expected to produce interrelated and profound niche shifts. Habitat loss and degradation can also effectively induce a *de facto* climate change by forcing populations to relocate to environmentally suboptimal habitats. Populations experiencing niche shifts due to range restrictions and geographic isolation become subject to a suite of factors that may act synergistically to amplify deleterious ecological effects of habitat loss. These factors tend to exert a greater influence on populations of rare or endemic species with inherently restricted ranges. The Puerto Rican parrot (*Amazona vittata*) is an example of a tropical, insular, endemic and critically-endangered species that has suffered from extensive habitat loss and degradation over the past century, resulting in a single relict wild population restricted for more than 70 years to the montane rainforest of the Luquillo Mountains in northeastern Puerto Rico. In this chapter, we examine the current ecological situation of this geographically and demographically isolated parrot population by reviewing the history of landscape-level changes in and around the Luquillo Mountains, and concurrent biotic and abiotic limiting factors in relation to both historical population trajectory and current prognosis for species recovery. We used a decade (2000-2009) of empirical data on parrot fledgling survival together with long-term climatological data to model effects of local climate on fledgling survival and gain insights into its influence on population growth. We also modeled hypothetical survival of parrot fledglings in the lowlands surrounding the Luquillo Mountains, areas currently deforested but previously occupied by parrots, to illustrate both quantitative and qualitative losses of reproductive habitat for the species. We illustrate and systematically discuss how progressive and sustained changes in landscape composition and associated limiting factors have effectively shifted and restricted the ecological niche of this species, and how this complex suite of ecological processes affects the Puerto Rican parrot in the Luquillo Mountains. Our niche restriction hypothesis is supported by the demographic response of Puerto Rican parrots recently (2006-2009) reintroduced in the lower elevation karst forest of northwestern Puerto Rico. Based on our findings, we present conservation strategies aimed at promoting the recovery of the species both in the Luquillo Mountains and elsewhere in Puerto Rico. Finally, we address the relevance of our findings to conservation of other endangered

species, particularly those threatened by both habitat loss and climate change.

Keywords: Allee effect, *Amazona vittata*, climate, competition, deforestation, extinction, fledging, habitat loss, mortality, population growth, predation, Psittacidae, rainfall, survival

INTRODUCTION

The factors that govern species distribution and abundance are myriad, and together constitute the ecological niche of a given species (Grinnell 1917). Hutchinson (1957) later redefined this concept as the ecological space, defined by both biotic and abiotic factors, within which a population can maintain a positive net rate of increase. Hutchinson (1957) further distinguished between the fundamental niche, defined by species-specific genetic attributes and physiological tolerances, and the realized niche, which includes limits imposed by biotic interactions such as competition and predation. At any given point in time, populations may occur at distinct points within the niche, relative to axial distances to niche boundaries (Hutchinson 1957, Pearman *et al*. 2007, Braunisch *et al*. 2008). Generally, populations occupying positions nearest the niche centroid have greater potential for growth. Conversely, populations occurring nearer to niche boundaries, especially "hard" boundaries delimited by abiotic factors (Brown *et al*. 1996, Holt *et al*. 2005, Tingley *et al*. 2009), are more likely to encounter lower potential for growth (Bridle and Vines 2007, Braunisch *et al*. 2008). This is particularly the case when niche boundaries shift towards the centroid or along axes that are narrow relative to niche breadth (Ackerly 2003). Niche shifts can be caused by habitat alterations, climate change, novel pathogens or predators, or competitively dominant invasive or exotic species (Case and Bolger 1991, Benning *et al*. 2002, Peterson 2003, Boland 2004, Pearman *et al*. 2007, Fitzpatrick *et al*. 2007, Tingley *et al*. 2009). In such events, niche boundaries may even shift beyond the niche occupancy point for a given population (Pounds *et al*. 1999, Braunisch *et al*. 2008, Tingley *et al*. 2009), resulting in a population existing outside its niche envelope (see Holt and Gomulkiewicz 2004, Holt 2009). When this occurs, the population must adapt, migrate or become extinct (Warner 1968, Taper, Bohning-Gaese and Brown 1995, Peterson *et al*. 1999, Martinez-Meyer *et al*. 2004, Phillips and Shine 2004, Pearman *et al*. 2007). Events in which populations either migrate to follow spatially changing niche boundaries, or become extinct *in situ*, are known as niche tracking (Tingley *et*

al. 2009). Positive niche tracking (*i.e*., migration) is an adaptive response documented mainly in highly vagile species with ample geographic ranges, or those with broad physiological tolerances (*i.e*., greater niche breadth). For example, in temperate forests of the Sierra Nevada of California, Tingley *et al*. (2009) found that 48 of 53 monitored bird species shifted their occupied geographic range in response to changing environmental niche axes. However, for species with extremely limited ranges and/or niche breadth, such as many tropical or insular species, positive niche tracking may be an extremely limited or impossible option (Janzen 1967, Johnson 1998, Murray 2001, Swihart *et al*. 2003, Hilbert *et al*. 2004, Thuiller *et al*. 2005, Urbina-Cardona and Loyola 2008, Essl *et al*. 2009, Anjos *et al*. 2010, Şekercioğlu *et al*. 2012). For such populations, *in situ* adaptation is frequently the only viable response to niche shifts (*e.g*., Jarvi *et al*. 2001, Shehata *et al*. 2001). In these cases, there emerge two temporally competing processes: those of adaptation and extinction (Holt and Gomulkiewicz 2004, Martinez-Meyer *et al*. 2004, Wiens and Graham 2005, Bridle and Vines 2007, Şekercioğlu *et al*. 2008). Although empirical evidence exists of rapid adaptations and niche expansions in response to niche boundary shifts (*e.g*., Thomas *et al*. 2001, Fitter and Fitter 2002, Ackerly 2003, Broennimann *et al*. 2007, Fitzpatrick *et al*. 2007, Steiner *et al*. 2008), such examples have primarily been *r*-selected species with short generation times, such as annual plants and insects (but see Phillips and Shine 2004, Spiegel *et al*. 2006, Smith *et al*. 2008). However, highly *k*-selected species are inherently disadvantaged when competing against extinction processes via *in situ* adaptations to rapid niche shifts (Murray 2001). This can result in localized extinctions and niche conservatism (Peterson *et al*. 1999, Martinez-Meyer *et al*. 2004, Martinez-Meyer and Peterson 2006, Pearman *et al*. 2007, Holt and Gomulkiewicz 2004, Wiens *et al*. 2010), in which the ecological niche of a species remains relatively constant over time.

Because abiotic factors are arguably the most profound of the factors influencing niche boundaries and thus, species' distributions (Swihart *et al*. 2003, Ahumada *et al*. 2004, Kearney and Porter 2004, Martinez-Meyer *et al*. 2004, Parra et al. 2004, Wiens and Graham 2005, Urbina-Cardona and Loyola 2008, Tingley *et al*. 2009, Essl *et al*. 2009), substantial changes in either climatic or habitat-related parameters can be expected to produce interrelated and profound niche shifts (Pounds *et al*. 1999, Ostendorf *et al*. 2001, Oberhauser and Peterson 2003, Thomas *et al*. 2004, Şekercioğlu *et al*. 2012). For instance, in montane tropical rainforests of Australia, Hilbert *et al*. (2004) projected significant reductions in breeding habitat for the Golden bowerbird (*Prionodura newtonia*) with increases in mean annual temperatures, leading to

probable extinction of the species. Habitat loss and degradation also can effectively induce a *de facto* climate change by forcing populations to relocate to environmentally suboptimal habitats (Warner 1968, Austin 2002, Braunisch *et al*. 2008), a form of "negative niche tracking". Negative niche tracking may also occur when optimal habitat is locally eliminated and significant dispersal barriers (*sensu* Janzen 1967) exist across an environmental gradient between suboptimal occupied and optimal unoccupied sites (Pulliam 2000, Peterson *et al*. 2002, Kambhampati and Peterson 2007, Holt 2009).

Populations experiencing niche shifts due to range restrictions and geographic isolation become subject to a suite of factors that may act synergistically to amplify deleterious ecological effects and reduce fitness (Pounds *et al*. 1999, van Riper and Scott 2001, Swihart *et al*. 2003). Such factors include greater vulnerability to climate change (Benning *et al*. 2002, Hilbert *et al*. 2004, Thuiller *et al*. 2005), increased competition and predation (Holt 1987, Ford *et al*. 2009), increased physiological stress (Warner 1968, Pounds *et al*. 1999, Benning *et al*. 2002), and greater susceptibility to Allee effects and inbreeding depression (Keller *et al*. 2002, Reed *et al*. 2004, Armbruster and Reed 2005, Bridle and Vines 2007). These factors tend to exert a greater influence on populations of rare or endemic species with inherently restricted ranges (Benning *et al*. 2002, Hilbert *et al*. 2004, Thuiller *et al*. 2005, Essl *et al*. 2009, Anjos *et al*. 2010, Şekercioğlu *et al*. 2012).

The Puerto Rican parrot (*Amazona vittata*; hereafter, PRP) is an example of a tropical, insular, endemic and critically-endangered species (IUCN 2009) that has suffered from extensive habitat loss and degradation over the past century (Snyder *et al*. 1987). Once abundant and widespread throughout all forested habitats of Puerto Rico, a single relict wild population has been confined to the upper Luquillo Mountains (also known as the Caribbean National Forest or El Yunque National Forest) for more than 70 years, during which the population declined precipitously from an estimated 2000 birds in 1937 to a low of 13 in 1975 (Snyder *et al*. 1987, Beissinger *et al*. 2008). Current (2013) population estimate in the Luquillo Mountains is 16–20 birds (USFWS unpubl. data). Additionally, approximately 50–70 parrots now also exist in a newly-reintroduced population in the karst forest region of northwestern Puerto Rico (PRDNER unpubl. data, Collazo *et al*. 2013). Designated as an endangered species in 1967, intensive recovery efforts began in 1973 and continue to date (Snyder *et al*. 1987, USFWS 2009a), and have thus far averted species extinction (Butchart *et al*. 2006). Recovery efforts are currently conducted by an interagency recovery team (hereafter referred to as

"managers") comprised of the U.S. Fish and Wildlife Service, the U.S.D.A. Forest Service-El Yunque National Forest and the Puerto Rico Department of Natural and Environmental Resources (PRDNER). However, despite over 40 years of intensive management, the total wild population has never exceeded 47 birds (USFWS 2009a), and remains in a severe population bottleneck (Beissinger *et al*. 2008). Although extensive and detailed accounts of all recovery actions to date are in Snyder *et al*. (1987), Wiley *et al*. (2004), Beissinger *et al*. (2008), and USFWS (2009a), some salient points and questions warrant reiteration.

Population estimates and trends subsequent to the geographic isolation of the PRP consist of anecdotal accounts from 1937–68 and regular systematic counts from 1968–present (Wadsworth 1949, Rodriguez-Vidal 1959, Snyder *et al*. 1987, USFWS 2009a). From these data, we find that once the PRP became limited to the Luquillo Mountains the species began a steady decline in numbers until 1975, when intensive management efforts began to stabilize losses and eventually result in modest, albeit variable, population gains (Snyder *et al*. 1987, USFWS 2009a). Despite continuing efforts, however, overall population growth has been only 1% annually since 1973 ($\lambda = 1.01$; USFWS 2009a). Indeed, growth during the past decade has been less encouraging ($\lambda = 0.94$; Collazo *et al*. 2010), placing the population at a high risk of extinction.

An intuitively obvious and fundamental question is thus: "Why has the PRP population in the Luquillo Mountains not demonstrated substantial growth after 40 years of intensive management"? To address this question, Beissinger *et al*. (2008) used life-stage simulation analysis to assess relative impact of various ecological factors on PRP population growth in the Luquillo Mountains. Using 27 years (*i.e*., 1973–2000) of data on PRP population trends, nesting success, survival estimates, and local climatological patterns, they identified four primary factors as instrumental in restricting population growth; namely, 1) reduced hatching success due to inbreeding, 2) low numbers of adults attempting to nest, 3) nest failures due to nongenetic factors, and 4) low survival of juveniles and adults (Beissinger *et al*. 2008). Moreover, both Beissinger *et al*. (2008) and Wiley *et al*. (2004) recommended continued nest guarding and active interventions to prevent nest failures, establishment of a second population (a process now well underway), and efforts to determine the causes of the low proportion of breeding birds, as necessary management actions to potentially increase population growth. However, these

measures and others have been applied with the Luquillo population for decades (see Wiley 1980, Snyder *et al*. 1987, Lindsey 1992, Vilella and Arnizaut 1994, Wiley *et al*. 2004, White *et al*. 2005a, White *et al*. 2006, USFWS 2009a), suggesting that the problems identified by Beissinger *et al*. (2008) may be symptomatic of a yet unidentified underlying ecological issue.

In this chapter, we examine the current ecological situation of this geographically and demographically isolated parrot population by reviewing the history of landscape-level changes in and around the Luquillo Mountains, including concurrent biotic and abiotic limiting factors, in relation to the historical PRP population trajectory. We also use a decade of empirical data on PRP fledgling survival in the Luquillo Mountains together with long-term climatological data to model the effects of local climate on fledgling survival and hence, population growth. Because of recent implementation of avian predator control as a management tool, we also model effects of this activity on fledgling survival. Additionally, we compare mortality patterns of wild fledglings and released captive-reared parrots (White *et al*. 2005b) to illustrate differential effects of mortality factors on these groups. We illustrate and systematically discuss how progressive and sustained changes in landscape composition and associated limiting factors have effectively shifted and restricted the ecological niche of this species, and how this complex suite of ecological processes affects the PRP and its future, both in the Luquillo Mountains and elsewhere in Puerto Rico. In doing so, we also compare and contrast the demographic responses of a newly-reintroduced population of PRPs in the northwestern karst region of Puerto Rico with contemporaneous data for the Luquillo population. In this chapter, we define "fundamental niche" as the phylogenetic space within which a population exhibits a positive rate of increase (*sensu* Holt and Gaines 1992). We define "realized niche" as the fundamental niche modified by changes in limiting factors or anthropogenic actions. We believe an analytically and conceptually holistic approach is essential in this case to accurately elucidate the underlying ecological and evolutionary issues affecting this population. Comprehensive approaches to understanding consequences of anthropogenic disturbances for the ecological and evolutionary processes that produce and maintain biodiversity have received little attention from conservationists (Mace and Purvis 2008, Smith *et al*. 2008). Finally, we address the relevance of our findings to conservation of other endangered species, particularly those threatened by both habitat loss and global climate change.

METHODS

Study Area and Environment

Our study focused on the Luquillo Mountains of northeastern Puerto Rico (18º18'N, 65º47'W), an isolated mountain massif (Figure 1) consisting of approximately 196 km^2 of primarily subtropical wet and subtropical montane rainforests (Ewell and Whitmore 1973). Elevations range from 200–1074 m a.s.l., with annual precipitation of 2000 mm at the lower elevations, and exceeding 5000 mm at the highest peaks (Snyder *et al*. 1987). Indeed, annual rainfall in the Luquillo Mountains is the greatest in Puerto Rico (Figure 1). However, we also gave particular attention to the approximately 8 km^2 area occupied year-round by the PRP in the western portion of the Luquillo Mountains, located at elevations from 500–700 m a.s.l. and with an average annual rainfall of 3500 mm (Figure 1). All known nesting by the PRP has occurred within this area since at least 1995 (White *et al*. 2006, USFWS 2009a).

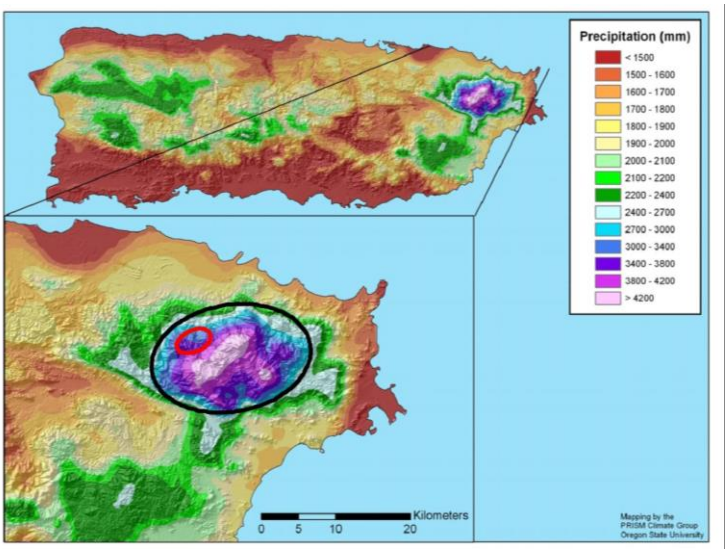

Figure 1. Location of the Luquillo Mountains in northeastern Puerto Rico (inset) and annual distribution of rainfall throughout Puerto Rico. Black oval denotes areal extent of Luquillo Mountains. Red oval denotes current breeding area of the Puerto Rican parrot within the Luquillo Mountains.

Landscape-Level Changes and Limiting Factors – Historical Perspective

To understand the current ecology of the PRP in the Luquillo Mountains, it is necessary to first examine the plethora of changes that have occurred within northeastern Puerto Rico over the past century (see Schrott *et al*. 2005, Groombridge 2007, Laurance *et al*. 2012). For this, we used historical data on landscape-level changes in northeastern Puerto Rico during the time period corresponding to the recorded isolation and decline of the PRP in the Luquillo Mountains (*ca.* 1935–present). Using both published and unpublished accounts, we also examined changes in the most important limiting factors to PRP population growth (Snyder *et al*. 1987, USFWS 2009) over the same time period. We categorized these factors into four main groups, namely: 1) primary abiotic factors, 2) secondary abiotic factors, 3) primary biotic factors, and 4) secondary biotic factors. Factors are discussed relative to their effect on PRP population ecology in the Luquillo Mountains.

