How to save the rarest Darwin's finch from extinction: the mangrove finch on Isabela Island

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Habitat destruction and predation by invasive alien species has led to the disappearance of several island populations of Darwin's finches but to date none of the 13 recognized species have gone extinct. However, driven by rapid economic growth in the Galápagos, the effects of introduced species have accelerated and severely threatened these iconic birds. The critically endangered mangrove finch (*Camarhynchus heliobates*) is now confined to three small mangroves on Isabela Island. During 2006–2009, we assessed its population status and monitored nesting success, both before and after rat poisoning. Population size was estimated at around only 100 birds for the two main breeding sites, with possibly 5–10 birds surviving at a third mangrove. Before rat control, 54 per cent of nests during incubation phase were predated with only 18 per cent of nests producing fledglings. Post-rat control, nest predation during the incubation phase fell to 30 per cent with 37 per cent of nests producing fledglings. During the nestling phase, infestation by larvae of the introduced parasitic fly (*Philornis downsi*) caused 14 per cent additional mortality. Using population viability analysis, we simulated the probability of population persistence under various scenarios of control and showed that with effective management of these invasive species, mangrove finch populations should start to recover.

Keywords: *Camarhynchus heliobates*; Galápagos; *Philornis*; population monitoring; population viability analysis; rat control

1. INTRODUCTION

Owing to their remote location, late colonization by humans and early conservation effort, the Galápagos still retain an almost intact original biodiversity (Bensted-Smith 2002). Anthropogenic activity has shaped Galápagos and its ecosystems during the past three centuries. The clearing of vegetation for agriculture, alongside the early removal of tortoises, introduction of goats and pigs for food, as well as the accidental release of invasive species have seriously affected native ecosystems, particularly those in the humid highlands (Stewart 1915; MacFarland *et al.* 1974; Campbell *et al.* 2004; Watson *et al.* 2010). However, more recently, drastic ecological change has been fuelled by the rise in tourism (from 40 000 in 1990 to over 145 000 in 2007; Watkins & Cruz 2007). Increased financial flow into the community

promotes unregulated growth and a high standard of living, making the islands attractive to immigrants from the Ecuadorian mainland: the local population has been increasing by 4 per cent every year (Watkins & Cruz 2007). The resulting decrease in isolation of the islands as a whole and increase in inter-island connectivity (Grenier 2000) favour the arrival and spread of exotic species. By 2006, more than 500 introduced animal and 700 plant species were recorded, of which 114 taxa were considered invasive and capable of causing severe impacts on the native biodiversity (Snell *et al.* 2002; Causton *et al.* 2006; Jiménez-Uzcátegui *et al.* 2007; Tye 2007). Introduced plant species now outnumber native ones, and 180 of the 500 native plant species on the islands are on the IUCN Red List of Threatened Species. Largely owing to the imminent threats posed by invasives, in 2007 the Galápagos were listed as a 'worldwide heritage in danger'.

Compared with other Pacific Islands, land bird communities in Galápagos have remained remarkably unaltered. However, on some islands such as Floreana

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(which has the longest settlement history), humans may have brought about the extinction of the island's large ground finch (*Geospiza magnirostris*), warbler finch (*Certhidea fusca*) and Floreana mockingbird (*Mimus trifasciatus*) (Grant *et al.* 2005), in addition to several reptile and plant species (Steadman 1986; Tye 2007). More recently, the medium tree finch (*Camarhynchus pauper*), a single island endemic also on Floreana, now qualifies as critically endangered, most probably due to rat predation but also from parasitism by the introduced dipteran *Philornis downsi* (O'Connor *et al.* in press). This fly was introduced into the islands in the 1960s (Causton *et al.* 2006) and is now on 11 islands across the archipelago (Wiedenfeld *et al.* 2007; B. Fessl 2008, unpublished data). Flies lay their eggs in nests with bird chicks, and the blood-sucking larvae cause reduced fledgling weights, anaemia and tissue damage, often leading to death and bill deformations that persist into adulthood (Dudaniec *et al.* 2006, 2007; Fessl *et al.* 2006; Galligan & Kleindorfer 2010). Rats and flies have also been implicated in the local extinction of the Floreana warbler finch (Grant *et al.* 2005).

The rarest of the Darwin's finches, the mangrove finch (*Camarhynchus heliobates*) (Hirschfeld 2008), originally occurred on Isabela and Fernandina Islands but has now disappeared from the latter (Grant & Grant 1997; Dvorak *et al.* 2004). Historically recorded in five mangrove forests on Isabela (including one close to the coastal village of Puerto Villamil), the species is now largely confined to two small habitat patches on the northwest coast of the island, with a very small number of birds in a southeastern coastal site (Bahía Carthago (BC); Dvorak *et al.* 2004). Exact causes for the reduction of the mangrove finch's range are unknown, but predation by black rats, cats (*Felis catus*), smooth-billed ani (*Crotophaga ani*), and insects such as *P. downsi*, the fire ant (*Solenopsis geminata*) and paper wasp (*Polistes versicolor*) have been implicated (Grant & Grant 1997; Dvorak *et al.* 2004). There is evidence that parasites, and in particular *P. downsi*, are paramount threats to the survival of the mangrove finch and other components of Galápagos' bird fauna (Wikelski *et al.* 2004).

