

An introduced parasitic fly may lead to local extinction of Darwin's finch populations

Jennifer A. H. Koop^{1†*}, Peter S. Kim^{2‡¶}, Sarah A. Knutie^{1§}, Fred Adler^{1,2} and Dale H. Clayton¹

¹Department of Biology, University of Utah, 257 South 1400 East, Rm 201, Salt Lake City, UT 84112, USA; and

²Mathematics Department, University of Utah, 155 South 1400 East, Rm 233, Salt Lake City, UT 84112, USA

Summary

1. Introduced pathogens and other parasites are often implicated in host population-level declines and extinctions. However, such claims are rarely supported by rigorous real-time data. Indeed, the threat of introduced parasites often goes unnoticed until after host populations have declined severely. The recent introduction of the parasitic nest fly, *Philornis downsi*, to the Galápagos Islands provides an opportunity to monitor the current impact of an invasive parasite on endemic land bird populations, including Darwin's finches.

2. In this paper, we present a population viability model to explore the potential long-term effect of *P. downsi* on Darwin's finch populations. The goal of our study was to determine whether *P. downsi* has the potential to drive host populations to extinction and whether management efforts are likely to be effective.

3. Our model is based on data from five years of experimental field work documenting the effect of *P. downsi* on the reproductive success of medium ground finch *Geospiza fortis* populations on Santa Cruz Island. Under two of the three scenarios tested, the model predicted medium ground finches are at risk of extinction within the next century.

4. However, sensitivity analyses reveal that even a modest reduction in the prevalence of the parasite could improve the stability of finch populations. We discuss the practicality of several management options aimed at achieving this goal.

5. *Synthesis and applications.* Our study demonstrates the predicted high risk of local extinction of an abundant host species, the medium ground finch *G. fortis* due to an introduced parasite, *P. downsi*. However, our study further suggests that careful management practices aimed at reducing parasite prevalence have the potential to significantly lower the risk of host species extinction.

Key-words: conservation, galápagos, *Geospiza fortis*, invasive species, medium ground finch, model, parasite, *Philornis downsi*, population viability model

Introduction

Introduced pathogens and other parasites pose a major threat to global biodiversity (Holmes 1996). The successful establishment of these species can trigger epidemics that cause the decline of even seemingly abundant host populations (Hochachka & Dhondt 2000). Co-evolved

hosts and parasites have adaptations that allow hosts to defend themselves and parasites to escape host defences. Co-evolutionary adaptations can lead to stable population dynamics of both the host and the parasite (Schmid-Hempel 2011). In contrast, naïve host populations may not have had time to evolve effective defences against introduced parasites. Under this scenario, parasites can cause host populations to quickly decline and even go extinct locally (Lyles & Dobson 1993; Mutze, Cooke & Alexander 1998; Atkinson & LaPointe 2009). Unfortunately, the threat of introduced parasites often goes unnoticed until host populations have already declined, making it difficult to gather data and assess the relative contribution of parasites and other factors to the decline (McCallum & Dobson 1995; Smith, Sax & Lafferty 2006).

*Correspondence author. E-mail: jkoop@umassd.edu

Present addresses: [†]Biology Department, University of Massachusetts-Dartmouth, Dartmouth, MA 02747, USA

[‡]School of Mathematics and Statistics, University of Sydney, Sydney, NSW, Australia

[§]Integrative Biology, University of South Florida, Tampa, FL, USA

[¶]Co-first author with JAHK.

Island populations of hosts are particularly at risk from introduced species of parasites, due to limited habitat size and a lack of genetic diversity (Paulay 1994; Blackburn *et al.* 2004; Steadman 2006; Pimm *et al.* 2014). For example, the extinction of half of Hawaii's endemic honeycreeper species has been attributed, in part, to the introduction of avian malaria and avian pox (Warner 1968; van Riper *et al.* 1986; Atkinson *et al.* 2000; van Riper, van Riper & Hansen 2002). Because 14 of 17 extant species of honeycreeper in Hawaii are endangered, these parasites continue to be a serious threat (Atkinson & LaPointe 2009). By comparison, the Galápagos Islands have suffered no recorded extinctions of birds (Parker, Whiteman & Miller 2006). However, with the number of tourists and island residents continuing to increase each year (Watkins & Cruz 2007), anthropogenic introductions of parasites are a growing concern.