Survival Data Acquisition and Analyses

Beginning in 2000, PRP nestlings in all wild nests were equipped with a radio transmitter approximately 4–7 days prior to fledging. Because all known wild nests (n = < 6) were monitored annually (White and Vilella 2004), we had access to all nestlings each year. We used Holohil SB-2C transmitters (Holohil Systems, Ltd., Ontario, Canada) which weighed 6 g (*ca*. 2 % body weight) and had a nominal lifespan of six months. Upon fledging, birds were closely monitored 2–3 times daily for the first two days, followed by once daily during the first week, then three times per week thereafter until death or loss of signal due to either censoring or end of transmitter life. During the initial week post-fledging, we obtained daily visual or auditory confirmation of the status (alive or dead) of each fledgling. Thereafter, if telemetry monitoring indicated that a bird was stationary we visually verified the status within 1–3 days and retrieved any remains in case of mortality.

We modeled the daily survival of Puerto Rican parrot fledglings using the nest survival model (Dinsmore *et al*. 2002) in Program MARK (White and Burnham 1999). We chose this model for our telemetry data because it relaxes the assumption that the exact failure date be known as in Kaplan-Meier approaches (Pollock *et al*. 1989).We modeled survival for a 90-day period post-fledging. For *Amazona* parrots, this period corresponds to the immediate post-fledging and dependence phases, during which fledglings acquire survival

skills and integrate into wild flocks (Snyder *et al*. 1987, Lindsey *et al*. 1991, Matuzak and Brightsmith 2007, Salinas-Melgoza and Renton 2005, 2007).We did not attempt to model survival beyond the 90-day period due to reduced sample sizes and attendant decreased precision in parameter estimates resulting from the combined effect of cumulative deaths and censored observations. On three occasions, a bird was known to have survived the 90-day period, but was censored before end of the period. In those cases, we censored the data at the last known telemetry detection.

In our analyses, we considered a suite of models to explain variation in parrot fledgling survival. Specifically, we investigated the survival consequences of fledgling age (*i.e*., days since fledging), daily rainfall, a 7-day post-fledging period when fledglings may be especially vulnerable (Lindsey *et al*. 1994, Salinas-Melgoza and Renton 2007), and years when Red-tailed hawks (*Buteo jamaicensis*) were and were not removed from the study area. The Red-tailed hawk (hereafter, RTH) is the primary predator of the PRP (Snyder *et al*. 1987, Lindsey *et al*. 1994, White *et al*. 2005b), and beginning in 2003 a program was initiated to reduce extremely high RTH population densities (see Snyder *et al*. 1987, Boal *et al*. 2003, Nimitz 2005), both within and adjacent to the parrot nesting area. We hypothesized that parrot survival would be enhanced in years with predator reduction (see Engemann *et al*. 2005, Livezey 2010, Pieron and Rohwer 2010).We modeled a daily fledgling age effect because we believed that as fledglings aged survival would increase, similar to patterns found in other psittacines (*e.g*., Myers and Vaughan 2003, Stahala 2005, Matuzak and Brightsmith 2007, Salinas-Melgoza and Renton 2007). Beissinger *et al*. (2008) reported that extremes in rainfall resulted in decreased adult survival of PRPs in the Luquillo Mountains. Accordingly, we hypothesized that increased precipitation would also have a negative impact on fledgling survival. Younger fledglings may be especially vulnerable to heavy rain events, as extremely wet periods can cause hypothermia, limited mobility and agility, and potentially increase vulnerability to predation (see Erikstad and Andersen 1983, Green and Cockburn 2001, McDonald *et al*. 2004).We thus modeled effects on survival of the first seven days post-fledging, and hypothesized that survival would be lower during this period. We also examined potential relationships between episodes of intense rainfall (*i.e*., >150% daily average) and fledgling deaths during the first three days post-fledging. During the first 3-4 days post-fledging, PRP fledglings are relatively sedentary and completely dependent on adults for care (Snyder *et al*. 1987).We used mean daily rainfall data from the El Verde meteorological station, located approximately 1 km from the study area, for the period 1990 to

2009 instead of data from individual years to better represent seasonal precipitation patterns.

We assessed the fit of the nest survival model to our parrot fledgling survival data using a modified chi-square test for independence of the fates of chicks within broods as a function of brood size (Erikstad and Andersen 1983, Dinsmore and Knopf 2005). We computed the expected values for the test statistic as the product of the number of broods in each clutch size (1–3 fledglings) and the probability of observing that outcome. The latter probability was calculated as the product of survival ($\#\text{surviving}/\text{total}$) and mortality ($\#\text{dying}/\text{total}$) within each possible brood outcome. For example, the probability (Pr) of observing a brood of three chicks where only one survived is $3*\Pr(\text{surviving})*\Pr(\text{dying})^2$. We estimated over-dispersion as: $\hat{c} = \frac{\chi^2}{\text{d.f.}}$; we calculated $\hat{c} = 0.45$ from this test and did not make any adjustments to the default value of 1 in MARK.

We used the methodology of Burnham and Anderson (2002) to identify competing models for inferences about the factors influencing parrot fledgling survival. We used Akaike's Information Criterion (AIC; Akaike 1973), corrected for possible small sample bias (AICc), to rank the set of candidate models. The nest survival model has no goodness-of-fit test (Dinsmore and Dinsmore 2007), so we relied on untested model assumptions as a basis for using this approach. We present model averaged estimates of effects (betas) across all candidate models (Burnham and Anderson 2002) and used them to make predictions about survival consequences for competing conservation scenarios.

We modeled averaged effects across the model set and used them to predict fledgling survival patterns for different scenarios. We plotted daily survival patterns for a 90-day fledgling period beginning on 27 May (mean fledging date), 27 April (1 month earlier than mean), and 27 June (1 month later than mean), and for each contrasted the effect of RTH control versus no control. These dates span the historical peak of the PRP fledging period (20 April–10 July), during which >80% of fledgings occur (Snyder *et al*. 1987, USFWS unpubl. data). We also computed the probability that a fledgling parrot would survive the 90-day fledgling period in each of six scenarios as the product of the daily survival probabilities. These scenarios were based on three fledging dates (*i.e*., mean date ± 1 mo.), both with and without hawk removal.

Using Program MARK, we also conducted supplemental analyses of the survival of 39 captive-reared PRPs released in the Luquillo Mountains during May–June from 2000–02 and in 2004 (White *et al*. 2005b, USFWS unpubl. data). To compare with wild fledglings, we examined influence of precipitation and time since "fledging" (*i.e.,* release) on survival of captive-reared parrots up to 90 days post-release. We were unable to model effects of predator removal on survival of released parrots because of insufficient temporal overlap between the captive releases and the removal program. Because all captive-releases occurred within the parrot nesting area and during the fledging period, both groups of parrots were subject to the same environmental conditions, thereby enabling comparisons of temporal patterns of mortality and cause-specific mortality factors between wild and captive-reared parrots (see Nicoll *et al*. 2004).

The potential demographic implications of niche restriction along the precipitation axis were explored in two ways. First, we projected the influence of the amount of rainfall (mm) on post-fledging survival at various locations in northeastern Puerto Rico, where parrots occurred historically (Wetmore 1927, Snyder *et al*. 1987) prior to deforestation. We used the average daily rainfall from 8 April to 17 October, the period encompassing the fledging period of parrots and 90 d post-fledging in the Luquillo Mountains. Second, we categorized locations according to the average number of days per year daily rainfall was > 14 mm during the seven days following chick fledging. The 14 mm is an empirically derived threshold associated with most wild PRP fledgling deaths recorded from 2000 to 2009. We used rainfall data from nine weather stations for these assessments (Figure 2). Eight of these stations locations represented the range of orographic rainfall patterns in northeastern Puerto Rico (Figure 1). Two sites within the Luquillo Mountains reflected rainfall patterns to which nesting parrots were exposed until 1995 (Pico del Este station), and to present (El Verde station). We also included the Dos Bocas station, near the Rio Abajo Commonwealth Forest, to gain insights about survival and rainfall exposure where parrots were reintroduced beginning in 2006. Survival projections were made using the equation relating rainfall to post-fledging juvenile survival during the first 90 days post-fledging. Daily rainfall averages for survival projections were based on a 30-year time series to capture long-term patterns in rainfall per location. We selected a 30-year time series for which data were available for most stations (*i.e*., 1975 to 2005). Two stations, Humacao and Fajardo, did not have data for the aforementioned time period, but instead from 1965 to 1995. The average number of days per year whose daily rainfall was >14 mm during the seven

days following chick fledging was calculated based on the same rainfall data series.

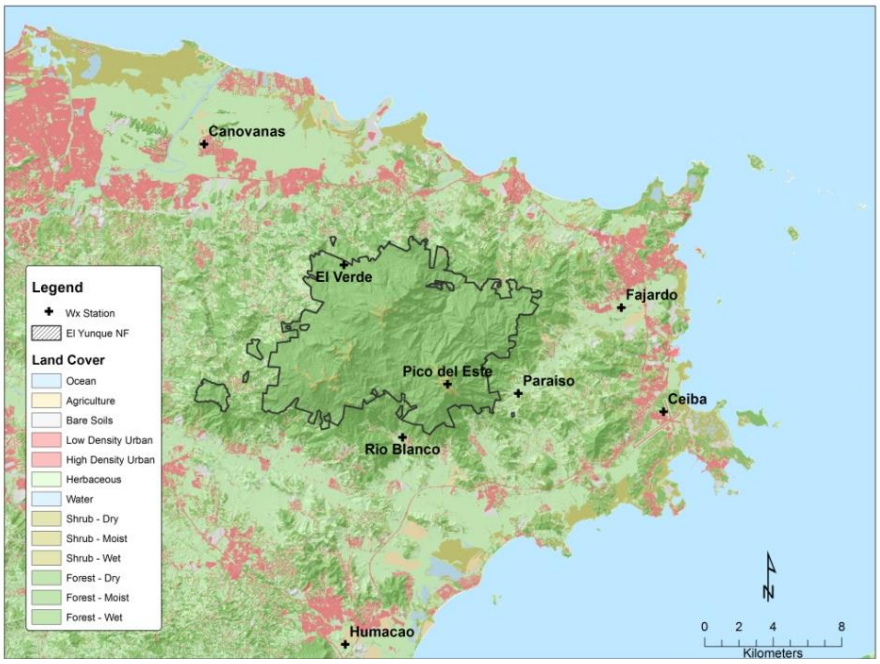

Figure 2. Locations of weather (Wx) stations used to project Puerto Rican parrot fledgling daily survival probability relative to local rainfall. Projections were based on a 30-year time series.

Finally, from 1991–99 a total of 88 chicks fledged from wild nests in Luquillo, many of which were fostered directly from the aviary captive population. Yet inexplicably, the total pre-breeding population grew by only 14 individuals (*i.e.*, 24 to 38) over the same period (USFWS 2009a). Although fledging success is often used as an indicator of recruitment (*e.g.*, Weatherhead and Dufour 2000), evidence exists that post-fledging mortality can invalidate this index, particularly for species with post-fledging dependency periods (see Keedwell 2003, Streby *et al*. 2009, Vormwald 2011). In the case of the PRP, could high fledgling mortality have been a factor in the apparent low recruitment during the 1990s? If so, could rainfall potentially have been a factor in fledgling mortality?

To answer these questions, we used observed (*i.e.*, 2000-09) patterns of fledgling survival relative to environmental conditions to also estimate or "backcast" hypothetical fledgling survival rates during the period 1991-99. To

do so, we used data from 77 fledglings for which exact fledging date was known (USFWS unpubl. data) together with daily precipitation records for the 90-day post-fledging period for 1991–99. We then applied the 2000–09 fledgling survival probabilities to the 77 fledglings, relative to their fledging date and contemporaneous rainfall. We did this to gain insights into potential interactions between environmental factors and population trends. Because of the relatively short and temporally continuous timeframe (*i.e*., 1991-2009), we assumed that overall effects of rainfall on fledgling survival were the same during both decades.

RESULTS

Landscape-level Changes

According to historical data, the extensive deforestation of Puerto Rico during the late 19th to early 20th centuries resulted in a net loss of more than 90% of the island's total forest cover, with only 1% remaining as virgin forest (Murphy 1916, Brash 1987). Only the higher elevations of the Luquillo Mountains, having been previously declared a protected forest reserve by the Spanish crown and later the United States government, remained relatively intact (Wadsworth 1949, Snyder *et al*. 1987). Consequently, by the beginning of the 20th century the PRP was restricted to five separate areas, and by 1940 existed only in the Luquillo Mountains (Snyder *et al*. 1987). Although other contemporaneous factors, such as nest robbing, shooting, and the occasional hurricane also took varying tolls on the species, habitat loss and degradation played the most significant role in the species' overall decline (Brash 1987, Snyder *et al*. 1987). This is because as a secondary cavity nester, the PRP is dependent upon mature forests for nesting, an ecological attribute that exacerbates impacts of deforestation. Comparing the PRP population trajectory in the Luquillo Mountains with surrounding deforestation patterns (Figs. 3, 4) reveals that the greatest decline occurred concomitant with the maximum deforestation during the first half of the 20th century. For example, during 1937 to 1950, when landscape isolation of the Luquillo Mountains reached its maximum level, the PRP population decreased by an order of magnitude (*i.e*., *ca*. 2000 to 200; Wadsworth 1949, Rodriguez-Vidal 1959). By 1975, the population had decreased by yet another order of magnitude, from approximately 200 to only 13 individuals, after which the decline was halted and tenuously stabilized by intensive and ongoing management efforts (Snyder *et al*. 1987, USFWS 2009a). According to Butchart *et al*. (2006), these past

and ongoing efforts effectively saved the species from imminent extinction. Indeed, a regression of the log-transformed population decline from 1937–75 indicates that had the observed decline continued, the population would likely have become extinct by 1990 ($y = 115 – 0.0578 * \text{year}$; $r^2 = 0.96$; $p = 0.002$). By this time, however, although some areas surrounding the Luquillo Mountains were beginning to show signs of fragmented secondary reforestation (Kennaway and Helmer 2007), many areas – particularly coastal – had also experienced a rapid increase in urbanization (Figs. 3, 5), effectively impeding and in some cases reversing a broader reforestation process that had been occurring elsewhere on the island (Lopez *et al*. 2001, Marcano-Vega *et al*. 2002, Lugo *et al*. 2004, Brandeis *et al*. 2007).

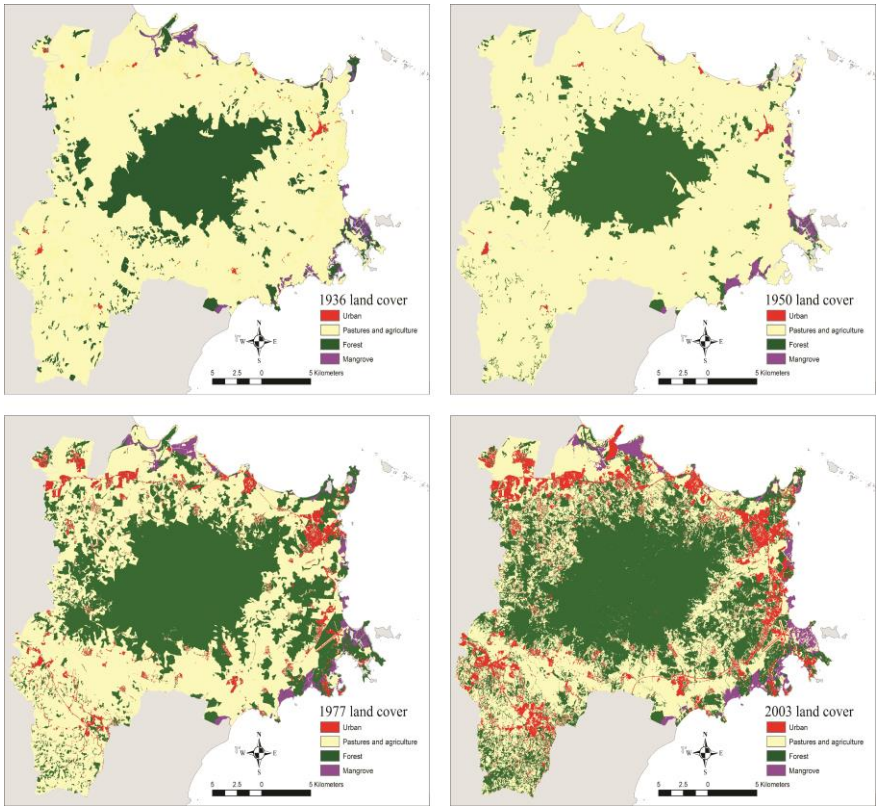

Figure 3. Chronological progression of landscape changes surrounding the Luquillo Mountains of northeastern Puerto Rico, 1936–2003. Figure modified from Gould *et al*. (2011).

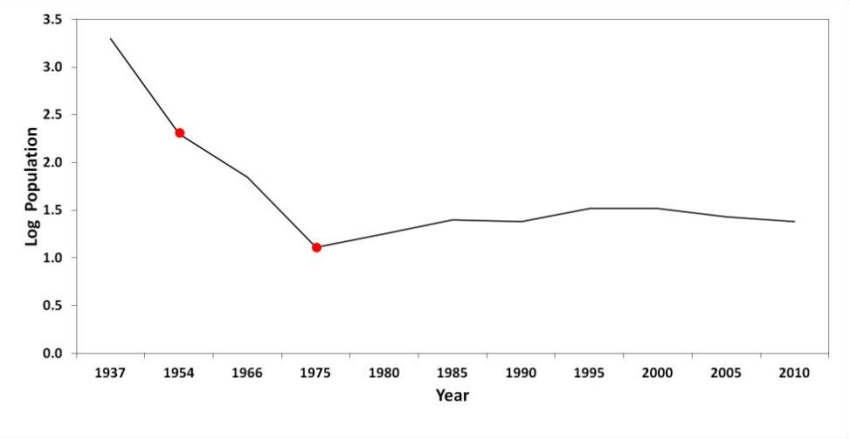

Figure 4. Population trajectory (log-transformed) of the Puerto Rican parrot in the Luquillo Mountains of northeastern Puerto Rico, 1937–2010. Populations at maximum landscape isolation (*ca*. 1954) and start of species recovery actions (*ca*. 1975) indicated.