While mangrove finches may never have been very abundant given the restricted occurrence of mangroves in Galápagos (Wium-Andersen & Hamann 1986), the size of the species' global population is thought to have fallen to a perilous level, with estimates ranging from 30 to 380 birds (Grant & Grant 1997; Dvorak *et al.* 2004). Given the observed declines in the species, including the disappearance of the Fernandina population, as well as the paucity of reliable population estimates, there was an urgent need to evaluate the species' actual population status and assess impacts of invasive predators. Here, we present results of the most systematic estimation of mangrove finch numbers to date, as well as data on nesting success in a large sample of finch nests both before and after rat control. Finally, by conducting population viability analysis (PVA), we simulated population trajectories under various scenarios of rat and *P. downsi* control, providing evidence that these interventions are viable management options to rapidly improve the survival prospects of the rarest Darwin's finch.

2. MATERIAL AND METHODS

(a) Study sites

We studied mangrove finch populations in the two main areas where the species occurs, Caleta Black (CB; 00°12' S, 91°23' W) and Playa Tortuga Negra (PTN; 00°14' S, 91°23' W) on the west coast of Isabela Island and in BC (00°41' S, 90°50' W) 70 km to the southeast (figure 1). CB is a 10 ha (500 × 300 m) dense red (*Rhizophora mangle*) and white (*Laguncularia racemosa*) mangrove stand, bordered by a beach to the west (distance to sea: 60–100 m), and surrounded by bare lava fields on the other sides. In most parts, the soil is always saturated with sea water. PTN to the south of CB is divided into a northern (PTN-B) and a southern block (PTN-A) of mangrove forest. PTN-B (approx. 5 ha) is a 250 m area of white and red mangrove stands bordered by beach and lava to the south. The northern and eastern sections are delimited by spiny shrub vegetation (*Scutia spicata*, family Rhamnaceae), and bare lava fields. PTN-A is an elongated mangrove patch (670 × 300 m, 15 ha) of red, white and black (*Avicennia germinans*) mangroves, of which 1.7 ha are lagoons. A beach (30–100 m wide) separates the forest from the sea in the west; the rest is surrounded by bare lava field, with *Scutia* vegetation along some parts of the eastern side.

Although separated from the sea by a beach, both mangrove finch sites are inundated on high tides. Plant debris (fallen leaves and timber) cannot be removed and therefore builds up on the forest floor, a phenomenon which is largely unknown for other mangrove forest sites. Three smaller mangrove patches (1.5–3.8 ha)—separated from the sea by a beach—also occur between the two main mangrove finch sites. We used the central one, Selvita (3.8 ha), a dense red and white mangrove stand, as a control site for rat monitoring and artificial nest trials (figure 1).

BC, a historical mangrove finch site (Dvorak *et al.* 2004), consists of various patches of mangroves totalling approximately 300 ha. Few singing male mangrove finches were encountered in the late 1990s (Dvorak *et al.* 2004). Mangrove stands consist mainly of white and red mangroves mostly connected to the sea. This finch population was included in our simulations.

(b) Mangrove finch population estimation

Territory mapping and distance sampling of mangrove finches in PTN and CB were undertaken during the birds' breeding season (December–April) every year from 2006–2009. We also conducted intensive searches for finches in mangroves in BC in February 2008 and 2009. A sound lure was broadcast for 5 min between 06.00–11.00 and 15.00–18.00 from points spaced 100 m apart at the edge of the mangrove.

At PTN and CB, transects approximately 50 m apart were partially cleared to allow access into the dense mangrove (former study). A total of 37 transects were used during the 2006/2007 season. In 2008/2009, another 12 transects (five in PTN and seven in CB) were cleared to improve nest searching and for placement of additional point counts. Observations

Figure 1. Map showing the main breeding population in CB and PTN (A + B) and the position of BC. Selvita was used as a control area for rat monitoring and artificial nest trials.

were carried out between 06.00 and 12.00 by walking along transects. Any mangrove finch sighted or heard singing was recorded on a map (prepared with Garmin global positioning system map 60CSx and ArcViewGIS). Plumage, colour, sex and singing pattern were also recorded.

In 2006/2007, territories were mapped by B.F. three times in PTN-A and PTN-B (December–February) and twice in CB (January, February). During 2007/2008, both sites were mapped three times (January, March–B.F., February–M.D.), and twice in 2008/2009 (January–B.F., February–M.D.) as song intensity ceased in March after a heavy storm destroyed active nests and many large trees. The onset of heavy rains, which triggers reproduction in the species, varied between years and was responsible for deviation in dates when birds could be counted. Data were interpreted following rules in Bibby *et al.* (2000) for inferring territory boundaries.

Distance sampling was performed in each of the three study seasons at 16 points in CB and 32 in PTN. All points, located along transects at least 40 m from the forest's edge, were separated by a minimum distance of 50 m between points. Each point was surveyed once in 2006/2007 (February), twice in 2007/2008 (January, March) and once in 2008/2009

(January) by a single observer (B.F.) between 06.00 and 12.00. After arriving at a point, the observer waited for 5 min before starting a count of 7 min. This period was considered by the observer to be the optimal length of time to ensure that all finches near to the point were recorded, and to provide a 'snapshot' of the number of finches around the point. The distance to each mangrove finch observed or heard was estimated and the individual's sex noted. In order to minimize bias in the estimation of distances, a second band was fixed in 10 m distance, and the observer conducted a short training session on distance estimation in the study sites before the start of each survey session.