Of particular concern in the Galápagos is the parasitic nest fly *Philornis downsi* (Diptera: Muscidae), which was first documented in the nests of birds in the Galápagos in 1997 (Fessl & Tebbich 2002). *Philornis downsi* has been found on most of the islands surveyed in the archipelago (Wiedenfeld *et al.* 2007; Causton, Cunninghame & Tapia 2013) and recorded in the nests of 14 species of land birds, including nine species of Darwin's finches (Koop *et al.* 2011). Adult *P. downsi* flies, which are not parasitic, lay their eggs in bird nests. Once the fly eggs hatch, the larvae develop in the nest, where they feed on the blood of nestlings and brooding adult females (Koop *et al.* 2013). Among years, the effect of *P. downsi* on finch nestling survival is highly variable. In some years, *P. downsi* reduces nestling survival to zero; in other years *P. downsi* has relatively little effect on nestling survival (Koop *et al.* 2011, 2013; Koop, Le Bohec & Clayton 2013). The highly variable climatic conditions of the Galápagos are thought to contribute to this variation (Koop, Le Bohec & Clayton 2013; Cimadom *et al.* 2014).

Infestation by *P. downsi* has been implicated in the decline of the mangrove finch *Camarhynchus heliobates* and the medium tree finch *Camarhynchus pauper* (Fessl *et al.* 2010; O'Connor *et al.* 2010). It may also play a role in the decline of several populations of other species of land birds in the archipelago (Dvorak *et al.* 2012; Cimadom *et al.* 2014). For many of these species, reservoir hosts, habitat degradation and invasive predators further contribute to population-level instability (Fessl *et al.* 2010; Cimadom *et al.* 2014). Fessl *et al.* (2010) used a population viability model (VORTEX v. 9.92) to predict the impact of high- and low-intensity rat control efforts, as well as *P. downsi* control efforts, on populations of the critically endangered mangrove finch. Because of the difficulty of accessing mangrove finch nests to regularly monitor the effects of *P. downsi* on nestlings, only nests containing dead nestlings were considered to have failed due to parasitism. Under this assumption, Fessl *et al.*'s model predicted that mangrove finch populations would recover only under conditions of high-intensity rat and fly

control. However, the presumed impact of *P. downsi* on mangrove finch reproductive success may be an underestimate since females are known to sometimes remove dead nestlings from nests (O'Connor, Robertson & Kleindorfer 2010). Directly measuring the effect of *P. downsi* on host fitness could provide more accurate parameter estimates for population viability models, increasing the accuracy of model predictions.

In this paper, we present a model that explores the effect of *P. downsi* on a large population of finches. Specifically, our model assesses the effect of *P. downsi* on the extinction risk of medium ground finches *Geospiza fortis* on the island of Santa Cruz. To estimate the various parameters of the model, we used 5 years of experimental data collected by members of our research group at a single study site (El Garrapatero). When available, we also used published data collected by other investigators to further inform parameter estimates. The goals of our model are to: (i) predict the long-term effect of *P. downsi* on medium ground finches at a population level and (ii) identify which variables should be the focus of conservation efforts.

Materials and methods

We formulated a mathematical model to predict population viability of medium ground finches based on the 5 years of data summarized in Table 1. We modelled only the female population in order to simplify parameter estimates (Doak 1989). However, by including only the female population, the model ignores potential frequency-dependent issues, such as an inability to locate a mate when populations become very small, which could lead to higher estimates of extinction risk. However, under monogamous conditions, with equal sex ratios, a model based on a single sex can provide a strong indication of the viability of the entire population (Brook, Burgman & Frankham 2000). The proportion of males and females in a given population was assumed to be approximately equal, such that all females of reproductive age are able to find a mate. Our field data consistently showed that females and males were captured in mist-nets in relatively equal proportions. Darwin's finches are typically monogamous with both sexes contributing to parental care of the offspring (Grant 1999). A diagram of the model is provided in Fig. 1.