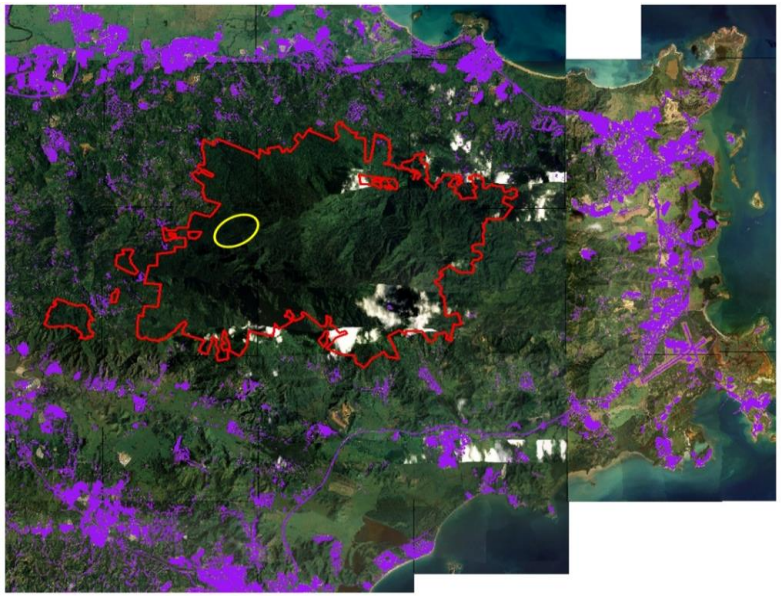

Figure 5. Current (2010) distribution of urbanized areas (purple highlights) surrounding the Luquillo Mountains in northeastern Puerto Rico. Official boundaries of the El Yunque National Forest are depicted in red. Yellow oval denotes current breeding area of the Puerto Rican parrot.

During the past 60 years, many formerly deforested areas of Puerto Rico have become largely reforested with secondary forests of varying ages (Aide *et al*. 1996, Marcano-Vega *et al*. 2002, Brandeis *et al*. 2007, Parés-Ramos *et al*. 2008). However, most such areas are in the western and central regions of the island. To date, the landscape surrounding the Luquillo Mountains has remained extremely fragmented and increasingly urbanized (Figs. 3, 5). According to Lugo *et al*. (2004), there was a 2185% increase in urbanization (*e.g.*, housing, industrial development, shopping centers, highways) surrounding the Luquillo Mountains from 1936 to 1995, much of which occurred on former agricultural lands (Lopez *et al*. 2001) originally covered by lowland broadleaf forests (*i.e.*, former parrot habitat). In fact, within this same area there was an additional 16% increase in urbanization during the period 1991 to 2003 (Gould *et al*. 2011). In effect, the Luquillo Mountains have become "an island within an island" (see Saunders *et al*. 1991, Gould *et al*. 2011).

Fledgling Survival and Mortality Factors

We monitored a total of 62 Puerto Rican parrot fledglings during the 10-year study (Table 1). During the study, an additional four chicks fledged without transmitters, and were not included in analyses. Thus, our sample constituted 93.9% of the total wild fledgling population. Of those monitored, 28 birds died and 34 (54.8%) survived the 90-day post-fledging period. Most (78.6%) deaths occurred within the first month post-fledging, with 60.7% occurring during the first week. Thus, 35.5% of all wild fledglings died within the first month, and 27.4% died within the first week after fledging. Further, fledgling deaths were not independent (G_1 = 6.32, p = 0.01) of episodes of intense rainfall (*i.e*., >14 mm/day; ≈ 1.5x mean daily rainfall) during the first three days post-fledging. Overall, rainfall events >14 mm/day resulted in first-week survival of 51%, compared to first-week survival of 86% in the absence of such events. Seven deaths (25%) were conclusively attributable to raptor predation (see White *et al*. 2005b). The causes of nine deaths could not be determined, although additional raptor predations or weather-related factors could not be ruled out (White *et al*. 2005b). The 90-day post-fledging period was 8 April to 17 October across all study years and mean fledging date was 27 May (SD = 21 days). Overall, the nest survival model fit our fledgling data well ($\chi^2_8 = 3.61$, p = 0.89); there was no effect of brood size on fledgling survival.

Our modeling results showed that fledgling survival was influenced by a combination of factors that included a quadratic age effect, a quadratic pattern of seasonal survival, daily rainfall, and RTH control (Table 2). In models with non-zero AICc weight, the quadratic term for seasonal variation, the linear term for age, and rainfall were "strong" effects and had 95% CIs that did not include zero. In the same subset of models, the linear term for seasonal variation, the quadratic term for age, the effect of the first 7 days post-release, and the effect of RTH removal were weaker because the 95% CIs barely included zero, although the point estimates matched our initial hypotheses (Table 3).

Table 1. Number of Puerto Rican parrot fledglings monitored via radio-telemetry in the Luquillo Mountains, Puerto Rico, 2000-2009

Year	[1]Survived	[1]Died	[2]Total
2000	1	7	8
2001	1	2	3
2002	1	1	2
2003	6	1	7
2004	2	5	7
2005	3	3	6
2006	6	2	8
2007	5	3	8
2008	4	2	6
2009	5	2	7
TOTAL	34	28	62

[1]Numbers of fledglings that survived or died during the 90-day post-fledging period.
[2]Totals do not include 4 parrots that fledged without transmitters: 2 in 2001, 1 in 2003, and 1 in 2006. Fates of these 4 fledglings are unknown.

Daily survival patterns were similar for birds fledging at the mean fledge date (27 May) and one month earlier, but substantially lower for birds fledging one month later (27 June). As expected, survival was greater in scenarios with hawk removals (Figure 6). With RTH removal the 90-day survival probabilities were 0.8201 (27 April), 0.6259 (27 May), and 0.0048 (27 June), whereas survival probabilities without RTH removals were 0.7699 (27 April), 0.5398 (27 May), and 0.0010 (27 June).

Table 2. Model selection results for survival of Puerto Rican parrot fledglings in the Luquillo Mountains, Puerto Rico, 2000-2009. Models are ranked by ascending ΔAICc values where *K* is the number of parameters and weight is the relative support for a model, scaled to sum to zero. Model factors included fledgling age (modeled as linear [Age] and quadratic [Age^2] functions), within-season daily variation in survival (modeled as linear [T] and quadratic [TT] functions), an effect of the first 7 days post-release (First 7d), daily rainfall (Rainfall), the effect of Red-tailed hawk removals (RTH), and a model with no effects

Model	[1]ΔAICc	*K*	Weight	Deviance
Age^2 + TT + First 7d + Rainfall	0.00	7	0.48	249.11
Age^2 + TT + First 7d + Rainfall + RTH	0.50	8	0.37	247.60
Age^2 + First 7d + Rainfall	3.71	5	0.07	256.83
Age^2 + First 7d + Rainfall + RTH	3.83	6	0.07	254.94
Age^2 + TT	11.70	5	0.01	264.82
Age^2 + Rainfall	12.96	4	0.00	268.09
Age^2 + First 7d	14.54	4	0.00	269.66
Age^2 + First 7d + RTH	15.00	5	0.00	268.12
Age^2	25.64	3	0.00	282.77
First 7d	27.00	2	0.00	286.14
Age + T	27.39	3	0.00	284.52
Age^2 + T	27.62	4	0.00	282.75
Age	41.28	2	0.00	300.41
Rainfall	61.44	2	0.00	320.57
RTH	66.40	2	0.00	325.53
T	68.87	2	0.00	328.00
TT	70.25	3	0.00	327.38
No effects	73.84	1	0.00	334.97

[1]The AIC value for the top model was 263.13.

In contrast, survival of released captive-reared parrots was less influenced by rainfall and even less by time since release than that of wild fledglings (Table 4). Moreover, of the 39 captive-reared parrots, 10 died and 29 (74.4%) survived the initial 90 days (13 weeks) following release. During the 90-day period, five deaths (50%) were caused by raptor predation (Figure 7). Causes of the remaining deaths could not be ascertained. Overall, 37 (94.9%) of the captive-reared parrots survived the initial 7-day post-release period, and 36 (92.3%) survived for at least one month after release (Figure 8).

Table 3. Model averaged estimates of parameters to estimate fledgling Puerto Rican Parrot survival in the Luquillo Mountains, Puerto Rico, 2000-2009. Model factors included fledgling age (modeled as linear [Age] and quadratic [Age^2] functions), within-season daily variation in survival (modeled as linear [T] and quadratic [TT] functions), an effect of the first 7 days post-release (First 7d), daily rainfall (Rainfall), and the effect of Red-tailed hawk removals (RTH).

Parameter	Beta	SE	
Intercept	4.33400	1.27124	
T	0.02083	0.03044	
TT	-0.00057	0.00021	
Age	0.11342	0.05755	
Age^2	0.00013	0.00034	
First 7d	-1.08281	0.67689	
Rainfall	-0.02227	0.00530	
RTH	0.27866	0.21507	

Table 4. Model averaged estimates of parameters to estimate survival (S) of captive-reared Puerto Rican Parrots released in the Luquillo Mountains, Puerto Rico, 2000-2004. Model factors included time since release (modeled as linear [Age] and quadratic [Age^2] functions), within-season daily variation in survival (modeled as linear [T] and quadratic [TT] functions), constant survival (.), and an effect of the first 7 days post-release (First 7d) and daily rainfall (Rainfall)

Model	[1]ΔAICc	*K*	Weight	Deviance
{S(Rainfall)}	0.00	2	0.34	117.43
{S(Rainfall + First 7d)}	0.28	3	0.29	115.71
{S(.)}	2.04	1	0.12	121.47
{S(First 7d)}	2.56	2	0.09	119.99
{S(T)}	3.73	2	0.05	121.16
{S(Age)}	4.03	2	0.04	121.47
{S(Age^2)}	5.11	3	0.03	120.54
{S(TT)}	5.73	3	0.02	121.16

[1]The AIC value for the top model was 121.43.

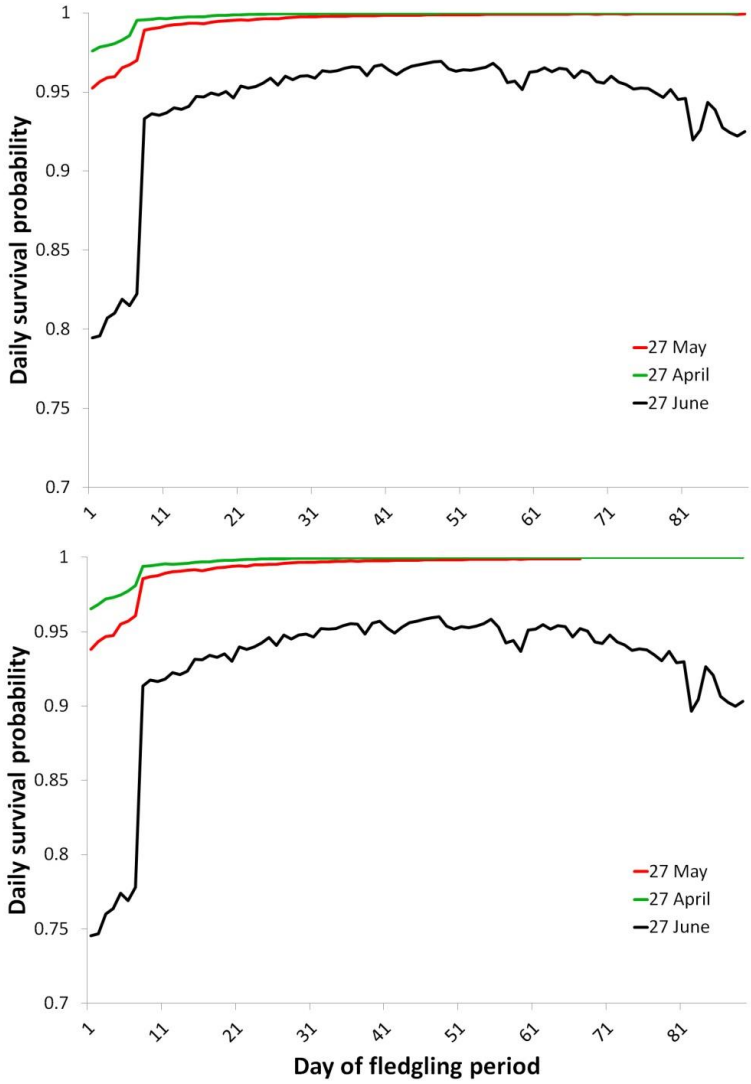

Figure 6. Predicted daily survival rates for Puerto Rican parrot fledglings during the 90-day post-fledging period in the Luquillo Mountains, Puerto Rico, 2000-2009. Survival patterns are illustrated for scenarios with (upper) and without (lower) Red-tailed hawk control and for the mean fledging date (27 May) plus (27 June) and minus (27 April) one month.

Based on current patterns of fledgling mortality relative to rainfall, we estimated an overall fledgling survival (90-day post-fledging) of approximately 41% during the previous decade (1991-99), slightly less than the current (2000-2009) estimate (55%). These estimates were within the range of historical estimates of first-year survival for the species (*i.e*., 35-65%; Snyder *et al*. 1987, Lindsey *et al*. 1994). Thus, approximately 36 of the 88 fledglings produced from 1991-99 likely survived for at least 90 days (Figure 9).

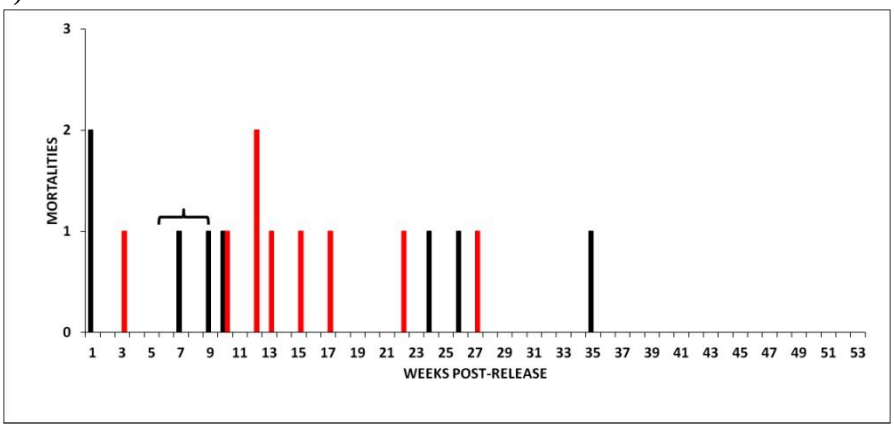

Figure 7. Temporal distribution and causes of post-release mortalities of 39 captive-reared Puerto Rican parrots released in the Luquillo Mountains, 2000-2004. Red bars indicate raptor predations. Black bars indicate unknown causes. Bracket marks 6–8 weeks following release, when parrots began dispersing from the release area.

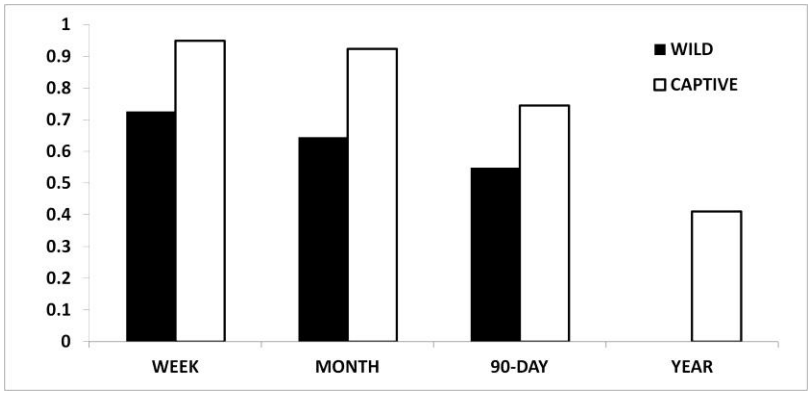

Figure 8. Weekly, monthly and 90-day survival for 62 wild fledglings and 39 released captive-reared Puerto Rican parrots in the Luquillo Mountains, 2000-2009. First-year (year) survival of captive-reared parrots included for comparative purposes.

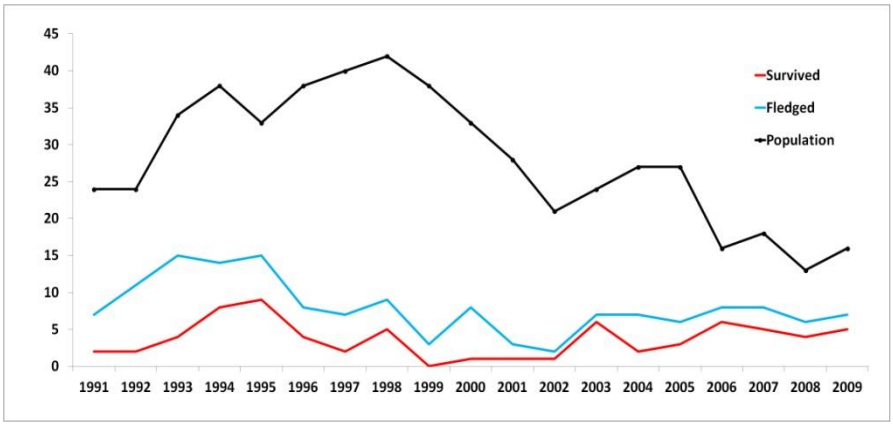

Figure 9. Number of chicks fledged, number of fledglings surviving for 90 days, and annual prebreeding population for the Puerto Rican parrot in the Luquillo Mountains, 1991–2009. Number that survived during 1991–99 was estimated based on observed (2000–09) relationship between fledging dates and precipitation relative to post-fledging survival.