Mangrove finch population size and density was estimated using DISTANCE 5.0 (Thomas *et al.* 2006). Radial distance data from the point counts were examined using a histogram of 20 intervals of equal width, to explore the data for any potential movement towards or away from the observer or rounding of distances to favoured values (e.g. 10 or 20 m). There was no evidence of either of these phenomena and thus distance data were analysed as ungrouped. Distance data were right-truncated to remove the largest 10 per cent of distances following the guidelines of Buckland *et al.* (2001). To allow for highly different

detection probabilities of male and female finches, multiple covariate distance sampling analysis was performed. According to the lowest Akaike information criterion (AIC) value, the half normal model was fitted to the distance data with sex as a factor covariate. Including this factor covariate into the analysis allows the detection probability to be modelled as a function of sex as well as distance. This was considered the optimal approach rather than estimating singing male density alone, as we did not want to make assumptions about sex ratio in order to estimate total population size. The global density estimate was post-stratified by year to derive annual population density and size estimates, and then by year and site in order to generate annual estimates for PTN and CB individually.

(c) *Evaluation of rat control efficacy*

To evaluate the efficacy of a rat control programme, we conducted live-trapping in PTN-A to estimate relative abundance of rats before and after poison was deployed. We trapped rats in November 2007, January, April and September 2008, in a 3 ha area of PTN-A using a 5×5 grid with 30 m spacing between traps ($41 \times 13 \times 13$ cm Tomahawk traps; Deluxe Single Door Chipmunk/Rat Live Traps). Traps were opened for three consecutive nights and checked each morning and late afternoon. We also trapped rats in Selvita, where no rat poisoning took place, to serve as a control. However, owing to logistical constraints, we were only able to carry out live trapping at this site once in November 2007. In Selvita, we were unable to cut transects through the mangrove and so 26 traps were deployed along a line 5 m from the edge of the mangrove, and arranged in 13 pairs each 30 m apart. Rats caught in live traps in PTN-A were killed, but released in Selvita after being marked by a numbered ear clip. We used a mixture of peanut butter and oat flour wrapped in wax paper as bait in the traps.

In late November 2007, after the rat trapping and artificial nest trials, permanent poison bait stations made from polyvinyl chloride piping (10 cm diameter; around 30 cm height) were placed on the ground or on trunks in an upright position every 50 m along transects, and along the mangrove edge in PTN-A ($n = 87$ bait stations), PTN-B ($n = 41$) and CB ($n = 89$). Rats can easily climb into the bait stations but they were inaccessible to birds. Each bait station contained 50 Klerat wax cubes (1 kg of the product contains 0.05 g brodifacoum). The poison cubes were secured so that they could not be carried away by rats. Bait stations were checked every month or two and if necessary refilled. Wax cubes not consumed after a six-month period were replaced. For logistical reasons, it was not possible to re-visit the bait stations between April and September 2008; therefore the bait stations were not re-filled with poison during this period.

In November 2007 and January 2008, an artificial nest experiment was conducted to identify nest predators and relative levels of nest predation before and after rat control in PTN-A, and also in Selvita where no rat control was conducted. Semi-closed nests were constructed from coconut fibre and hung at 2–3 m height in mangrove trees in PTN-A and Selvita.

Each nest contained two Plasticine eggs (Acrilex modelling clay) layered with egg albumen, similar in size and shape to mangrove finch eggs. All nests and eggs were handled with surgical gloves to avoid them being tainted with human odour. We systematically placed 36 artificial nests in a 4 ha area in PTN-A, with each nest at least 30 m apart. In Selvita, 15 nests were placed along a line 1–5 m from the forest rim and at least 30 m apart. Nests were checked 3, 6 and 9 days after deployment, before being removed. Damaged ('predated') eggs found at 3 and 6 days were removed from nests and replaced with new eggs. Signs of predation on artificial eggs were identified as caused by (i) rats, if clear rat tooth marks were present, (ii) birds, if single puncture(s) marks were present, or (iii) unidentified. We calculated the percentage of predated nests (i.e. at least one artificial egg predated per 9-day period) in each site and also the number of predation events over the whole 9-day period per site.

(d) *Nesting success*

During the 2006/2007 and 2007/2008 breeding seasons, we monitored the outcomes of 105 mangrove finch nests encountered during the population surveys in PTN-A ($n = 68$ nests), PTN-B ($n = 4$) and in CB ($n = 33$). A total of 44 nests were followed in 2006/2007 and 61 in 2007/2008. On encountering a nest, we identified the occupying bird species (mangrove finch, woodpecker finch *C. pallidus*, or ground finch *Geospiza* spp.) and breeding stage (nest building, presence of a pair, incubating eggs, feeding nestlings). Mangrove finch nests were visually checked every other day, until nesting activity ceased. Nests were classified as (i) abandoned—eggs in the nest, birds building new nest nearby; (ii) predated (incubation and feeding phase separately)—empty nest with no fledglings in surrounding area and adults building new nest nearby; (iii) death by parasite infestation—dead nestling(s) but parents building new nest; and (iv) successful—empty nest and fledglings seen around the nest site (three nests that had begging nestlings greater than 8 day old in 2008/2009 after the study had ended were considered successful and included in our analyses). The locations of nest sites were recorded with a global positioning system and used as additional information when drawing territory maps. Fifteen nests were collected after chicks fledged ($n = 7$), or activity ceased ($n = 8$). We used an aluminium ladder (8 m) and a 5 m extension stick to collect the non-active nests, but because nests were built very high up on the trees (average height: 13.13 ± 5 m, $n = 64$), this limited the number of accessible nests. Collected nests were dismantled to search for parasitic fly larvae, and their numbers counted. Breeding started in December and lasted till the end of April. Mean clutch size was 2.13 ± 0.51 (s.d., $n = 30$).