The populations of steps (1), (2), (4) and (5) of Fig. 1 were updated by binomial random variables as follows: $C_n = c_n \times \text{Bin}(A_n, p_n)$, $I_n = \text{Bin}(C_n, q_n)$, $U_n = C_n - I_n$ and $A_{n+1} = \text{Bin}(F_n, S_n^f) + \text{Bin}(A_n, S_n^a)$. A description of each variable is found in Table 2. We assumed that the population is maintained at equilibrium by a density-dependent mortality rate that primarily affects the fledgling population. That is, the more adults in a given population, the lower the probability that a fledgling will survive the first year and be recruited into the breeding population the following year. As a result, fledgling survival probability depended on the adult population in a logistic fashion as follows: $S_n^f = \max[S_n^0(1 - A_n/K), 0]$. Furthermore, since females can reproduce as early as 1 year of age, we assumed that all surviving female fledglings can become part of the potential adult breeding population A_{n+1} in the following year (Grant & Grant 1992).

Table 1. Summary of results from 5 years of data on the effects of *Philornis downsi* on medium ground finch reproductive success (Koop *et al.* 2011, 2013; Kntutje *et al.* 2014, 2015)

Year* treatment	Parasite prevalence [†]	Mean parasite abundance [‡]	Mean parasite intensity [¶]	Proportion of nests with fledglings [§]	Mean # of fledglings per nest
2008 Treated	0.83 (20 of 24 nests)	21.8	26.2	0.33	0.79
Control	0.96 (23 of 24 nests)	37.5	39.13	0.04	0.13
2009 Treated	0.00 (0 of 7 nests)	00.0	00.0	0.14	0.29
Control	0.83 (5 of 6 nests)	30.5	36.6	0.16	0.33
2010 Treated	0.10 (2 of 21 nests)	0.23	2.5	1.00	2.67
Control	1.00 (22 of 22 nests)	38.5	38.5	00.0	00.0
2012 Treated	0.08 (1 of 12 nests)	0.25	3	0.92	3.08
Control	0.83 (10 of 12 nests)	26.2	31.4	0.50	1.08
2013 Treated	0.00 (0 of 20 nests)	00.0	00.0	0.95	2.50
Control	0.88 (15 of 17 nests)	17.0	19.3	0.65	1.71

*In 2008, treated nests were fitted with nylon liners to reduce parasite abundance in nests, while control nests were left unlined (Koop *et al.* 2011). In later years, treated nests were sprayed with dilute permethrin to kill parasites in nests, while control nests were sprayed with water.

[†]Proportion of infested nests out of all nests (following treatment).

[‡]Mean number of *P. downsi* per nest.

[¶]Mean number of *P. downsi* per infested nest.

[§]Fraction of nests that fledged at least one offspring.

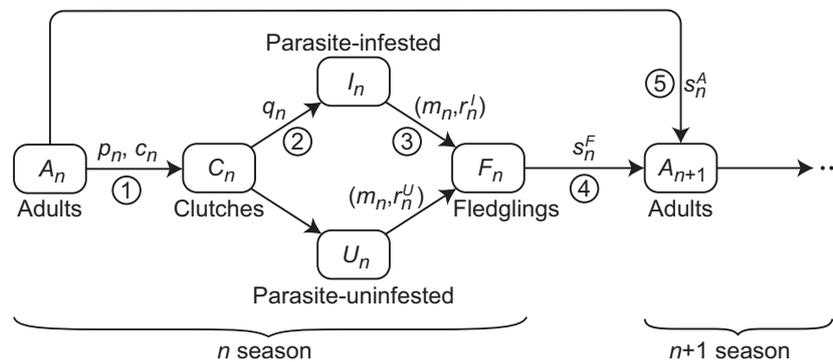


Fig. 1. Diagram of model predicting finch annual reproductive success. The variable A_n is the number of female adults in the population at the beginning of year n , which is equal to the carrying capacity K in our model. The model accounts for the following processes: (1) Each breeding season, a certain fraction of female adults breed (p_n) and produce a mean number of clutches per adult (c_n) for a cumulative number of C_n clutches in a breeding season. (2) In a given year, a fraction (q_n) of clutches will become infested (I_n) by *Philornis downsi* or remain uninfested (U_n). (3) Each infested (m_n, r_n^I) and uninfested (m_n, r_n^U) clutch successfully produces a certain number of female fledglings (F_n) in a given year. Each clutch is capable of producing a maximum number (m_n^I) of nestlings and r_n^I and r_n^U refer to the probabilities that female nestlings fledge from infested and uninfested nests, respectively. (4) A fraction of female fledglings (S_n^F) from year n survive to become adults at the beginning of year $n + 1$. (5) A fraction of female adults (S_n^A) from year n survive to year $n + 1$.