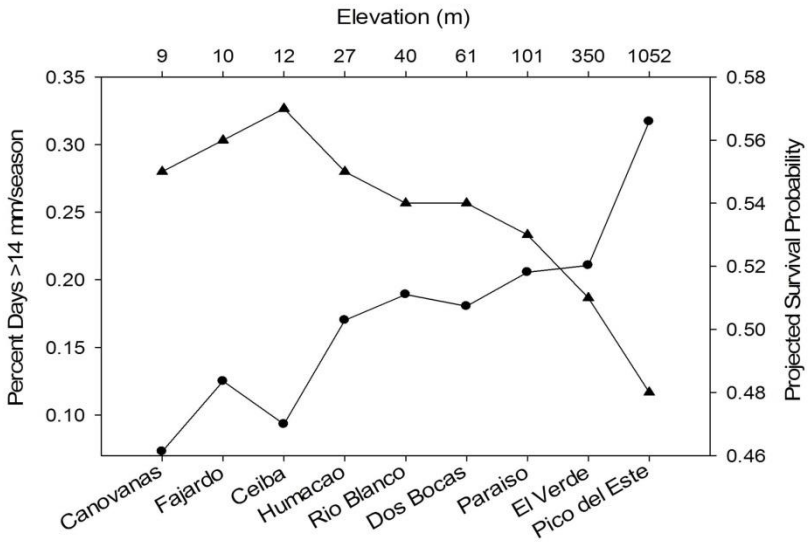

Figure 10. Relationships between elevation, rainfall patterns (percent days >14 mm/season), and projected 90-day fledgling survival probability (line with triangles) for Puerto Rican parrots in northeastern Puerto Rico. Percent days >14 mm (line with dots) represents index of rainfall during the initial week post-fledging.

Projections of fledgling daily survival based on regional precipitation patterns suggest potentially higher survival at lower elevations with an overall drier climate during the post-fledging period (Figure 10). Conversely, higher elevations (*e.g.*, El Verde, Pico del Este) with higher rainfall were associated with lower projected daily survival. Based on rainfall patterns, the Rio Abajo reintroduction area (*i.e.*, Dos Bocas station) occupied an intermediate position within the range of projected fledgling survival (Figure 10).

DISCUSSION

Deforestation and Historical Population Decline

Encompassing approximately 8900 km^2, and with elevations ranging to more than 1300 m a.s.l., Puerto Rico is a relatively small oceanic island with substantial topographic and habitat diversity. It follows that the fundamental niche of the PRP evolved to include the full range of inherent environmental variation present on the island (Holt and Gaines 1992, Brown *et al*. 1996, Pulliam 2000, Holt and Barfield 2008). Psittacines are highly vagile, and historically, PRPs at virtually any point in the island would have had access to a wide array of habitats, ranging from montane forests to coastal scrub and mangroves, resulting in an ideal free distribution (Fretwell and Lucas 1970, Kawecki 1995, Bonebrake and Beissinger 2010). Indeed, historical accounts include several references to substantial movements of the PRP across elevational and habitat gradients (Snyder *et al*. 1987). For example, Wetmore (1927) reported numerous observations of PRPs in the coastal Mameyes Swamp, located approximately 7 km north of the Luquillo Mountains and stated: "When it rained heavily in the mountain, many birds descended to the warmer valleys, returning when the weather cleared". Wetmore (1927) also collected several parrots in the Mameyes area, and found seeds of tabonuco (*Dacryodes excelsa*) in their crops. As tabonuco is a species of the lower montane rainforest (Little and Wadsworth 1964), this was clear evidence that the parrots had returned to the coastal lowlands after foraging at higher elevations.

Following geographic isolation in the upper Luquillo Mountains, however, the PRP was effectively forced into a form of negative niche tracking. The relict population then became subject to a suite of new and additional factors – both biotic and abiotic – acting synergistically to further constrict niche space and limit population growth. The plight of native Hawaiian forest birds

following introduction of mosquitoes (see Warner 1968, Camp *et al*. 2010) provides a functionally analogous ecological scenario. In that case, habitat *per se* was not eliminated, but rendered inhospitable by presence of lethal mosquito-borne pathogens.

The most precipitous population decline of the PRP coincided with the period of maximal landscape isolation of the Luquillo Mountains (Figs. 3, 4). Similar patterns of deforestation also occurred in Costa Rica during the latter part of the past century (Sader and Joyce 1988). Rates of species loss subsequent to forest fragmentation and isolation are time-dependent and sensitive both to fragment size and degree of spatial isolation, with loss rates generally increasing over time and as fragment size decreases and insularity increases (Saunders *et al*. 1991, Newmark 1996, Schrott *et al*. 2005), a phenomenon often referred to as "extinction debt" (Hanski and Ovaskainen 2002, Malanson 2008, Ford *et al*. 2009). Leck (1979) also found that species with larger body sizes (relative to other species within their guild) and/or large territorial requirements suffered disproportionately higher local extinction rates in an isolated tropical forest in Ecuador. Amongst those species suffering post-isolation declines, Leck (1979) reported at least three psittacines, including one *Amazona*. It is noteworthy that the last known sighting of the White-necked crow (*Corvus leucognaphalus*) in Puerto Rico occurred in the Luquillo Mountains in 1963, shortly before the near-extinction of the PRP, and contemporaneous with the extirpation (*ca*. 1959) of the Limpkin (*Aramus guarauna)* on Puerto Rico (Brash 1987, Snyder *et al*. 1987).

The temporal pattern of PRP population decline is also consistent with predictions of Brooks *et al.* (1999) regarding rates of faunal relaxation in isolated tropical forests. In their study, Brooks *et al*. (1999) reported that, for avian communities, approximately 50% of species losses (*i.e.*, half-lives) would occur during 25–100 years post-isolation, with corresponding decreases in half-lives as fragment size decreased and distance to nearest patch increased. Schrott *et al*. (2005) reported similar time-dependent effects of habitat loss on population stability, and found that some populations could remain relatively stable for 50–60 years with slow rates (*e.g*., 0.5% per year) of habitat loss, but would decline rapidly (*i.e*., nonlinearly) in less than 20 years with higher (*e.g*., 5% per year) rates of loss. In this study, the nadir – and near extinction – of the PRP in the Luquillo Mountains occurred approximately 25–50 years after maximum isolation (Figs. 3, 4). A similar time lag in post-isolation extinctions was reported by Willis (1974), who found that 22% of forest bird species were lost on Barro Colorado Island over the period 1923–71 following its isolation by Lake Gatun in 1914. Rapid and

severe population declines of numerous avian species following landscape-level habitat conversions have also been documented throughout Europe (Donald *et al*. 2001).

Primary Abiotic Factors – Climate

Survival of PRP fledglings in the Luquillo Mountains was affected both by the amount of rainfall and its temporal distribution, with increasingly negative effects on survival with increases in fledging date and attendant higher rainfall. Beissinger *et al*. (2008) also reported that extremes in rainfall adversely affected survival of adult PRPs in the Luquillo Mountains. Adverse effects of inclement weather on avian reproductive success and post-fledging survival have also been reported for Australian brown falcons (*Falco berigora*; McDonald *et al*. 2004), Willow grouse (*Lagopus lagopus*; Erikstad and Andersen 1983), Capercaillie (*Tetrao urogallus*; Moss 1986), Lark buntings (*Calamospiza melanocorys*; Yackel-Adams *et al*. 2006), Grasshopper sparrows (*Ammodramus savannarum*; Hovick *et al*. 2011), Eastern meadowlarks (*Sturnella magna*; Suedkamp-Wells *et al*. 2007) and Mountain plovers (Dinsmore *et al*. 2002). In particular, rainfall exceeding 150% of the daily average within three days of fledging significantly reduced PRP post-fledging survival. Similar results were reported by Nicoll *et al*. (2003), who found that post-fledging survival of Maritius kestrels (*Falco punctatus*) was affected by the temporal distribution of rainfall, and that above average numbers of rain days reduced survival of fledgling cohorts. As with Maritius kestrels, parrots which fledged later in the fledging season were more vulnerable to rainfall effects because the probability of higher daily rainfall generally increased over time during the fledging period (8 April – 19 July), particularly during early July (Figure 11). However, post-release survival of captive-reared parrots released contemporaneous with the fledging of wild parrots was notably higher than that of the wild cohorts (Figure 7), and with less influence of precipitation on survival (Table 4). Notwithstanding, cumulative losses of captive-reared parrots to raptor predation eventually reduced overall survival of released cohorts to levels comparable to those of wild fledglings (Figs. 6, 7; see also White *et al*. 2005b).

Differences in survival and relative influence of cause-specific mortality factors between wild fledglings and captive-reared parrots likely arise from inherent differences in "pre-release" conditions. For example, released captive-reared parrots were exposed and acclimated to local rainfall and attendant physiological stressors for at least one year – in some cases more –

prior to release (White *et al*. 2005b, USFWS unpubl. data). In contrast, wild parrots fledging directly from cavity nests were "environmentally naïve", and thus immediately subjected to inclement weather conditions of the Luquillo Mountains during the critical time in which flight and foraging skills develop (Wunderle 1991, Lindsey *et al*. 1994, Myers and Vaughan 2004, Salinas-Melgoza and Renton 2007). However, wild fledglings had the putative benefit of immediate and close association with adult wild birds which may have reduced initial losses to avian predators via more effective predator detection and avoidance (Westcott and Cockburn 1988, Caro 2005). Captive-reared birds were presumably without such advantage, and suffered higher overall losses to avian predators relative to other factors, with at least 50% of captive-reared parrot deaths caused by raptors, compared to 25% for wild fledglings. Thus, while differing in cause-specificity of mortalities, both wild and captive-reared PRPs were equally affected by inherent limiting factors in the Luquillo Mountains.

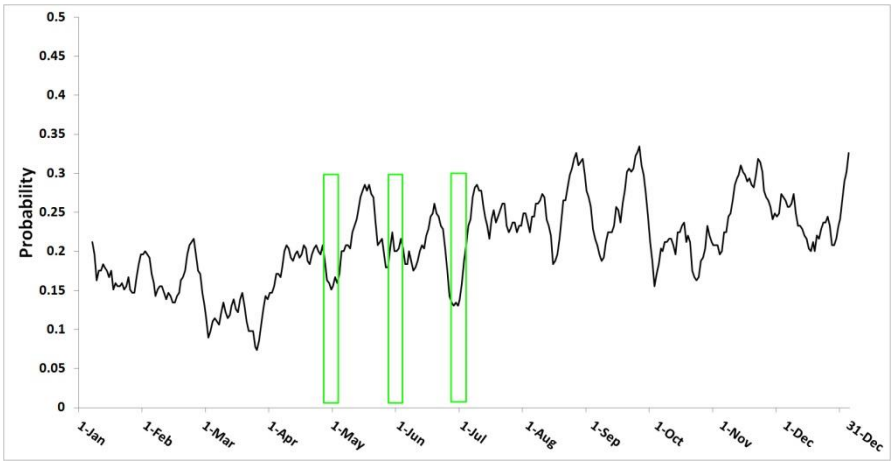

Figure 11. Annual distribution of the probability of daily rainfall >14mm (*i.e*., >1.5x mean daily) at the El Verde meteorological station, approximately 1 km from the Puerto Rican parrot nesting area. Probabilities are based on a 30-year time series with a 7-day running mean. Vertical green boxes span the initial week post-fledging for the mean fledging date (27 May; center box) and one month before and after mean fledging date. These dates were used to model parrot fledgling survival relative to rainfall and raptor removal efforts.

Our findings were similar to those of Lindsey *et al*. (1994), who reported PRP fledgling survival of 43–100% during a three-year study (1985–87) in the

Luquillo Mountains. However, the study of Lindsey *et al*. (1994) also included former PRP nesting areas that were no longer used at the time of our study. Examination of the data of Lindsey *et al*. (1994) for the same nesting area sampled in our study (*i.e*., South Fork) indicates an overall fledgling survival of 56%, nearly identical to that (55%) of our study. As in our study, Lindsey *et al*. (1994) also reported that most deaths (60%) occurred during the first month post-fledging. It is noteworthy that Lindsey *et al*. (1994) monitored fledgling survival using radio-transmitters of the same weight and configuration as those of this study, thereby eliminating any potential bias between studies due to transmitter differences and attendant effects on survival.

Our findings contrast with those of Nicoll *et al*. (2004), who reported no difference in survival rates between released captive-reared and wild-fledging Maritius kestrels. However, there was no temporal overlap between groups of released and wild kestrels, an important factor recognized by Nicoll *et al*. (2004) as possibly masking potential differences due to differing environmental conditions of sampling periods. Although Nicoll *et al*. (2004) attempted to analytically account for this difference, their results were nevertheless inconclusive. In this study, both because of the temporal and spatial overlap of the captive releases and wild fledgings, and the high proportion of the total population sampled (*i.e*., 100% captive-reared; 94% wild), we were able to directly compare survival of these groups relative to post-release/fledging environmental conditions.

Our hypothetical projection of past (1991–99) fledgling survival based on known fledging dates and attendant rainfall suggests that weather-related early post-fledging mortality likely contributed to observed population trends (Figure 9). That is, if one assumes that 36 (41%) of the 88 fledglings produced during that time period survived the initial 90-day post-fledging period, then the total number of juveniles recruited into the population would likely have been some lesser, albeit unknown, number. This is because although we were unable to assess fledgling survival past the 90-day period, it would be biologically unrealistic to assume no additional deaths occurred subsequent to this period (see Lindsey *et al*. 1994). Indeed, the net increase in the pre-breeding population was only 14 individuals over this period (USFWS 2009a), indicating an additional loss of 22 birds. Given that potential juvenile losses after the 90-day post-fledging period were undetected, and that PRP subadult mortality is – as in most avian species – higher than that of adults (Snyder *et al*. 1987, Lindsey *et al*. 1994), we believe the loss of an additional 2–3 birds/year to combined juvenile, subadult and adult mortality was quite probable (see Snyder *et al*. 1987), not to mention the additional hurricane-

related losses in 1998 (see Beissinger *et al*. 2008). Interestingly, Lindsey *et al*. (1994) reported that although 73 PRPs fledged into the wild population during 1979–88, the pre-breeding population grew by only 11 birds, indicating a proportionally identical recruitment (*i.e*., 15–16%) as during the 1990s. These findings suggest that despite intensive nest monitoring and aggressive fostering of captive-produced chicks (Lindsey 1992, Wunderle *et al*. 2003, USFWS 2009a), wild nest productivity and juvenile survival during the 1990s (and apparently 1980s) only marginally exceeded overall mortality. Indeed, the pre-breeding population exhibited a distinct downward trend concurrent with several years (1999–2002) of relatively low productivity and fledgling survival (see Figure 9). Thus, our results further corroborate the findings of Beissinger *et al*. (2008) regarding the strong effect of climate on PRP population growth in the Luquillo Mountains.

Climatic factors also affect PRP reproductive success and population growth in the Luquillo Mountains in ways other than fledgling and adult mortality. For instance, Snyder *et al*. (1987) reported that prior to intensive nest management and enhancement which began in 1973 (and continues to date), nesting success (*i.e*., % of nests fledging young) of the PRP in Luquillo was only 11–26%, with 21–32% of overall nesting failures due to extremely wet nest cavities, resulting in poor egg hatchability or nestling deaths (see also Beissinger *et al*. 2008). Indeed, Snyder *et al*. (1987) reported that of 302 tree cavities inspected in the Luquillo Mountains, more than 68% had wet or damp bottoms that limited their suitability as potential nest sites. Snyder *et al*. (1987) also estimated that, due to accelerated decay from wet conditions, the useful life of natural cavities in the Luquillo Mountains was only 10–15 years. Since 1976, however, virtually all PRP nesting in the Luquillo Mountains has occurred in either artificial or rehabilitated natural nests, and subsequent nesting success has averaged 75–80% (Snyder *et al.* 1987, USFWS 2009a). Moreover, since 2001 all PRP nesting in the Luquillo Mountains has occurred in standardized polyvinyl chloride (PVC) artificial nest cavities (White *et al*. 2005a, USFWS 2009a) with a specially-prepared nesting substrate which is replaced with fresh material 3–4 times during the three-month nesting season. The nest substrate management is necessary for yet another climate-related factor: high relative humidity. Humidity in the upper Luquillo Mountains regularly reaches 100%, often for extended periods (Snyder *et al*. 1987), and the resultant prolonged dampness inside nest cavities promotes growth of pathogenic (to nestlings) bacteria and fungi, particularly the fungus *Aspergillus* (A. Rivera, USFWS veterinary consultant, pers. commun.,). During this study, 18 wild nestlings died from respiratory or gastrointestinal

infections, with an additional 7 requiring either *in situ* treatment or removal to the aviary, representing 29% of the total wild productivity from 2000–2009 (USFWS unpubl. data). Thus, even before fledging, environmental factors adversely affected nearly a third of all nestlings. To counter this problem, since 2010 all nesting substrate has been autoclaved and treated with a fungicide as a prophylactic measure, and nestling respiratory and gastrointestinal infections have thus far been dramatically reduced, with only two of 31 wild nestlings (6%) suffering such infections over the past four (2010–2013) breeding seasons (USFWS unpubl. data). In contrast, only two (3%) of the 67 nestlings produced from 2008 to date by the recently reintroduced PRP population in the drier karst region of northwestern Puerto Rico have suffered from respiratory or gastrointestinal infections (PRDNER unpubl. data), and all nests were in artificial nest cavities identical to those used in Luquillo. Clearly, the climatic factor permeates all aspects of PRP reproductive ecology in the Luquillo Mountains.