(e) *Population viability analysis*

We modelled the probability of persistence of the mangrove finch populations (PTN, CB and BC) over a 100-year time period using VORTEX v. 9.92 (Lacy *et al.* 2005). VORTEX is an individual-based simulation

Table 1. Parameter input values for the baseline VORTEX model used for the mangrove finch.

parameter ^a	value
inbreeding depression	six lethal equivalents with 50 per cent lethal alleles
EV concordance of reproduction and survival	yes
EV correlation among populations	0.75
number of catastrophes	0
breeding system	monogamous
age of first reproduction for ♀/♂	1 year/2 years
maximum age of reproduction	15 years
maximum number of eggs per ♀ per year	nine (the sum of three clutches of three eggs per year)
sex ratio at birth	1 : 1
density-dependent reproduction	no
percentage of adult ♀ breeding in non-La Niña years	90% ± 10
percentage of adult ♀ breeding in La Niña years	0%
mean clutch size in non-El Niño years	3.14 ± 1.19
mean clutch size in El Niño years	4.7 ± 1.19
percentage annual mortality ♀/♂ ± EV	
0–1	84 ± 5.04/84 ± 5.04
1–2	18.37 ± 2.25/12.79 ± 2.25
2–3	12.79 ± 2.25/12.79 ± 2.25
percentage of ♂ in breeding pool	100%
initial population size (n_0)/carrying capacity (K)	
PTN	48/74
CB	34/40
BC	10/135

^aEV = environmental variation.

model for PVA (Miller & Lacy 2005). Our model was parameterized using estimates of finch vital rates generated from our own and other field studies (table 1). The level of inbreeding depression was increased from the default level in VORTEX of 3.14 lethal equivalents to 6, following recommendations by O'Grady *et al.* (2006) and discussions with population viability modelling experts (B. Lacy 2008, personal communication). This was to reflect possible high levels of inbreeding depression likely to be typical in the small mangrove finch population. The correlation of environmental variation (EV; defined as the annual variation in the probabilities of reproduction and survival that arise from random variation in environmental conditions) among populations was set at 0.75. This reflected the probable high correlation between variation in reproduction and survival between the three geographically close and ecologically similar study sites.

To deal with the effects of El Niño (hot and rainy years for Galápagos) and La Niña (cold and dry years) events on reproduction, we entered a function into the model that increased the quantity of eggs that females lay on average per year when a strong El Niño event occurs (every 20 years; Vargas *et al.* 2006), and reduced the percentage of adult females breeding to 0 per cent during a strong La Niña event (every 14 years; Vargas *et al.* 2006). No data exist on mortality rates of mangrove finches beyond fledging so we based mortality rates from 1 year and above on those observed in *G. scandens* and *G. fortis* on Daphne Mayor Island by Grant & Grant (1992). Similarly, the maximum age of reproduction for the mangrove finch is not known, and this was set at 15 years based on the study of *G. scandens* (Grant & Grant 1992). We predicted the probability of

population persistence of the mangrove finch under four scenarios of juvenile (0–1 year) mortality to investigate the potential impact of varying degrees of invasive alien species control:

- *Baseline model of no intervention.* Juvenile mortality was set at 84 per cent based on the estimates of mangrove finch nesting success data in PTN and CB in 2006/2007 before rat control was implemented.
- *Low intensity rat control.* Juvenile mortality was set at 76 per cent based on the estimates of mangrove finch nesting success data in PTN and CB in 2007/2008 after rat control was implemented.
- *High intensity rat control.* Juvenile mortality was set at 68 per cent under the assumption that high levels of rat control (increased levels of poisoning of rats within PTN and CB and around the site to prevent recolonization) could reduce mortality by a further 8 per cent (the difference between juvenile mortality before and after low intensity rat control at PTN and CB).
- *High intensity rat control and control of *P. downsi*.* Juvenile mortality was set at 57 per cent to reflect a further reduction (from high intensity rat control) in mortality of 11 per cent (the level of mortality observed at PTN in 2006/2007 owing to *P. downsi* infestation of nests; this was indicated by very high numbers of parasites found in the nest; however, as we did not find dead nestlings, these nests were subsequently classified as predated during nestling phase).

As the impact of these control measures is not likely to be immediate, a function was introduced into the model where the baseline model mortality (84%)

decreased linearly over a 10-year period to the prescribed level. Carrying capacity estimates of the three study sites were calculated by dividing the total surface area of suitable mangrove habitat by the mean mangrove finch territory size estimated from the territory mapping data collected in PTN and CB. Initial population sizes for PTN and CB were set according to our population estimates from distance sampling; they were set at 10 for BC as we assumed that five females accompanied the five singing males recorded at this site in 2008. All four models were run over 100 years and with 500 iterations, and mean probability of persistence curves over this time interval were produced.