The projected higher post-fledging survival in the drier coastal lowlands surrounding the Luquillo Mountains (Figure 10) further highlights the long-term ecological impact to the PRP of the loss of mature coastal forests and associated nesting cavities throughout northeastern Puerto Rico. In this case, habitat loss effectively induced a *de facto* climate change for the PRP by limiting the relict population to an area of suboptimal environmental conditions. Although reforestation often provides hope of recovery for many populations affected by habitat loss (see, *e.g*., Impey *et al*. 2002), the increasingly widespread and irreversible urbanization of previously occupied parrot habitat in the lowlands of northeastern Puerto Rico (see Wetmore 1927, Snyder *et al*. 1987) means that most of what were likely favorable nesting areas for the species have been permanently lost throughout the region (Figure 5; see also Lopez *et al*. 2001, Gould *et al*. 2011).

Secondary Abiotic Factors – Hurricanes

The interaction of geographic location and topography of the Luquillo massif makes it the most hurricane-prone site in Puerto Rico, in terms both of frequency of occurrence and damage vulnerability (Boose *et al*. 2004). Indeed, in Puerto Rico the frequency of hurricane-induced damage equivalent to the F3 level on the Fujita scale (Fujita 1971) is at least three times greater in the northeastern quadrant of the island (*i.e*., Luquillo Mts.), compared to the rest of the island, with wind damage at higher elevations being further exacerbated by extensive deforestation within the surrounding coastal plain and lower

elevations (Boose *et al*. 2004). Some researchers (*e.g*., Meyers *et al*. 1993, Wunderle 1999, Beissinger *et al*. 2008) have suggested that hurricanes can have positive effects on forest and parrot ecology by temporarily increasing forest productivity, and creating potential new cavities. For species with robust and amply distributed populations this may be true. However, we believe the immediate negative effects of these powerful atmospheric events (see Collazo *et al.* 2003, White *et al*. 2005c) on such a small and demographically vulnerable population as the PRP in Luquillo far outweigh any putative benefits accrued via short-term gains in primary productivity. Of particular relevance was the loss of nearly 50% of the relict PRP population (*ca*. 47 birds) immediately following hurricane Hugo in 1989 (USFWS 2009a). Although the population initially exhibited some degree of post-hurricane recuperation (Meyers *et al*. 1993, Vilella and Arnizaut 1994), based on the latest (2013) population estimate (*i.e.*, 16–20 birds), it is unlikely that the current population could sustain such a proportional loss. Furthermore, the apparent positive demographic response of the PRP in the years immediately following hurricane Hugo (Beissinger *et al*. 2008) did not, for reasons yet unclear, occur following hurricane Georges in 1998 (Figure 9). Indeed, Beissinger *et al*. (2008) considered hurricanes to be one of the most important factors limiting PRP population growth. Recent trends and observations predict increasingly frequent and destructive hurricanes in the tropical Atlantic (Goldberg 2001, Emanuel 2005), with ominous implications for the PRP in the Luquillo Mountains. Similar examples of insular avian populations that remain highly vulnerable to extinction from stochastic environmental factors include the Montserrat oriole (*Icterus oberi*; volcanic activity), Cozumel thrasher (*Toxostoma guttatum*; hurricanes), and the Northern royal albatross (*Diomedea sanfordi*; intense storms; see Hilton *et al*. 2003). In effect, it is the unique combination of geographic location, topography and higher frequency of occurrence for hurricanes in the Luquillo Mountains – relative to other parts of the island – that exacerbates both short- and long-term impacts of these recurrent natural phenomena on the relict PRP population.

Primary Biotic Factors – Native Predators, Competitors and Parasites

Predator control, in the form of Red-tailed hawk removals, positively affected post-fledging survival over the course of the fledging season, regardless of fledging date (Figure 6). Overall gains in 90-day post-fledging survival ranged from approximately 0.4 – 8.6%, depending on fledging date.

Indeed, for parrots fledging late in the season (27 June), survival – albeit low – was nearly five times greater with predator control than without. Raptors also caused the loss of over 20% of all captive-reared parrots released in the Luquillo Mountains (Figure 7). For small critically-endangered populations all mortality is additive, and any increases in survival should be considered biologically significant (see, *e.g*., Pimm *et al*. 1988, Goodrich and Buskirk 1995, Sinclair *et al*. 1998). Clearly, raptor predation is exerting a quantifiably negative effect on fledgling survival and thus, PRP population growth in the Luquillo Mountains.

Cumulative landscape-level changes in northeastern Puerto Rico have likely been instrumental in fostering and maintaining an extremely high population of Red-tailed hawks within the Luquillo Mountains. With a reported density >1.1 hawks/km^2, the Luquillo Mountains contains the highest RTH population density ever reported within the species' geographic range (Nimitz 2005). Indeed, Boal *et al*. (2003) stated that the RTH population in the Luquillo Mountains was "at or near saturation". Factors promoting the high RTH density in the Luquillo Mountains include abundant and easily accessible prey, constant trade winds with associated uplifts which maximize foraging efficiency and the absence of significant interspecific competition or depredation by similar-sized raptors (Santana and Temple 1988, Nimitz 2005). The increasingly close proximity to – and even within – the Luquillo Mountains of human dwellings and associated activities (see Figure 5) also provides additional resources (*e.g*., domestic poultry, household pets, rodents) for RTH. Based on historical trends (Wetmore 1927, Danforth 1931), the RTH population has apparently increased throughout Puerto Rico since the 1940s, presumably due to conversion of many former agricultural lands to a matrix of open areas and second-growth forests (Santana *et al*. 1986). Further, the RTH is a habitat generalist with a relatively broad niche, making the species inherently adaptable in dynamic landscapes (Bednarz and Dinsmore 1982, Swihart *et al*. 2003, Suarez-Rubio and Thomlinson 2009), such as those of northeastern Puerto Rico. However, Santana *et al*. (1986) believed that the increasing urbanization of lowlands in Puerto Rico would progressively reduce nesting habitat for RTH in such areas. If so, then this may increase future density of the RTH in the Luquillo Mountains as displaced coastal hawks increasingly shift to montane forests for nesting, thereby further increasing predation pressure on the PRP and potentially nullifying any survival gains accrued from the RTH control program.

While the RTH is a direct predator of both fledgling and adult parrots, the Pearly-eyed thrasher (*Margarops fuscatus*) is a major nest predator and direct

competitor with the PRP for nesting cavities (Arendt 2000, 2006). A relatively large (≈ 110 g) and aggressive cavity-nesting passerine with an omnivorous diet and the capacity to produce multiple broods per year, the Pearly-eyed thrasher is a constant threat to nesting parrots (Wiley 1985, Snyder *et al*. 1987, Arendt 2006), and continual management actions (*e.g*., alternative nest boxes, lethal control) have long been required to minimize this threat (Snyder *et al*. 1987, USFWS 2009a). Though recorded as "scarce" and patchily distributed in Puerto Rico early in the past century, by the early 1950s the Pearly-eyed thrasher population had experienced a substantial increase in the Luquillo Mountains (Snyder *et al*. 1987, Arendt 2000, 2006). A classic avian "supertramp" (Arendt 2006), the Pearly-eyed thrasher quickly colonizes and effectively exploits disturbed, simplified, and species-poor habitats. The landscape-level changes which occurred both within and surrounding the Luquillo Mountains over the past several decades (Figure 3) have most likely promoted the proliferation of the thrasher. For example, the extensive planting of exotic ornamentals associated with coastal urban development and attendant native forest conversion have provided the thrasher with additional food sources and nesting sites, while the close proximity of the Luquillo Mountains offers a relatively species-poor and readily available habitat for dispersing individuals (see Crooks *et al*. 2004, Arendt 2006, Suarez-Rubio and Thomlinson 2009). In fact, population densities of Pearly-eyed thrashers in the upper Luquillo Mountains are among the highest in Puerto Rico, although signs of a slight decline in numbers have been recently detected (Arendt 2006). An aggressive predator and competitor, the thrasher is known to adversely impact several island endemic and endangered species – and not just on Puerto Rico. The apparent extirpation of a subspecies of the Puerto Rican screech-owl (*Megascops nudipes newtoni*) from the U.S. Virgin Islands has been attributed, in part, to nest predation by the Pearly-eyed thrasher (Raffaele 1998, Arendt 2006). On Montserrat, the Montserrat oriole – the sole endemic bird – has also suffered significant reproductive losses to Pearly-eyed thrashers in the aftermath of recent volcanic eruptions which have altered the local habitat to the benefit of the thrasher (Hilton *et al*. 2003, Arendt 2006). Moreover, the thrasher is believed to have also played a role in the disappearance of the White-necked crow from its last known stronghold in Puerto Rico – the Luquillo Mountains (Arendt 2006). It is noteworthy that in those cases where populations have been extirpated by thrashers, it is usually after such populations have been significantly reduced or otherwise debilitated by other factors, such as habitat loss or parasitism. Thus, by creating environmental conditions more favorable to the Pearly-eyed thrasher, past and

current landscape-level changes in northeastern Puerto Rico have apparently amplified effects of thrasher competition and nest predation on the relict PRP population in the Luquillo Mountains (see Evans 2004, Fischer and Lindenmayer 2007). Adverse synergistic effects of nest predation and competition have also been reported for a similarly isolated small population of the Orange-breasted falcon (*Falco deiroleucus*) in Belize (Berry *et al*. 2010), as well as for native psittacines in Australia (Pell and Tidemann 1997).

For both the PRP and the thrasher alike, ectoparasitic infestations of nestlings by botfly (*Philornis pici*) larvae can cause significant pre-fledging losses, both from direct tissue damage and secondary infections (Snyder *et al*. 1987, Arendt 2000, 2006). Even when nestlings survive a heavy infestation, they are often permanently impaired due to atrophied flight musculature (Snyder *et al*. 1987, Rabuffetti and Reboreda 2007, Quiroga and Reboreda 2012). In the Luquillo Mountains, Arendt (2000, 2006) found that botfly numbers and infestation rates were positively correlated with rainfall and attendant high humidity, as also reported in Argentina (Antoniazzi *et al*. 2011). Because rainfall in the Luquillo Mountains generally increases over the course of the PRP nesting season (January-July; Figure 11), broods which hatch (and thus fledge) later in the nesting season become subject to not only increased post-fledging mortality due to rainfall (Table 3), but also potentially higher incidence of debilitating botfly infestations and attendant effects on survival, as reported also by Rabuffetti and Reboreda (2007) for Chalk-browed mockingbirds (*Mimus saturninus*). Furthermore, Streby *et al*. (2009) found that Ovenbird (*Seiurus aurocapilla*) fledglings which had been previously infested with botfly larvae had lower post-fledging survival and movement rates than non-infested individuals. It is noteworthy that during the 1990s, botfly infestations of PRP nestlings were common (Wunderle *et al*. 2003, USFWS unpubl. data) and although most nestlings treated *in situ* for infestations later fledged, post-fledging survival during that time was apparently low (Figure 9) and may have been compromised, in part, by the sublethal effects of botfly parasitism (see Streby *et al*. 2009, Quiroga and Reboreda 2012). Indeed, the restriction of the relict PRP population to the "wettest" area of Puerto Rico (Figure 1) likely exacerbates the incidence of botfly parasitism, compared to drier habitats elsewhere on the island. Merino and Potti (1996) also found that variations in rainfall affected ectoparasitic infestation rates of passerine birds in Spain. Although recent management practices for the PRP have minimized the threat of botfly infestations (see White *et al*. 2005a), constant vigilance by management personnel is

nevertheless required throughout the parrot nesting season, as occasional infestations yet occur (USFWS unpubl. data, THW pers. obs.).

Secondary Biotic Factors – Invasive Predators and Competitors

For most island-evolved species, the introduction of exotic predators and competitors constitutes a daunting ecological challenge to which they have few, if any, adaptive responses. Global biogeographic history is replete with examples of the often rapid extinction of endemic insular species by novel invasives – including humans (see, *e.g*., Olson 1989, Pimm *et al.* 1995, Steadman 1995, Fritts and Rodda 1998, Sax *et al*. 2002, Blackburn *et al*. 2004, Lugo *et al*. 2012).

Deliberately introduced to Puerto Rico in 1877, the small Indian mongoose (*Herpestes javanicus*) is a now well-established and ecologically novel mammalian predator in Puerto Rico (Pimentel 1955, Vilella 1998, Lugo *et al*. 2012). A strictly diurnal and terrestrial species, the mongoose is both an opportunistic predator and scavenger, preying on small birds, lizards and arthropods, while also feeding on fresh carrion and fallen fruits (Vilella and Zwank 1993, Vilella 1998). In the Luquillo Mountains, Vilella (1998) reported bird remains (ostensibly of *Geotrygon montana*) in 33% of mongoose stomachs sampled within the current area occupied by the PRP. Although the sampling period of Vilella (1998) also coincided with the fledging season of the PRP, he found no parrot remains in the mongooses sampled. More recently however, Engeman *et al*. (2006) reported six instances during 2000–03 in which remains (including radio-transmitters) of PRP fledglings were found inside mongoose burrows, and argued that the predatory potential of the mongoose on parrot fledglings in the Luquillo Mountains was generally underestimated. In fact, since the study of Engeman *et al*. (2006), there have been an additional 12 cases in which remains of PRP fledglings were found within mongoose burrows (USFWS unpubl. data). Like Engeman *et al*. (2006) however, we are uncertain whether such events constitute actual predation or scavenging of parrot fledglings by mongooses. Lindsey *et al*. (1994) also found remains of two PRP fledglings which had been consumed beneath a root mass, but also could not determine whether this was due to predation or scavenging, nor the species which had consumed them.

If the mongoose is terrestrial and only opportunistically predatory on birds, how might fledglings of a canopy-dwelling species such as the PRP be found in mongoose burrows? We believe a plausible explanation lies in the observed negative relationship between heavy rainfall and PRP fledgling

survival. In this study, most (61%) fledgling deaths occurred during the initial week post-fledging, particularly when accompanied by heavy (*i.e.*, >1.5x daily mean) rainfall. In such events, young naïve fledglings with wet plumage would have greater difficulty flying, feeding and thermoregulating (Erikstad and Andersen 1983, Nicoll *et al*. 2003, Boal *et al*. 2005, Glenn *et al*. 2011), thereby increasing the probability of them being encountered at or near ground-level and within the foraging zone of mongooses (see Snyder *et al*. 1987). Indeed, although reportedly "terrestrial", mongooses have been observed climbing up to 2 m above ground amongst dense tangles of branches and lianas (Engeman *et al*. 2006, THW pers. obs.). Moreover, during our study it was often necessary to "rescue" clumsy first-day parrot fledglings that had fallen to the ground (USFWS unpubl. data, THW pers. obs.), either by placing them back inside the nest, or on higher branches within the midstory strata (*i.e.*, 3-4 m agl). In a least one such case, a mongoose was observed attempting to predate a fallen PRP fledgling (H. Abreu, USFWS, pers. commun.). In all such cases however, fledglings continued to be attended to and fed by the adults, even when near ground-level. Because the ecological niche of the PRP evolved in the absence of mammalian predators, such post-fledging behaviors would only recently have become maladaptive. Accordingly, the PRP now faces an ecologically novel predation threat (Engeman *et al*. 2006). Before the introduction of mammalian predators to Puerto Rico it was quite probable that, given time, at least some fallen fledglings would have survived – a currently improbable outcome with mongoose present. Ecologically similar scenarios have been reported in New Zealand with predation of endangered Kakapo (*Strigops habroptila*), Mohua (*Mohoua ochrocephala*) and Kaka (*Nestor meridionalis*) by introduced stoats (*Mustela erminea*; Lloyd and Powlesland 1994, Elliot 1996, Wilson *et al*. 1998).

As with the mongoose, black rats (*Rattus rattus*) were also introduced to Puerto Rico, albeit inadvertently, and currently occur at very high densities in the Luquillo Mountains (Snyder *et al*. 1987, Engeman *et al*. 2006, Lugo *et al*. 2012). Like the mongoose, the black rat is an opportunistic scavenger and predator; yet unlike the mongoose, is scansorial and adept at entering tree cavities. Ample evidence exists of the detrimental effects of introduced rats on endemic insular fauna, including psittacines (*e.g.*, Atkinson 1985, Goodman 1995, Robinet *et al*. 1998, Heath *et al*. 2008). In the Luquillo Mountains, Rodriguez-Vidal (1959) attributed the loss of 25% of monitored parrot nests (4/16) to rat predation, and both Snyder *et al*. (1987) and Engeman *et al*. (2006) likewise documented episodes of rat-parrot agonistic interactions at nest cavities and attempts by rats to attack and (presumably) consume parrot

eggs and chicks. Consequently, management efforts (*e.g*., trapping, poison bait stations) were initiated at the beginning of the PRP recovery program to control this potential nest predator near active parrot nest sites (Snyder *et al*. 1987), and continue to date.

Snyder *et al*. (1987) and Engeman *et al*. (2006) also reported the widespread occurrence of feral cats (*Felis catus*) in the Luquillo Mountains, including the PRP nesting area (THW pers. observ.). The close proximity of residential and urbanized areas to the parrot nesting area (Figure 5) likely facilitates colonization of the forest by feral cats. The negative impact of feral cats on island avifauna is well-documented (*e.g*., Tideman *et al.* 1994, Smucker *et al*. 2000, Keedwell 2003, Nogales *et al*. 2004, Vázquez-Domínguez *et al.* 2004). For example, a single cat is believed to have extirpated the last population of the Stephan Island wren (*Traversia lyalli*; Fuller 2000). Amongst psittacines, the endangered kakapo (*Strigops habroptila*) in New Zealand has suffered significant losses to feral cats (Karl and Best 1982). Although Rodriguez-Vidal (1959) documented at least one incident of cat predation on a nesting adult PRP in Luquillo, we found no recent direct evidence of cat predation on parrots. However, not all causes of mortalities of wild fledglings or released parrots could be conclusively determined (Lindsey *et al*. 1994, White *et al*. 2005b), and feral cats may also have preyed on some parrots.