3. RESULTS

(a) *Mangrove finch population estimates*

A total of 40, 41 and 39 territories were mapped in the three study seasons in PTN and CB (table 2). Mean territory size was 0.39 ha (s.d. = 0.19 ha, $n = 120$). Whereas mean territory size in CB and PTN-A was comparable (mean for all years: 0.38 and 0.34 ha), in PTN-B it was more than double (mean: 0.83 ha). There were no differences in territory size within sites between years (analysis of variance (ANOVA): $F_{\text{site}} = 18.54$, $p < 0.001$, $F_{\text{year}} = 2.4$, n.s., $F_{\text{site} \times \text{year}} = 1.24$, n.s.).

In the three study seasons, a total of 215 males and 12 females were recorded during the distance sampling surveys of PTN and CB (table 2). We estimated the combined population size of PTN and CB to be 93 birds (95% confidence intervals (CI): 48, 182) in 2006/2007, 120 (95% CI: 78, 185) in 2007/2008 and 99 (95% CI: 59, 165) in 2008/2009. Population estimates for CB and PTN individually in each year are given in table 2.

In 2008, searches and play-back surveys of BC revealed the existence of four or five singing male mangrove finches, but a year later only two males were located. No females were recorded at this site in either year.

(b) *Evaluation of rat control efficacy*

In November 2007, before rat poisoning commenced, rat numbers were similar in PTN-A and Selvita, with 20.0 and 26.9 rats trapped per 100 trap nights, respectively (per cent difference test: n.s.). In January 2008, two months after the deployment of rat poison bait stations in PTN-A, the number of rats caught in this site fell markedly to only 1.0 rats trapped per 100 trap nights (per cent difference test: $p < 0.05$). Rat numbers remained low in April 2008 at 6.0 rats per 100 trap nights but increased markedly in September 2008 to 28.0 rats per 100 trap nights (per cent difference test: $p = 0.0001$) after a six-month hiatus in the deployment of rat poison. In January 2009, four months after poisoning resumed, no rats were caught at all during a 3-day trapping session.

The proportion of artificial nests in November 2007 predated was very high in both PTN-A (77%) and Selvita (87%) (per cent difference test: n.s.). The distance between artificial nests and the mangrove's edge varied between sites (1–5 m in Selvita, and 1–100 m in PTN-A); however, we found no evidence that rat

Table 2. Estimates of numbers of mangrove finch territories derived from territory mapping, and population density and size estimates from distance sampling in Caleta Negra (CB) and Playa Tortuga Negra (PTN) in 2006/2007, 2007/2008 and 2008/2009. Territory boundaries were drawn according to observations: sightings of males (one, two or three times during different mapping events), females (one, two or three times; no male singing), pairs (at least in one mapping event, a pair was encountered) and nests (at least in one mapping event, a nest was encountered); 95% CIs of population estimates are given in parentheses.

site	year	territory mapping		distance sampling		
		number of territories	types of observations	number of observations	density (birds ha ⁻¹)	population size
CB	2006/2007	15	11 nests, two pairs, one male 3×, one male 1×	12	4.3 (1.3, 13.9)	42 (12, 139)
	2007/2008	15	10 nests, one pair, two males 2×, two males 1×	42	4.8 (2.5, 9.1)	48 (25, 91)
	2008/2009	16	six nests, two pairs, seven males 2×, one male 1×	28	4.9 (2.4, 10.1)	49 (24, 101)
PTN	2006/2007	25–26	17 nests, two pairs, four males 3×, one male 1×, two females 2×	25	2.8 (1.3, 6.2)	53 (24, 117)
	2007/2008	26–27	20 nests, one pair, five males 2×, one male 1×	64	3.8 (2.2, 6.7)	72 (41, 127)
	2008/2009	23	17 nests, one pair, five males 2×	32	2.7 (1.3, 5.5)	51 (25, 103)

Figure 2. Proportional outcome of nests with eggs or nestlings for the breeding season 2006/2007 (open bars) and 2007/2008 (black bars).

predation events were correlated with distance (multiple regression: $r^2 = 0.02$, $F_{2,48} = 0.49$, $p = \text{n.s.}$; distance $\times$ site: $p < 0.01$). In PTN-A and Selvita, respectively, 64 per cent and 66 per cent of predated eggs showed rat bite marks, 11 per cent and 19 per cent bird peck marks, and 25 per cent and 15 per cent had unidentifiable signs.

In January 2008, two months after installation of rat poison station, in PTN and CB, the proportion of artificial nests predated remained high in Selvita at 73 per cent but dropped to 28 per cent in PTN-A (per cent difference test: $p < 0.01$). All predated eggs at Selvita had clear rat tooth marks compared with only 50 per cent of eggs at PTN-A.

(c) Nesting success pre- and post-rat control

Before rat control commenced (2006/2007), only five of the 44 monitored nests at PTN and CB were successful, producing only 10 fledglings in total. We identified several possible causes for this low productivity (figure 2). In addition, during the pairing phase in 2006/2007, 18 per cent of displaying males with a nest never found a mate. Eighteen per cent of pairs with a nest abandoned it before egg laying in 2006/2007 and 26% of pairs left their empty nest in 2007/2008. During the nesting phase, most nests were predated during incubation and in three cases eggs did not develop. Only 10 nests made it to the nestling phase; five were either predated or succumbed to *P. downsi* parasitism. We did not find dead nestlings to confirm the cause of mortality in these five nests; however, two empty nests contained a very high number of *P. downsi* larvae.

Nest success of mangrove finches increased markedly after rat control in PTN and CB (figure 2). Compared with 2006/2007 values, significantly more nests reached the nestling phase in 2007/2008 (one-tailed per cent difference test: $p < 0.03$) with the proportion of successful nests (excluding nests with displaying males or pairs only) doubling from 18 to 37 per cent (one-tailed per cent difference test: $p = 0.05$). This was largely due to a substantial decrease in the proportion of nests being predated during the incubation phase and a drop in the

proportion of nests with eggs being abandoned (figure 2). We found dead nestlings (seven nestlings in total) which appeared to have succumbed to *P. downsi* infection in 14 per cent of nests with eggs or nestlings monitored in 2007/2008. Mean parasite number per nest was 40.8 (s.d. = 15.3, $n = 15$). Five more nests in this breeding season were thought to have been predated by rats during the feeding phase.

(d) Population viability analysis

In the baseline scenario (juvenile mortality rate at 84%), mangrove finch populations in CB and BC were predicted to have a probability of persistence of zero over 100 years and very near zero for PTN (figure 3). Only nine of 500 simulations for PTN showed population persistence of over 100 years. In the 'low intensity rat control' scenario (i.e. levels of rat control undertaken during this study), which coincided with juvenile mortality dropping to 76 per cent, the PTN population was predicted to stabilize with a probability of persistence of nearly unity. Under this scenario, persistence probability was elevated in CB and BC, although it was still predicted to remain low at 100 years (figure 3). In a high intensity rat control scenario, we assumed that juvenile mortality would reduce to 68 per cent following elevated rat control (e.g. poisoning in adjacent mangrove patches to prevent re-colonization), the probability of persistence of mangrove finch populations in 100 years at PTN and CB was predicted to be unity and very nearly unity and above 0.5 at BC (figure 3). In the final scenario of high intensity rat control and *P. downsi* eradication, we assumed that juvenile mortality would drop to around 57 per cent (an upper value of mortality in *G. scandens* from 0 to 1 year reported by Grant & Grant (1992)), and the probability of persistence remained at unity for CB and PTN and near to unity for BC for the duration of 100 years.

4. DISCUSSION AND CONCLUSION

(a) Mangrove finch population estimates

Territory mapping indicated the existence of around 40 mangrove finch breeding territories in PTN

Figure 3. Predicted probability of persistence of mangrove finch populations in PTN, CB and BC over 100 years under scenarios of no intervention and three levels of invasive species control. (a) Playa Tortuga Negra, (b) Caleta Black and (c) Bahía Carthago. Filled square, high rat and fly control; open diamond, high rat control only; open circle, low rat control only; filled circle, no intervention.

and CB, with perhaps four or five in BC. For PTN and CB, this may be a slight underestimate as the interpretation of territory boundaries was conservative (i.e. validated with confirmation of nest sites). In 1997 and 1998, Dvorak *et al.* (2004) estimated the existence of 52–58 territories, although the difference with the current study could be due to subsequent population decline. Our distance sampling estimates point to a population of around 100 individuals in PTN and

CB. The disparity between numbers of territories and estimates of total population size indicates the presence of non-territorial birds, including singing males, in the breeding sites.

During the surveys, males vocalized regularly whereas females remained largely silent and were only observed at distances very close to the point, resulting in highly different encounter rates and detection probabilities. We dealt with this in the analysis by modelling detection probability as a function of sex as well as distance, but the small total number of female observations resulted in our estimates having relatively wide CIs. This was particularly true for the individual annual estimates for PTN and CB, and thus we recommend that survey effort should be increased in future monitoring to boost numbers of female observations and improve precision. Nevertheless, there is broad agreement between territory mapping and distance sampling estimates and we consider it unlikely that the global population of the mangrove finch numbers varies greatly from 100 individuals, confirming that this species is one of the rarest birds in the world.

(b) Impact of invasive species on nesting success

Black rats are probably the main invasive predator of birds' nests in the Galápagos and worldwide (Martins *et al.* 2006; Towns *et al.* 2006) and our data indicate this to be the case with the mangrove finch, although information on impacts of other predators such as cats and smooth-billed anis is still missing. The proportion of artificial eggs damaged by rats was very high before rat control commenced. Furthermore, around 70 per cent of nests with eggs or nestlings appeared to have been predated, which was the main reason for the low nesting success in 2006/2007 when only 18 per cent of nests produced fledglings. Our PVA model predicted that at this level of juvenile mortality, the species has almost no chance of surviving the next 100 years. Owing to a lack of data on survival rates of the mangrove finch at different life stages, we could not incorporate any measure of mortality between fledging and 1 year of age into the model. Given levels of post-fledging mortality (up to 1 year of age) observed in similar bird species including Darwin's finches (Newton 1989; Grant & Grant 1992; Berkeley *et al.* 2007), it is likely that very few or no mangrove finch fledglings from this cohort would have survived to 1 year. Therefore, if the low nesting success observed in 2006/2007 is typical, the predictions of the PVA model under the scenario of no intervention may in fact be optimistic.