Introduced to the Americas during the 1600s (Goulson 2003), the honey bee (*Apis mellifera*) is a nonnative cavity-occupying species in Puerto Rico. In both their native and introduced ranges, honey bees actively compete with other cavity-using species (see Oldroyd-Benjamin *et al*. 1994, Yamashita and de Barros 1997, Goulson 2003, Pinho and Noguiera 2003, Sanz *et al*. 2003, Vaughan *et al*. 2003, Barré *et al*. 2010). Although honey bees have been present in Puerto Rico and the Luquillo Mountains for centuries (Snyder *et al*. 1987, Lugo *et al*. 2012), the widespread loss of former PRP nesting habitat and consequent restriction of the PRP to the suboptimal habitat of the upper Luquillo Mountains placed the PRP in direct competition with honey bees for the few suitable (for the PRP) existing natural cavities (see Wiley 1985, Snyder *et al*. 1987). Moreover, arrival of the more prolific and aggressive Africanized strain of honey bee in the early 1990s has exacerbated existing competition between bees and the PRP for nest cavities (Arendt 2000, USFWS 2009a). Habitat disturbances associated with recent hurricanes (*i.e*., Hugo – 1989; Georges – 1998) also apparently increased the frequency of avian nest cavity usurpations by honey bees in the Luquillo Mountains (Arendt 2000, USFWS unpubl. data). Because most swarming of honey bees occurs after

parrot chicks have fledged (Snyder *et al*. 1987, USFWS 2009a), nest cavity usurpations usually do not directly threaten active PRP nests (but see Arendt 2000 for an exception); rather, honey bee occupation renders otherwise suitable cavities unavailable for future nesting by PRPs (Wiley 1985, Snyder *et al*. 1987). For example, during the course of this study (2000-09), there were on average two PRP nests per year in which honey bees had to be removed prior to the parrot nesting season (USFWS unpubl. data). In any given year, this represents 10-17% of the total available nest sites managed for the PRP (White *et al*. 2006, USFWS unpubl. data). Thus, honey bees have been – and continue to be – a significant limiting factor to successful nesting by PRPs in the Luquillo Mountains.

Current Urbanization Trends and Long-term Impacts

The current and projected land use patterns surrounding the Luquillo Mountains offer a poor prognosis for significant ecological restoration of coastal forests in northeastern Puerto Rico, or for meaningful landscape connectivity between the Luquillo Mountains and other potentially suitable areas for the PRP. Further, most areas of northeastern Puerto Rico with potentially – and likely historically – the highest fledgling survival for PRPs (*e.g*., Canovanas, Fajardo, Ceiba; see Figs. 2, 10) have now been extensively urbanized (Figure 5). Alas, even the Mameyes Swamp – once habitat of the PRP during the time of Wetmore (1927) – has long since been irreversibly drained and filled for housing, commercial development and golf course construction.

Fahrig and Merriam (1994) reported that increased rates of landscape change concomitantly decreased the probability of regional survival of isolated populations, and predicted that if increases in dispersal capability of a species were less than the rate of surrounding landscape change, isolated regional populations would not survive, a scenario currently unfolding with isolated populations of ocelots (*Leopardus pardalis*) in southern Texas, USA (Janečka *et al*. 2011). Fischer and Lindenmayer (2007) also described cascading ecological effects on native species as result of changes in both vegetative cover and landscape connectivity. The recent extirpation of the Middle-spotted woodpecker (*Dendrocops medius*) in Sweden offers a dramatic example of how the effects of adverse environmental and demographic factors can be exacerbated by population isolation (Pettersson 1985).

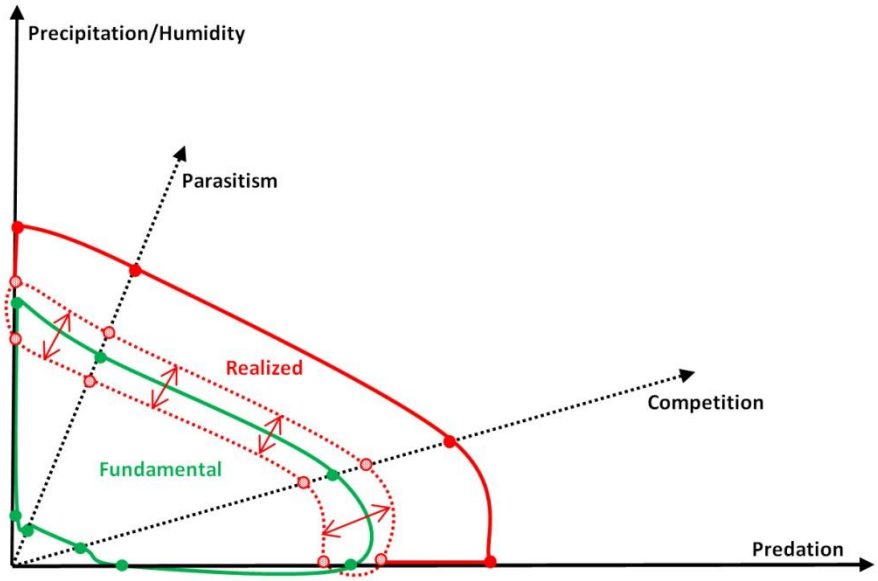

Figure 12. Schematic representation of niche shifts of the Puerto Rican parrot along four primary axes. Realized niche represents current ecological space occupied by the relict population in the Luquillo Mountains. Fundamental niche represents space in which population growth is possible. Dotted bordered area represents a dynamic realized niche boundary subject to management efforts and stochastic fluctuations along abiotic and biotic niche axes. Positive population growth occurs when niche boundaries overlap. Negative growth occurs during periods of non-overlapping niche boundaries.

The increasing urbanization of surrounding lands (Figs. 3, 5) may also further affect PRP persistence within the Luquillo Mountains in a markedly nonlinear fashion. For instance, in isolated tropical forest tracts, Laurance *et al*. (2011) reported significant biotic and abiotic effects arising from relatively small changes in surrounding land-use practices. Laurance *et al*. (2011) also found that in the case of birds, the more wide-ranging species – as are parrots – were more susceptible to adverse effects of increasing fragmentation and isolation, as also reported by Saunders *et al*. (1991) and Christiansen and Pitter (1997) and referred to as the "island effect" by Willis (1974). Indeed, in the Luquillo Mountains, recent changes in temperature and precipitation patterns have been documented and attributed, in part, to changes in the albedo of surrounding areas due to deforestation (van der Molen 2002, F. Scatena, *in litt*.). Moreover, marked increases have also been documented in the amount of airborne dust with exotic bacterial and fungal spores, including the pathogenic

fungus *Aspergillus*, arriving eastern Puerto Rico due to increased deforestation and desertification in sub-Saharan Africa (Shinn *et al*. 2000, Stallard 2001). As mentioned, respiratory infections due to *Aspergillus* have been frequent in wild PRP nestlings – particularly during periods of prolonged rainfall and attendant high humidity – and have necessitated additional management responses in order to counter them. Given the inherent ecological complexities of tropical rainforests (Odum 1970, Pounds *et al*. 1999, Ostendorf *et al*. 2001, Laurance *et al*. 2011), the long-term implications of these environmental changes for the PRP in the Luquillo Mountains remain speculative.

Species Prognosis in the Luquillo Mountains and Conservation Implications

Over the course of at least the past century, the ecological niche of the relict PRP population has experienced progressive and sustained multiaxial shifts. The ecological niche of the species has shifted and contracted along primary axes associated with precipitation, humidity, predation, competition and parasitism (Figure 12), as well as experiencing reductions in both nesting and foraging habitat diversity. These shifts have occurred as result of an inexorable "ecological cascade" which was set in motion by the rapid and extensive deforestation of Puerto Rico during the past 150 years (Brash 1987). Deforestation not only geographically and demographically isolated the PRP, but also contributed to biotic and abiotic changes in and around the Luquillo Mountains that have proven detrimental to the isolated population. Indeed, Laurance *et al*. (2012) reported that environmental changes outside tropical forest reserves also strongly affected ecological processes within such forests. From the historical trajectories of deforestation and landscape isolation processes, and concomitant and ongoing ecological responses, it is likely that the future of the PRP in the Luquillo Mountains was already determined by around 1950, indeed perhaps even earlier. By 1950, the landscape isolation of the upper Luquillo Mountains had reached its zenith (Figure 3), and the attendant long-term and time-dependent biotic responses were already becoming evident (Brash 1987, Snyder *et al*. 1987). As such, the fate of the PRP in Luquillo is consistent with and parallels that of many tropical species following extensive and sustained deforestation and habitat degradation (see, *e.g*., Willis 1974, Leck 1979, Christiansen and Pitter 1997, Brooks *et al*. 1999, Harris and Pimm 2008, Laurance *et al.* 2011). Based on our and other's findings, we believe that the PRP population in the Luquillo Mountains currently exists on a dynamic and ephemeral fringe of its fundamental

ecological niche , as clearly even a minimally positive rate of population growth is possible only with continuous intensive management and "immigration" (*i.e*., fostering/captive releases) from a source population (*i.e*., aviaries). Accordingly, the Luquillo Mountains constitute quintessential "sink" habitat (*sensu* Pulliam 1988) for the PRP. Consequently, we further posit that the PRP population in Luquillo represents the ecological paradox of a wild population whose current realized niche not only extends beyond the limits of its fundamental niche with respect to precipitation and humidity, but has also further shifted and contracted along biotic axes of predation, competition and parasitism (Figure 12; see also Holt and Gaines 1992, Dias 1996, Holt and Gomulkiewicz 2004); yet, the population persists. In the case of the PRP, how might this paradox exist, and how is it maintained?

Population persistence in sink habitats is generally thought to be maintained only by immigration from outside source populations (see, *e.g*., Pulliam 1988, Dias 1996, Holt 1996, Runge *et al*. 2006); however, to this we would also add the influence of direct conservation efforts. Such efforts (*e.g*., artificial nests, predator and parasite control) can achieve the effect of "expanding" niche space along specific axes (*e.g*., competition, predation), thereby *temporarily* allowing positive growth in sink habitats (see, *e.g*., Snyder *et al*. 1987, Beissinger *et al*. 2008). We emphasize temporarily, because in the absence of local adaptation, artificial gains in population persistence via direct interventions and "forced immigration" (*e.g*., fostering, translocations) can be maintained in sinks only as long as such efforts continue; otherwise, niche axes will again contract and negative growth resume (see, *e.g*., Westemeier *et al*. 1998, Holt *et al*. 2004, Holt 2009). In the case of the PRP, management interventions have historically shown variable degrees of success at promoting population growth (see Snyder *et al*. 1987, Beissinger *et al*. 2008, USFWS 2009a), depending upon relative strength of limiting factors and intensity of countering efforts. Accordingly, stochastic fluctuations in specific limiting factors (*e.g*., drier/wetter years, more/less thrashers) – combined with continuous management interventions – can result in realized niche boundaries periodically shifting into and out of fundamental niche space with corresponding variations in population growth (Figs. 9, 12).

Maintenance of maladapted populations in sink habitats can, over time, result in selective adaptation to sink conditions, a phenomenon often called "evolutionary rescue" (Gomulkiewicz and Holt 1995, Holt and Gomulkiewicz 1997, Holt *et al*. 2002). However, immigrants from source populations can also maintain maladaptive phenotypes in sinks if immigrants are likewise maladapted to local sink conditions, as is generally the case (see Holt and

Gaines 1992, Dias 1996, Holt and Gomulkiewicz 1997, Gomulkiewicz *et al*. 1999). With the PRP, the fostered and released parrots from the captive source population may potentially maintain stability of maladaptations to local conditions in the Luquillo Mountains. This is because selection during captive breeding – either intentionally or unintentionally – most often favors phenotypes and characteristics most adapted to captive conditions (*e.g*., docility, tractability) rather than those most adapted to the wild (see Tufto 2001, Ford 2002, Araki *et al*. 2007, Frankham 2008). Indeed, over the past decade there has been a substantial increase in captive productivity of the PRP (USFWS 2009a). Although improvements in husbandry techniques have likely played a role in increasing production, increased adaptation to captive conditions may also have been a factor. In some species, this "relaxation" of natural selection and associated reduction in wild fitness can occur rapidly. For example, Araki *et al*. (2007) reported a significant decline in salmonid (*Oncorhynchus* spp.) reproductive success in the wild after only three generations of captive breeding. Similarly, Kraaijeveld-Smit *et al*. (2006) documented erosion of predator defense behaviors in the Mallorcan midwife toad (*Alytes muletensis*) after 9 to 12 generations in captivity. By comparison, the PRP has now been captive-bred for 5–7 generations. Such declines in fitness tend to occur more rapidly in the absence of genetic infusion from outside populations (Ford 2002, Frankham 2008). With the PRP, the current "source" population (captive-reared) – which was derived directly from a subset of the relict sink population – is considered "nearly devoid of genetic diversity" (see Beissinger *et al*. 2008) and also receives recurrent migration (*i.e*., "reciprocal dispersal") from the sink population in the form of "rescued" and back-fostered nestlings (Figure 13). In such cases, relict sink populations become the major source – both past and present – of species genetic diversity, in contrast to "classical" source-sink relationships in which sink populations contribute little to the genetic future of the species (see Dias 1996, Gaggiotti and Smouse 1996). With the PRP, the back-dispersal from sink-to-source (*i.e*., wild-to-captive) has also consisted primarily of rescued nestlings which were either gravely ill or otherwise moribund (Wunderle *et al*. 2003, USFWS unpubl. data). As such, these individuals represent birds that would otherwise have died and hence, were potentially maladapted to sink conditions. These surviving rescued individuals then become part of the captive population and sources of future immigrants back to the sink population via captive releases and fostering (Figure 13). This phenotypically-skewed feedback loop may

effectively inhibit or otherwise retard local adaptation to sink conditions via perpetuation of maladaptive phenotypes (Dias 1996, Ford 2002, Lenormand 2002, Holt 2009). When captive-breeding critically-endangered species such as the PRP, this presents managers with a conservation dilemma: whether to produce the *most* individuals possible, or the *best* individuals possible (see, *e.g.*, Meretsky *et al*. 2000, 2001). In maladapted populations, however, the extinction process in the absence of counteracting immigration or other interventions can exceed the local adaptation process; particularly with highly *k*-selected species (such as psittacines) with longer generation times. In such cases, producing the most individuals possible initially provides a demographic buffer against imminent extinction whilst efforts at selective breeding attempt to unravel the more complex issues of genetic diversity and phenotypic adaptability (Meretsky *et al*. 2001, Tufto 2001, Ford 2002).

Direct interventions (*i.e.*, conservation actions) can also effectively alter time to extinction and/or adaptation for niche-restricted populations, often nonlinearly (Figure 14; see also Holt and Barfield 2008). For example, while the provisioning and intensive management of artificial nests has substantially increased nesting success of the PRP, ostensibly delaying extinction, the apparent fixation of the wild population for this reproductive trait (see White *et al*. 2006) and consequent increasing dependence on direct interventions, ironically also increases adaptation time to local sink conditions in the Luquillo Mountains by altering selection pressures on reproductive behavior. Ideally, optimal conservation actions are those that simultaneously increase time to extinction *and* decrease local adaptation time (see Figure 14). We believe that correctly identifying and implementing such optimal long-term actions remains one of the greatest challenges in the conservation of not only the PRP, but many other endangered species as well.

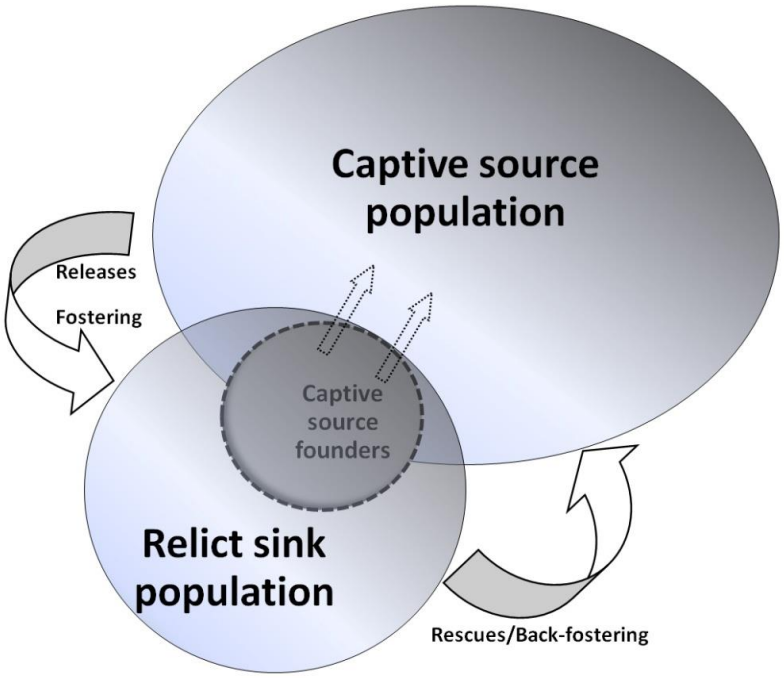

Figure 13. Schematic representation of population exchange between captive and wild populations of the Puerto Rican parrot.