The rat trapping and artificial nest data indicated that the poisoning campaign was reasonably successful in reducing rat numbers and their potential impacts on nests. Given the difficulty and cost of accessing the breeding sites, it was important to test the ability of the invasive species management teams to control rat numbers at least in the short term. Following the reduction in rat numbers, mangrove finch nesting success increased significantly in 2007/2008 with 37 per cent of nests producing fledglings. Using this as the level of juvenile mortality (i.e. from 0 to 1 year) expected under a scenario of low intensity rat control,

the PVA model predicted reasonable gains in persistence probability over 100 years, particularly at PTN which approached unity. Under a scenario of high intensity rat control (juvenile mortality reduced by a further 8%), the predicted probability of persistence of the CB population over 100 years also approached unity. Finally, we reduced juvenile mortality by a further 11 per cent to reflect the added potential impacts of successfully controlling *P. downsi*. This level of juvenile mortality was comparable with levels observed in *G. scandens* (from 0 to 1 year) on Daphne Mayor Island (Grant & Grant 1992). Under this scenario, CB and PTN populations are predicted to certainly persist and that of BC has a high chance of persisting.

Modelling the population viability of threatened species, when data are often lacking, is problematic, and the utility of PVA for informing conservation action has been widely debated in the literature (e.g. Brook *et al.* 2000; Coulson *et al.* 2001; Reed *et al.* 2002). To supplement the sparse population data available for the mangrove finch, we parameterized our model using data on mortality rates from *G. scandens* (Grant & Grant 1992) but there remain a number of issues with our model. For example, owing to a lack of data, we assumed no movement of individuals between populations. As PTN and CB are only 2 km apart, this seems unlikely for the mangrove finch, and such movement may be an important factor in stabilizing the two individual populations (i.e. rescue effect; Brown & Kodric-Brown 1977). We also did not include any possible catastrophes in the model (e.g. arrival of a disease or volcanic activity), nor did we include potential changes in the frequency and severity of El Niño and La Niña events predicted to occur as a result of climate change. However, we did not aim to draw inferences about mangrove finch persistence probability *per se*, but rather investigate the relative effects of invasive species control on mangrove finch viability, an approach thought to more reliably contribute to conservation planning (McCarthy *et al.* 2003). Our PVA model predicted that significant and important gains in persistence probability of the PTN and CB populations can be achieved by increasing the intensity of rat control by levels considered feasible by the invasive species management teams in Galápagos.

One factor we did not include in the model was any potential nonlinear increases in mortality owing to *P. downsi* infestation of nests as a result of an increased number of nests reaching nestling stage following rat control. The number of parasites found per mangrove finch nest in CB and PTN was high and comparable with numbers observed in nests of several finch species on Santa Cruz Island (Dudaniec *et al.* 2007). In the current study, partial and complete brood loss was linked to infestation by *P. downsi* resulting in an important proportion of mortality during the nestling phase in 2007/2008. Furthermore, this source of mortality may be underestimated as parents may remove dead nestlings from the nests, leading to observers recording a predation rather than a parasite event. Further increases in infestation rates may offset the potential gains in nesting success through rat control. Additionally, post-fledging survival might be negatively affected by blow

fly infestation (Streby *et al.* 2009). Thus, alongside rats, control of the blood-sucking larvae of *P. downsi* must be a high priority. Currently, we do not have any control agent applicable for the mangrove finch. Research is underway to develop *P. downsi* control methods over the short term (e.g. pheromone traps) as well as long term (e.g. sterilization programme).

Despite the increase in reproductive success observed in 2007/2008, population estimates in 2008/2009 were not different to those before rat control. Darwin's finches are long-lived species (10–15 years; Grant & Grant 1992) and tend to start to reproduce at 2–4 years with females generally being reproductively active earlier than males (Grant & Grant 1992). Males will start to sing in their second year (B. Fessl 2008, personal observation) and eventually establish a territory then. Thus, young males will not be counted during territory mapping or point count sampling. Consequently, changes in productivity might not be evident in terms of population growth for several years. However, observations of yearlings as well as adult birds in mangrove stands adjacent to PTN and CB in 2008/2009 indicate that the population is increasing and dispersing following the intervention of rat control. In fact, it is the first time that birds have been regularly seen in these mangrove stands in the past 10 years (H. Vargas 2008, personal communication). Further annual monitoring of this species is clearly required to evaluate the outcome of the rat control campaign.

(c) Genetic factors

The effective population size (N_e) at the remaining mangrove finch sites is unknown. Although processes including geographical isolation, migration and founding of new populations are natural, we can assume that a dramatic reduction of numbers has occurred in the near past and only a sample of the genetic information or gene pool of the original population currently exists. Loss of genetic variability in such a small and historically declining population through dramatic El Niño/La Niña events and years of poor recruitment through predation may have already affected the future potential of the species. Such decrease in diversity results in a loss of evolutionary potential for individuals within that population which may be then less likely to adapt to any environmental changes. Additionally, smaller populations also implicate greater random genetic drift. Thus, though in normal populations the size is often large enough to minimize the effect of drift, in disturbed or fragmented populations the population size may be small enough for the effect of drift to become important. Grant & Grant (1992) suggest that for Darwin's finches, effective population size could be as low as a quarter of the actual population size.

There is strong evidence that the remaining mangrove finches are considerably inbred given their low F_{st} values (<0.01 , K. Petren 2009, unpublished data). Studies, including those of Darwin's finches, have shown a significant correlation between inbreeding and reduced reproductive fitness (Keller 1998; Markert *et al.* 2004; Swinnerton *et al.* 2004) or reduced immune response (Hale & Briskie 2007)—eventually strongly linked with

environmental conditions (Keller *et al.* 2002). Studies on whether inbreeding is causing a decrease in fecundity and increase in mortality, over and above deaths caused by invasive predators as shown in this study, are fundamental to resolve for the mangrove finch. Hybridization may, however, counteract the effects of inbreeding (Grant *et al.* 2003). Preliminary results of mangrove finch samples suggest that there is introgression from the woodpecker finch (13%, K. Petren 2008, personal communication). Analyses of the current effective population size of the mangrove finch and the significance of introgression from woodpecker finch genes need to be determined urgently.

(d) *Emerging threats*

The risk of catastrophic new threats reaching the diminished populations of mangrove finch is real, with disease representing an emerging problem. Introduced pathogens can lead to the extinction of many species (McCallum & Dobson 1995; Atkinson *et al.* 2000; Daszak *et al.* 2000). Avian pox, which has been present for several decades in Galápagos, causes high mortality in species such as mockingbirds (Vargas 1987; Curry & Grant 1989) and possible fitness reduction in finches (Kleindorfer & Dudaniec 2006). In 2004, pox was reported in PTN (14% prevalence in ground finches; G. Jiménez *et al.* 2004, unpublished data) and a mangrove finch was seen with symptoms in 2009 (B. Fessl 2008, personal observation). It is currently unclear what impact this disease could have on the population, but its closest relative, the woodpecker finch, is thought highly susceptible (B. Fessl 2008, personal observation). The recent discovery of *Plasmodium* sp., a still unidentified species from the genus causing avian malaria, in the Galápagos penguin (*Spheniscus mendiculus*) (Levin *et al.* 2009) and potential for transmission to the mangrove finch may also be significant given that the species share the same environment (B. Fessl 2008, personal observation).

Pathogens and parasites detected in domestic poultry in Galápagos (11 to date) pose a realistic threat of spreading to wild birds (Vargas & Snell 1997; Gottdenker *et al.* 2005; Soos *et al.* 2008). Additionally, because several wild animal diseases require insects as vectors (Whiteman *et al.* 2005; Kilpatrick *et al.* 2006; Deem *et al.* 2008; Bataille *et al.* 2009), the recent establishment of the mosquito *Culex quinquefasciatus* in Galápagos (Thiel *et al.* 2005), which spreads *Avipoxvirus* spp. and is a potential vector for avian malaria and West Nile virus, represents a major risk to the island's native avifauna (van Riper *et al.* 2002; Pollock 2008).

Climate change will result in a higher frequency of El Niño; thus, vectors for pox, *Plasmodium* and other diseases might be able to increase their range (Freed *et al.* 2005), and conditions for the establishment of diseases and parasites will be improved (Holmes 1996). On the other hand, El Niño conditions result in prolonged breeding of finches (Grant & Grant 1987) and might thus be beneficial for the recovery of the mangrove finch given that rat control is intensified at the same time. However, the favourable conditions for finches might increase *P. downsi* infestation (Dudaniec *et al.* 2007), outbalancing the positive effect.

(e) *Conclusion and future prospects*

Although the Galápagos retains a high percentage of its pre-human species assemblages, this is very likely an effect of its recent discovery (Snell *et al.* 2002). If extinction rates of the recorded biological histories are compared between archipelagos, few have current higher extinction rates than Galápagos. At the present rate of extinction, 50 per cent of the Galápagos vertebrate fauna could disappear, with Darwin's finches being among the most vulnerable (Snell *et al.* 2002). Our study has shown that the rarest of Darwin's finches, the mangrove finch, is in a particularly perilous state, with a highly restricted range, tiny population size and very low nesting success owing mainly to the impacts of the invasive black rat and *P. downsi*. Furthermore, a number of introduced pathogens recently arrived in the Galápagos could cause catastrophic impacts on this small population. The genetic consequences of the historical decline in this species and their impact on population growth are not understood.

We have demonstrated that effective rat control is possible at the mangrove finch's remote breeding sites, which probably lead to a marked increase in nesting success during this study. However, predictions of PVA models suggested that rat control would need to be intensified and possibly *P. downsi* control initiated in order to reduce nesting mortality sufficiently to secure the species. Because invasive species control measures are time intensive and costly, especially in the harsh and remote environments of the mangrove finch sites, the application of adaptive management strategies is imperative. If these interventions successfully lead to mangrove finch population growth at CB and PTN, the small area of suitable habitat restricts the number of finches able to occupy these sites. Birds might re-colonize Fernandina Island, only 7 km from PTN; however, mangroves (three patches, together approx. 170 ha) are mostly located around lagoons and thus seem less suitable for mangrove finches. Birds might migrate southwards along the coast (H. Vargas 1998, personal observation), and reach Bahía Urbina (patch of approx. 70 ha at 18 km distance). Yet, this and other patches on the northwestern coast are isolated, some of them difficult to access (for restoration actions), but most importantly have long since had no mangrove finch records. For the population to grow further and therefore to reduce extinction risk, other historically occupied mangrove sites need to be restored. Rat control is planned for a number of potentially suitable mangrove sites in BC following translocations of juvenile mangrove finches from PTN and CB. Combined with intensive monitoring to evaluate outcomes, these actions may enable us to save the mangrove finch from the brink of extinction, and in so doing learn how to protect other Darwin's finches from similar threats.

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