The Puerto Rican parrot is not the only endemic insular species to have suffered a drastic population reduction and subsequent bottleneck following widespread environmental degradation. However, several such species have since made impressive recoveries, notably the Echo parakeet (*Psittacula eques echo*; Woolaver *et al*. 2000), Seychelles kestrel (*Falco araea*; Groombridge *et al*. 2009), Rodrigues fody (*Foudia flavicans*; Impey *et al*. 2002), Ouvéa parakeet (*Eunymphicus uvaeenis*; Barré *et al*. 2010) and the Kakerori (*Pomarea dimidiata*; Robertson *et al*. 1994). Why did these species recover rapidly from a decimated population, in some cases with minimal intervention (see, *e.g*., Groombridge *et al.* 2009), while the PRP has not? We posit that this may be due, in part, to relative differences in "niche scale". For example, the islands of Rodrigues and Ouvéa have landmasses of 109 and 130 km^2, respectively, while that of Rarotonga (home of the Kakerori) is only 67 km^2, compared to 8900 km^2 for Puerto Rico. Accordingly, the refugia of relict populations on small islands such as Rodrigues and Rarotonga comprised a greater overall proportion of the island's landmass and intrinsic environmental

heterogeneity (see Robertson *et al*. 1994, Impey *et al*. 2002, Barré *et al*. 2010), and hence likely retained a greater volume of the species' fundamental niche, than that of the PRP in the Luquillo Mountains (see Holt and Gaines 1992). Moreover, for the aforementioned species the major limiting factors were categorically few (*i.e*., predators, habitat) and later successfully remediated, either through extensive reforestation (*e.g*., Rodrigues) or effective control of predators or nest poaching (*e.g*., Rarotonga, Ouvéa). Thus, fundamental niches may have remained relatively intact and accessible for rapid reoccupancy by relict populations (a type of "quasi-ecological release") following reduction or control of key limiting factors. Had other isolated populations of the PRP persisted elsewhere on Puerto Rico (*e.g*., karst region, central mountains), it is possible that these would have benefitted from the widespread reforestation and attendant restoration of landscape heterogeneity and connectivity which has occurred in those areas over the past 60 years, and demonstrated recoveries similar to those of island species elsewhere. The observed demographic response of the newly-reintroduced PRP population in the karst forest region of northwestern Puerto Rico provides an intriguing and encouraging indicator of this potential. Parrots released in the karst region have not only attained higher post-release survival than parrots released in Luquillo, (White *et al*. 2012, PRDNER unpubl. data) but also have formed more breeding pairs than the relict population (Figure 15). Indeed, in less than five years after the initial reintroduction (2006) the number of PRP breeding pairs in the karst region had exceeded the maximum number ever recorded for the relict population since recovery efforts began (Figure 15), and with higher nesting success and fledgling survival than the relict population (Collazo *et al*. 2010, 2013; PRDNER unpubl. data) as predicted, in part, from the rainfall-fledgling survival relationship (Figure 10). A strikingly similar scenario occurred with the relict population of the endemic Lord Howe Island woodhen (*Tricholimnas sylvestris*). Limited to sink habitat on the summit of Mount Gower, the woodhen was in precipitous decline until populations were reestablished at lower, more hospitable elevations following the elimination of feral pigs (*Sus scrofa*), whose presence in the lowlands had displaced and restricted woodhens to the highest elevations on the island (Miller and Mullette 1985). In the Luquillo Mountains, however, a major portion of the PRP fundamental niche is no longer accessible, and – unlike the removal of pigs from Lord Howe Island – ongoing patterns of development in northeastern Puerto Rico will most likely render this situation permanent.

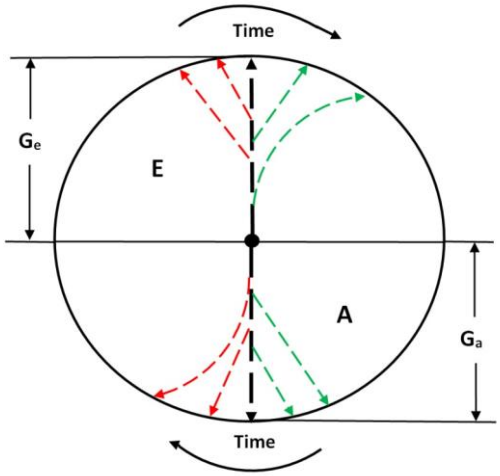

Figure 14. Extinction (hemisphere E) and adaptation (hemisphere A) processes in niche-restricted populations. Vertical opposite vectors represent generations (G) to extinction (upper) or adaptation (lower). Outer circle represents time (T) continuum. Population adapts (survives) when $G_a < G_e$. Diagonal vectors (red, green) represent conservation actions that alter – either linearly or nonlinearly – extinction or adaptation times. Green vectors represent beneficial actions which increase time to extinction while decreasing adaptation time (adaptation zone). Red vectors represent adverse actions that decrease time to extinction while increasing adaptation time (extinction zone). Earlier and continual actions proportionately alter either time to extinction and/or adaptation, respectively. Optimal outcome of actions is: $A_{A(t+i)} < A_{E(t-i)}$; where effect of action (A) on increases in adaptation time < effect on decreases in time to extinction.

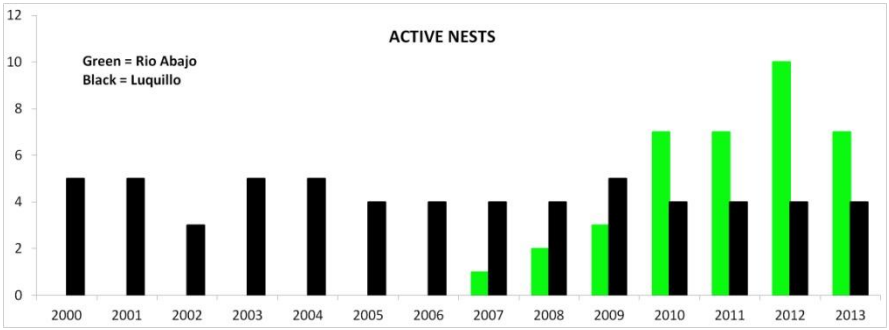

Figure 15. Total active nests of Puerto Rican parrots in the Luquillo Mountains (Luquillo) and the Rio Abajo Commonwealth Forest (Rio Abajo), 2000-2013. Parrots were reintroduced in Rio Abajo beginning in 2006.

A logical question at this point is: "If the Luquillo Mountains have always been within the range of habitats historically occupied by the PRP, how can they now be considered beyond the fringe of the species' fundamental niche"? Revisiting the concepts of ideal free distributions and the evolution of ecological niches provides some useful insights into this question. For example, with historically panmictic insular species such as the PRP, ecological niches evolved to encompass island-wide environmental heterogeneity (Holt and Gaines 1992). In this sense, the key elements are "heterogeneity" and "free access" by such species to an associated diverse array of habitat conditions. For the PRP, historically this meant access to *both* coastal and montane forests, as reported by Wetmore (1927) and Snyder *et al*. (1987). This adaptive habitat selection would have allowed the PRP to select from an array of habitats according to temporally-varying degrees of fitness, as would be associated with distinct foraging and nesting areas. In an evolutionary context, such behavioral habitat selection promotes niche conservatism (see Kawecki 1995, Peterson *et al*. 1999, Holt and Barfield 2008, Wiens *et al*. 2010). This is particularly true in species exhibiting strong natal philopatry, such as the PRP (see Snyder *et al*. 1987), as in such cases selection on reproductive success is always greater in source versus sink habitats (Holt and Gaines 1992). We have no doubt that the Luquillo Mountains have always been of value to the PRP as foraging habitat; indeed, the area contains over 65 plant species consumed year-round by the PRP (Rodríguez-Vidal 1959, Snyder *et al*. 1987, USFWS unpubl. data). However, the Luquillo Mountains are undeniably of extremely poor quality as nesting habitat. Unfortunately, land use practices in northeastern Puerto Rico have rapidly (in evolutionary time) eliminated the historical connectivity between and access to *both* high-quality foraging *and* nesting habitats, thereby relegating the relict population to completing its entire life cycle within an increasingly harsh sink habitat with attendant niche conservatism and restriction (Figure 12; see also Holt and Gomulkiewicz 2004, Holt 2009).

Collateral Endogenous Factors

The PRP population in the Luquillo Mountains has also exhibited not only a marked stasis relative to its traditional breeding area, but also an inexplicable demographic inertia in terms of breeding pairs (Snyder *et al*. 1987, Beissinger *et al*. 2008). As mentioned earlier, since 1995 all known nesting has occurred within an 8 km^2 area (Figure 1), and the number of breeding pairs has never exceeded six, regardless of changes in total population (Beissinger *et al*. 2008,

USFWS 2009a).Why are there so few breeders, and why do they consistently utilize the same limited area for nesting? We will now posit answers to these questions by considering some of the endogenous factors also affecting this niche-restricted population.

The PRP, like most psittacines, is a highly social and flocking species. For such species, flocking behavior and associated intraspecific interactions are highly adaptive in terms of habitat selection, foraging efficiency, predator avoidance, and breeding-pair formation (*e.g.*, Bayer 1982, Evans 1982, Westcott and Cockburn 1988, Danchin *et al*. 1998, South and Pruett-Jones 2000). In Cliff swallows (*Petrochelidon pyrrhonota*) for instance, selection of breeding sites is influenced by conspecific breeding performance, with sites having higher nesting success being selected more often and by more individuals (Brown *et al*. 2000), as reported also by Salinas-Melgoza *et al*. (2009) for Lilac-crowned parrots (*Amazona finschi*). Similarly, Black-billed gulls (*Larus bulleri*) also use cues from conspecifics for locating food resources (Evans 1982). With the PRP, 87.5% of successful nest sites (*i.e*., that fledge young) are re-used the following year; either by the same nesting pair or another pair (White *et al*. 2006). In fact, as of 2013 there were two nest sites (*i.e*., SF2-A, SF2-B) with over 15 years of continuous use. Moreover, PRPs also tend to select nest sites near their own natal site (Snyder *et al*. 1987, USFWS unpubl. data, THW pers. observ.), as expected in philopatric species. Thus, like Cliff swallows and Lilac-crowned parrots, PRPs apparently also use conspecific presence and breeding success (including their own) in selecting nesting areas and sites (but see Meyers 1996 for an exception). Importantly, because of management efforts, even for first-time nesters suitable nest sites are readily available within the current PRP nesting area (see White *et al*. 2006, Beissinger *et al*. 2008). For small isolated populations with no evidence of nest-site limitation, these behaviors should result in nesting areas which are highly stable over time, as individuals would have little biological incentive to colonize new areas (see Danchin *et al*. 1998). Danchin *et al*. (1998) also found that temporal autocorrelation in nest sites may vary with changes in relative quality (and breeding success) of nesting areas. Consistent with these predictions, over the course of the PRP recovery program there has been a gradual contraction in the total area used for nesting, with several former areas (*i.e*., West Fork, North Fork, East Fork; see Snyder *et al.* 1987) abandoned by the PRP over 18 years ago; in some cases much earlier. Since then, only the two adjacent valleys of South Fork and Quebrada Grande have been used for nesting. Moreover, since 2009 we have observed a further contraction in the overall nesting area, as some traditionally-used peripheral sites (*e.g*., Quebrada

Grande) have remained unused, with all known nesting activity now concentrated within <0.3 km^2 (USFWS unpubl. data). Further, once fledglings become fully vagile, individual PRP family groups occasionally leave the traditional nesting area and engage in wide-ranging extraterritorial forays to unoccupied (by PRP) areas of the Luquillo Mountains (USFWS unpubl. data). However, in all such cases sojourning birds have returned to their traditional nesting area and conspecifics prior to the next breeding season. This strong temporal autocorrelation in nesting sites further contributes to maintaining the current PRP population within the sink conditions of the upper Luquillo Mountains. Ironically, the necessary intensive management of PRP nesting cavities also plays a likely role in maintaining stability of the current nesting area by artificially increasing "habitat quality" and thereby promoting reproductive success – and site fidelity – in otherwise sink habitat.

As sink populations become smaller and more isolated, they also become increasingly subject to additional factors that manifest themselves at lower population densities. For example, in prey species, larger groups (to a point) typically experience a lower *per capita* predation rate due to risk-dilution (Courchamp *et al*. 1999, Stephens and Sutherland 1999, Caro 2005). In highly-vocal species such as primates and psittacines, larger groups also facilitate earlier detection and avoidance of predators via the "Trafalgar effect", whereby alarm calls from members nearest to a perceived threat alert more distant members in turn (see Caro 2005). As group size declines, however, these anti-predation mechanisms erode and individuals become subject to an often nonlinearly increasing predation risk (Stephens and Sutherland 1999). This phenomenon, known as the "Allee effect", encompasses a variety of situations in which fitness is reduced at low (or high) densities or below a threshold population size (*i.e.*, inverse density dependence; see, *e.g.*, Courchamp *et al*. 1999, Stephens and Sutherland 1999, Dennis 2002, Armstrong and Wittmer 2011).With the PRP, it is noteworthy that greater raptor predation on released captive-reared parrots occurred upon parrots' dispersal from the release area and resultant flock dilution (Figure 7). Indeed, captive-reared parrots preyed upon by raptors were either solitary or with only one other parrot (White *et al.* 2005b), as reported also by Lindsey *et al*. (1994) for wild PRP fledglings.

Low population not only increases *per capita* predation risk for the PRP, but also magnifies the demographic effect of predation events. For instance, the loss of even a single breeding bird to predation would represent loss of 10-17% of the entire relict breeding population in any given year, based on annual numbers of breeding pairs (*i.e.*, 3–5) over the course of this study. In the

Luquillo Mountains, the high density of predators – relative to PRP numbers – may further exacerbate predation-related Allee effects (see Courchamp *et al*. 1999). Indeed, Dennis (2002) regarded Allee effects as constituting yet another form of "extinction vortex" (*sensu* Gilpin and Soulé 1986).

Mate selection and reproductive efforts can also be disrupted by Allee effects. For example, populations of the Kakapo – the world's largest psittacine – experience decreased probability of finding suitable mates at low population densities, as well as biased sex-ratios due to demographic stochasticity (Courchamp *et al*. 1999). Moreover, individual groups of the cooperative-breeding African wild dog (*Lycaon pictus*) experience higher pup mortality and face greater risk of extinction once group size falls below a critical threshold level (Somers *et al*. 2008). In psittacines, little is currently known of how complex social interactions may be affected by low population densities (Beissinger *et al*. 2008). However, in the isolated PRP relict population, low numbers coupled with innate inbreeding avoidance mechanisms (see Pusey and Wolf 1996) may inherently limit options for optimal mate choice in this monogamous species. PRPs, like most psittacines, have individually-distinguishable vocalizations (Snyder *et al*. 1987) which they may use to identify closely-related individuals (Beissinger *et al*. 2008). Beissinger *et al*. (2008) suggested that environmental factors rather than inbreeding avoidance most likely influenced breeding effort in the PRP, based on increased reproduction and population growth following hurricane Hugo in 1989. However, this demographic response did not occur following hurricane Georges (1998; see Figure 9). Regardless, even if so, for a population of a *k*-selected species to be dependent upon infrequent stochastic events for population growth would imply serious maladaptation to local environmental conditions. Beissinger *et al*. (2008) also argued that the rapid replacement of mates by PRPs following loss contradicted evidence that inbreeding avoidance influenced numbers of breeding pairs. However, this assertion is based on the assumption that PRPs correctly recognize closely-related potential mates. Over the course of at least the past two decades, however, fostering of captive-produced eggs and nestlings to wild nests, and cross-fostering of eggs and nestlings amongst wild nests has been regularly employed to maximize nest productivity (Wunderle *et al*. 2003, USFWS 2009a). Inbreeding avoidance based on kin recognition (see, *e.g*., Holmes and Sherman 1983, Barnard and Fitzsimons 1988, Price 1999) is effectively undermined in such case, as nestlings are often reared with unrelated nest-mates (whom they perceive as related), while siblings may fledge from different nests, and later be perceived as unrelated and acceptable as mates. Thus, in the PRP, "inbreeding

avoidance" may indeed limit optimal mate selection in some cases; while in others fail to deter suboptimal pairings. Recent cases of low hatchability (Beissinger *et al*. 2008) and infertile pairs (USFWS unpubl. data) suggest that this is occurring.

To date, the most compelling evidence of a demographic Allee effect restricting breeding efforts in the Luquillo population is the demographic response of the newly-reintroduced PRP population in the karst region. As we have seen, in the Luquillo Mountains the total PRP population has never exceeded 50 individuals since the beginning of recovery efforts, and there have never been more than six breeding pairs in any given year. However, during the previous (2012) breeding season there were 10 pairs of PRPs nesting in the karst population, compared to only four in Luquillo (Figure 15). Why the dramatic difference in breeding effort between the Luquillo and karst populations? We believe a plausible answer lies in the concept of a "threshold population" or critical density, below which intraspecific interactions such as pair-formation are disrupted or inhibited (McCarthy 1997). Also known as "social facilitation", this phenomenon has been documented in numerous social species (see, *e.g*., Courchamp *et al*.1999, Waas *et al*. 2000, Somers *et al*. 2008). In the case of the PRP, the karst region reintroduction took place on the grounds of one of the two captive-rearing facilities for the species (USFWS 2009a). At that site, there are currently (2013) over 150 captive PRPs (R. Valentin, PRDNER, pers. commun.) housed in outdoor cages immediately adjacent to the release site. To date, a total of 108 captive-reared parrots have been released, of which 50–55 have formed a resident flock centered at the aviary (PRDNER unpubl. data). Released parrots freely fly throughout the aviary grounds, and there is substantial visual and vocal contact between released and captive birds. Consequently, the *total number* of PRPs interacting in this "flock" is around 200–205 (Figure 16), including the captive population and the released birds and their offspring. Thus, we hypothesize that this number (or density) of PRPs surpasses an inherent social threshold that stimulates increased pair formation and resultant breeding efforts. Because the released parrots cannot actually mate with the captive population, the mechanism is apparently social, rather than merely a function of increased availability of potential mates. We do not know the magnitude of such a threshold, but it would appear to be at least >50, based on history of the Luquillo population. Of course, an alternative hypothesis would be that greater breeding effort by the karst population is due to site-specific environmental factors (see Beissinger *et al.* 2008, Whitehead *et al.* 2012). Indeed, there are substantial differences between the Luquillo Mountains and the karst region

both in climate and the biotic factors which impinge upon PRP population growth (see Trujillo 2005). If this alternative is true, then it would also be consistent with our earlier hypothesis of a "quasi-ecological release" in recovering niche-restricted populations, and constitute further evidence of niche restriction and conservatism in the relict Luquillo population.

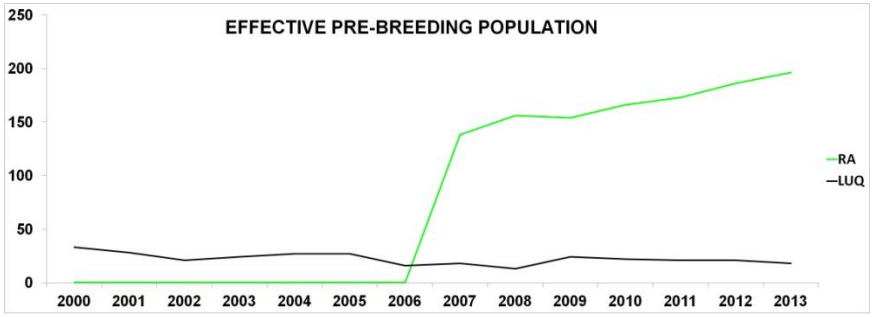

Figure 16. Effective pre-breeding population of free-flying Puerto Rican parrots in the Luquillo Mountains (LUQ) and the Rio Abajo Commonwealth Forest (RA), 2000-2013. Parrots were reintroduced in Rio Abajo beginning in 2006. Total population for Rio Abajo also includes individuals held in the captive breeding facility where all reintroduced parrots were released.

CONCLUSION

Conservation strategies

Given our findings, what should – or even can – be done regarding the Luquillo population of the Puerto Rican parrot? The scientific evidence suggests that without continued management interventions the wild PRP population in the Luquillo Mountains would soon decline to extinction. Based on current population size and the historical population trajectory prior to recovery efforts (Figure 4), local extinction could likely occur within 15–20 years following cessation of supportive efforts. Indeed, such an outcome could occur even with supportive efforts due to stochastic events such as hurricanes or a novel pathogen. Thus, managers' current overarching strategy is in accord with Beissinger *et al*. (2008) in that for the Luquillo wild population to be maintained – albeit tenuously – continued intensive management and "immigration" from the captive population will be necessary despite potential maintenance of stable maladaptations (see Holt and Gomulkiewicz 1997,

Lenormand 2002, Holt *et al*. 2004). The risk of extinction from stochastic factors (environmental and demographic) is simply too great at the present time to curtail management interventions or population supplementations (see Lande 1993, Beissinger *et al.* 2008).

Cognizant of the factors contributing to this ecological reality, managers have adopted some additional short- and long-term strategies, based on our research and current literature and expertise, which could maximize persistence and ecological value of the relict population. First, the practice of cross-fostering eggs and chicks *among* wild nests is now to be avoided, and used only as a temporary emergency measure to prevent imminent loss of an active nest. Allowing wild siblings to fledge from different nests may eventually (if not already) erode innate inbreeding avoidance mechanisms with consequent adverse effects on population fitness. However, fostering from the captive population to maximize nest success in the wild will continue, and careful evaluation of the known PRP pedigree is being used to select the most genetically appropriate individuals possible for fostering into wild nests. Because fledgling survival is not affected by brood size, maximizing individual nest productivity in the wild via fostering will continue to be a tactical management priority, as recommended by Beissinger *et al*. (2008).

Beissinger *et al.* (2008) also recommended capturing one member of infertile or otherwise poorly-productive wild pairs and moving them to captivity, ostensibly to promote re-pairing of the remaining bird with a presumably less-related mate. However, this approach has some potential flaws. Decades of captive breeding of the PRP have shown that reproductive problems are not limited to genetic incompatibility, and can also result from physiological factors such as poorly-developed testes or ovaries, and even behavioral idiosyncrasies. In such cases, capturing one member of a reproductively dysfunctional pair yields a 0.5 probability of removing the "defective" individual, and with no assurance that subsequent mate replacement will result in a more genetically-optimal pairing. An alternative strategy, however, has already proven successful in practice. For example, during the past six nesting seasons (2008-2013) there have been two infertile pairs of wild PRPs. One pair consisted of a previously productive female which, following mate replacement in 2009, thereafter produced only infertile eggs. Another pair which began nesting in 2008 was consistently infertile until 2012, when they unexpectedly produced – and fledged – three of their own chicks. However, rather than removal to captivity, these infertile pairs were used to foster fertile eggs to the wild from the captive population. In fact, these pairs successfully fledged a total of 18 chicks – and thus contributed

demographically – to the wild population during their infertile nesting seasons. This strategy also avoids unnecessary capture-related risks, does not disrupt nesting efforts, does not numerically reduce the total wild population, and most importantly, avoids potential reduction in the number of breeding pairs in any given season. Moreover, this strategy also provides unique opportunities for slowing loss of genetic diversity in the wild population through selective fostering.

A remaining unknown in the ecology and management of the PRP is to what extent inbreeding depression and genetic drift may have affected adaptive plasticity relative to rapidly changing niche dimensions (see Both *et al*. 2006, Salinas-Melgoza *et al*. 2013). Based on a recent (2008) pedigree analysis of the captive PRP population (Schloss *et al*. 2008), mean kinship was 0.13, indicating that the average relatedness of any two captive individuals is equivalent to half-siblings. Because the captive population was derived from the relict wild population, and because of the continuous exchange of individuals between captive and wild populations (Figure 13), it is reasonable to assume that similar – if not greater – kinship exists in the wild population. To date however, there have been no comprehensive genetic analyses at the molecular level that could provide a quantitative and reliable assessment of current genetic diversity in the relict population (but see Brock and White 1992). Loss of genetic diversity and coadapted gene complexes can adversely affect immunological responses to pathogens and parasites, reproductive success, and behavioral and phenotypical adaptations to novel challenges and changing environmental conditions (Lande and Shannon 1996, Westemier *et al*. 1998, Bijlsma *et al*. 2000, Keller *et al*. 2002, Keller and Waller 2002, Armbruster and Reed 2005). Moreover, the effects of inbreeding depression are usually more pronounced in populations inhabiting stressful environments (see Armbruster and Reed 2005), such as the PRP in the Luquillo Mountains. Accordingly, inbreeding depression may have played an as yet undetermined role in amplifying deleterious effects of niche restriction on the relict PRP population. Thus, comprehensive molecular genetic analyses of the PRP are being considered to not only rigorously assess current genetic composition and attendant fitness implications, but also to aid in more effective genetic management of the captive PRP population, as also suggested by Schloss *et al*. (2008). Comparison of contemporary genetic analyses with samples from museum specimens of the PRP could also reveal the extent of any isolation and bottleneck-related genetic erosion in the relict population (see Tracy and Jamieson 2011).

There will eventually come a time at which a fundamental decision will be required of managers and policy-makers regarding the direction of overall species recovery efforts relative to the relict population. Time is a critical parameter in the extinction process, and future efforts to reestablish additional wild populations elsewhere in Puerto Rico will require yet additional time and resources (Beissinger *et al*. 2008, USFWS 2009a). A second incipient wild breeding population has now been established, and plans for yet a third such population are now underway (USFWS 2009a, White *et al*. 2010). Indeed, a key criterion for delisting the species is the establishment of at least "three interacting populations" in the wild (see USFWS 2009a). Based on our findings however, the potential for meaningful interaction between the Luquillo population and populations elsewhere in Puerto Rico (*e.g*., karst region) is virtually nonexistent under current and projected regional land use patterns. This is because populations of non-migratory philopatric species with strong conspecific attraction tend to expand spatially via a diffusion process, rather than through long-range dispersal of propagules (Howard 1960, Caughley 1978); a process effectively impeded by the current landscape of northeastern Puerto Rico (see Sutherland *et al*. 2000). In practical terms, this will require existence of least *four* populations (including Luquillo) to meet the stated species recovery objective. Thus, given that the Luquillo population will most likely remain isolated in sink habitat with the attendant ecological consequences, how might such a population best contribute to overall species recovery?

Managers believe the long-term ecological and evolutionary value of the relict population can best be maximized via a strategic two-level process. For example, although captive and wild PRPs share most – if not all – genetic attributes, these two groups are nevertheless qualitatively dissimilar in terms of behavior and vocalizations, with wild parrots having a complex range of vocalizations far exceeding that of the captive population (Snyder *et al*. 1987, THW pers. observ.). This is not surprising, given the far less complex and less challenging captive environment. Nevertheless, over the course of releasing captive-reared PRPs to the wild, observations indicate a gradual convergence by released parrots to behaviors and vocalizations consistent with (at least to human observers) the wild population. The successful breeding between released and wild parrots (see White *et al.* 2005b, Beissinger *et al*. 2008) is indeed evidence of functional convergence and attendant cultural transmission of behavior and survival skills from wild to captive-reared birds. Not unknown in psittacines, vocal or behavioral convergence by individuals introduced into a new population or social group has also been documented in Budgerigars

(*Melopsittacus undulates*; Hile and Striedter 2000), Ringneck parrots (*Barnardius zonarius*; Baker 2000), and Yellow-naped parrots (*Amazona auropalliata*; Wright 1996). Accordingly, the relict wild PRP population constitutes an invaluable "ethological template" through which species-specific wild behaviors are culturally transmitted to fostered and released captive-reared parrots and hence, preserved and perpetuated. Thus, maintaining the current relict population and its ethological attributes via active management and the fostering and release of captive-reared parrots is the logical first level of a longer-term strategy. In the near term, this approach also provides valuable opportunities for testing novel experimental techniques and strategies for releasing captive-reared parrots. Such techniques may prove useful for establishing and managing future populations of PRPs elsewhere in Puerto Rico, as well as those of other psittacines for which reintroductions or supplementations are contemplated. As an example, since 2008 experimental "precision releases" of small groups (*i.e.*, 2–3) of subadult captive-reared parrots have been conducted at wild nest sites immediately upon fledging of the last chick. Results to date have been encouraging, with higher post-release survival than previous "traditional" releases (*e.g.*, White *et al.* 2005b) and with immediate interactions between wild and captive-reared birds (USFWS unpubl. data).

The process of reestablishing additional populations of PRPs is currently limited to only captive-reared birds as founders (USFWS 2009a), and will likely continue to be so for the foreseeable future. However, unlike captive-reared parrots released or fostered into the relict population, parrots in reestablished populations (*e.g.*, karst region) have no direct exposure to wild birds, nor opportunities for cultural acquisition of species-specific wild behaviors. If the ultimate goal of PRP population reestablishment is "species" conservation, then this includes not only genetic but also phenotypic aspects such as wild behaviors (see Meretsky *et al.* 2001). So, if captive-reared founders have no contact with wild conspecifics, how might wild behavioral traits be instilled into such populations? Managers believe this may be accomplished through strategic translocations from the relict wild population to newly-established populations elsewhere on the island. However, this recommendation is not without important caveats.

First, to maximize the probability that wild behaviors will ultimately be retained by translocated individuals, managers intend to translocate intact breeding pairs, as opposed to juveniles or adult singletons. Releasing random individual wild birds into populations comprised entirely of captive-produced birds may result in a reversal of the previously observed didactic gradient (*i.e.*,

wild-to-captive), with behavioral convergence by wild individuals to that of the recipient population (see Baker 2000, Salinas-Melgoza *et al*. 2013). Importantly however, Baker (2000) and Bradbury *et al*. (2001) found that psittacine flight calls serve to coordinate movements of mated pairs. If so, then wild breeding pairs should maintain their original wild flight calls following translocation. Because behavioral convergence is driven largely by social factors (Hile and Striedter 2000, Bradbury *et al*. 2001, Salinas-Melgoza *et al*. 2013), interjection of intact breeding pairs may thus minimize social pressure for convergence by wild birds, and increase the potential for cultural transmission to the recipient population of desired behaviors such as wild vocalizations. Importantly, any offspring subsequently produced by the translocated wild pair would also learn appropriate species-specific behaviors from wild parents, further perpetuating such behaviors. Obviously, although no one can guarantee that cultural transmission of wild behaviors to captive-produced birds will occur following translocations, it is certain that cultural transmission will *not* occur *without* such translocations.

We do not yet understand the adaptive significance of the complex vocal repertoire or subtle behavioral nuances of the relict wild PRP population. However, given the evident harshness of sink conditions within the Luquillo Mountains, selection on adaptive behavioral attributes may be substantial (see Kawecki 1995). Faced with this uncertainty, managers aim to preserve as much as possible of the species' innate "biological culture" and avoid complete loss of the last wild population of the species. In the words of Leopold (1949): "To keep every cog and wheel is the first precaution of intelligent tinkering".

Because of the demographic fragility of the relict wild population, "harvesting" of breeding pairs for translocations would most likely further jeopardize population persistence (see Beissinger *et al*. 2008). Accordingly, barring unforeseen catastrophes, translocations from the relict population are not anticipated until such time as three additional *breeding* populations (including the current karst population) have been established outside the Luquillo Mountains. At such time, the requisite number of spatially-distinct populations will exist to meet species recovery objectives (USFWS 2009a), even in the event of loss of the Luquillo population. Using the last remnants of the relict wild PRP population to "seed" populations established at more ecologically-benign sites in Puerto Rico would constitute the most optimal use of this invaluable ecological and evolutionary resource, and provide the most likely means by which wild phenotypes can be perpetuated outside the Luquillo Mountains.

From a practical perspective, the challenges to preventing the extinction of species for which no wild populations remain are daunting and well-documented (see, *e.g*., Frankham 2008). Once limited to only captive-reared individuals, species recovery efforts become far more ecologically complicated, lengthy, costly and with fewer management options. For example, recovery efforts for the critically-endangered Ἀlalā (*Corvus hawaiinensis*) are hampered by lack of a wild population into which captive-reared individuals can be released, or from which additional genotypes can be drawn to invigorate the captive-breeding program (USFWS 2009b). Loss of the last wild Ἀlalā occurred in 2002, and future attempts to reestablish "wild" populations of Ἀlalā now face the inherent and significant challenges of releasing only captive-adapted individuals into unoccupied habitat (see Tufto 2001, Frankham 2008). Meanwhile, the small captive population remains highly vulnerable to stochastic environmental, demographic and genetic events (USFWS 2009b), as do the remaining captive individuals of the Spix's macaw (*Cyanopsitta spixii*; ICMBIO 2012). Burger and Hemmer (2006) similarly described the urgent conservation status of the last remaining captive individuals of the Barbary lion (*Pantera leo leo*), which became extinct in the wild over 70 years ago, and whose relict lineage in captivity is now also in danger of disappearing.

Managers have at times been asked: "Why not simply release enough parrots to establish a population at some lower (*i.e.*, ostensibly "drier") elevation within the Luquillo Mountains"? After careful consideration of this option, managers concluded that establishing another population within the Luquillo Mountains would only be meritorious if its population growth rate exceeds rates at alternative release sites throughout the island. However, Collazo *et al*. (2013) did not find support for this option after evaluating alternative reintroduction strategies. Moreover, establishing a "satellite population" elsewhere within the Luquillo Mountains (assuming enough birds could be released and subsequently survive and breed) would only minimally address – if at all – one axis of niche restriction, that of precipitation, which at any point within the Luquillo Mountains still exceeds that of virtually anywhere else on the island (see Figure 1). Meanwhile, the remaining limiting factors (*e.g*., hurricane vulnerability, raptors, thrashers) would nevertheless continue to synergistically restrict population growth. In fact, from analyses of factors promoting reintroduction success in psittacines, White *et al*. (2012) found that predation and habitat quality were the two most important factors governing success, and reintroductions at sites with high predation threat and low habitat quality (*e.g*., Luquillo Mountains) were highly unlikely to succeed.

Finally, as alluded to previously, releasing enough parrots to overcome initial Allee effects (see Armstrong and Wittmer 2011) and establish yet another tenuous population in the sink habitat of the Luquillo Mountains would divert critical resources – both biological and financial – away from ongoing and future efforts to establish and secure ecologically essential additional populations elsewhere on the island (see Wiley *et al.* 2004, Beissinger *et al.* 2008, USFWS 2009a).

Concluding Remarks

Our findings are at once foreboding and encouraging. They are foreboding in that with current and increasing rates of habitat loss and degradation coupled with global climate change, it is certain that more species – especially those that are inherently rare, endemic or already endangered – will experience future niche shifts and restrictions and the attendant deleterious effects on fitness and population persistence (see, *e.g.*, Brooks *et al.* 1997, Hilbert *et al.* 2004, Şekercioğlu *et al.* 2012, Wiens *et al.* 2012, Foden *et al.* 2013). In fact, during only the course of this study (2000-09) there was a 71% and 86% increase in the number of species worldwide in the categories of Critically Endangered and Endangered, respectively (IUCN 2009). Thus, like Mace and Purvis (2008), we encourage conservationists and policy-makers to adopt a conceptually and analytically comprehensive niche-based approach for accurately identifying the ultimate causes of a species' endangerment, and thereby develop more effective conservation measures consistent with species-specific ecological and evolutionary realities. Otherwise, efforts to prevent extinctions can become analogous to placing a bandage on a carcinoma; that is, treating the evident symptoms without addressing more serious underlying issues. However, our findings are also encouraging because they further demonstrate that anthropogenic extinctions are preventable and, given sufficient resources, it is indeed possible to maintain a wild population of a critically-endangered species beyond its fundamental niche for an extended period, effectively providing more of what is increasingly becoming the most valuable resource of all in preventing species extinctions: time.

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