We modelled the number of fledglings produced in each clutch (step 3, Fig. 1) in the following manner. During year n , each clutch i was capable of producing a maximum number (m_n^i) of nestlings, some of which may successfully fledge. We assumed that all nestlings within a nest had the same probability of fledging. We let r_n^I and r_n^U be the probabilities that female nestlings fledge from infested and uninfested nests, respectively. As a result, the total number of fledglings produced by all clutches in year n was $F_n = \sum_{i=1}^{I_n} \text{Bin}(m_n^i, r_n^I) + \sum_{i=I_n+1}^{I_n+U_n} \text{Bin}(m_n^i, r_n^U)$. Further details of parameter estimation and methods for calculating the expected annual population growth rate (r) are provided in Appendix S1 in Supporting information.

Breeding and survival of finches is highly influenced by variation in annual environmental conditions, such as rainfall (Grant & Boag 1980; Dudanic, Fessl & Kleindorfer 2007; Cimadom *et al.* 2014). In general, years characterized by relatively high

rainfall lead to increased food supply and higher rates of breeding and survival. In contrast, extremely dry or extremely wet years lead to a scarcity of resources and lower rates of breeding and survival (Gibbs & Grant 1987; Grant & Grant 1992; Grant 1999). To simulate the high variability of conditions and the subsequent effects on population growth rates from year to year, we assumed each year in the simulation had a certain probability of being like year 2008, 2009, 2010, 2012 or 2013. We used parameters from the corresponding column of Table 2 for each simulated year. We considered three scenarios for making model predictions: (i) equally weighted years, in which each of the 5 years had the same probability of being chosen; (ii) weighted towards bad years, in which we used the probability weightings 3/15, 4/15, 5/15, 2/15 and 1/15 for 2008, 2009, 2010, 2012 or 2013, respectively (the weightings were ranked in order of decreasing probability of fledging from an infested nest, such that

Table 2. Parameter estimates for model predicting mean time to extinction for medium ground finches on Santa Cruz Island

Param. Variable	Description	Estimates				
		2008	2009	2010	2012	2013
p_n	Probability of breeding	0.95	0.29	0.95	0.95	0.95
c_n	Mean number of clutches per breeding adult	2	1	2	2	2
q_n	Probability of infestation	0.96	0.83	1.00	0.83	0.88
m_n^i	Max number of fledglings per clutch i	2.96*	2.23	3.40	3.38	3.08
r_n^I	Probability of fledging from an infested nest	0.05	0.15	0.00	0.22	0.50
r_n^U	Probability of fledging from an uninfested nest	0.00 (0.73) [†]	0.13	0.68	0.87	0.83
S_n^F	Survival probability of fledglings	0.36	0.36	0.36	0.36	0.36
K	Estimated population carrying capacity	271 400	271 400	271 400	271 400	271 400
S_n^A	Survival probability of adults	0.69	0.69	0.69	0.69	0.69

*Actual values were randomly sampled for each year from the histogram in Fig. S1. The mean values for each year are presented here.

[†]In 2008, only a single parasite-free, treated nest was included in the study, from which no nestlings fledged (0.00). Therefore, we also consider an alternative estimate of fledging probability averaging across all 5 years (0.73). See Supporting Information for further detail.

Table 3. Table of expected annual growth rate r and predicted mean time to extinction (results of 1000 simulations are shown in the form of mean \pm standard deviation) under three scenarios

	With parasites		Without parasites		Without parasites*	
	r	Time (years)	r	Time (years)	r	Time (years)
Equally weighted [†]	0.86	80 \pm 15	1.14	>1000	1.32	>1000
Weighted towards bad years [‡]	0.78	50 \pm 7	1.07	>1000	1.23	>1000
Weighted towards good years [§]	0.96	244 \pm 90	1.22	>1000	1.41	>1000

*Calculated using the alternative estimate of $r_n^U = 0.73$ for the probability of fledging from uninfested nests in 2008 (Table 2).

[†]Every year is assumed to have an equal probability of being like the years 2008, 2009, 2010, 2012 and 2013.

[‡]Years with lower probability of fledging from infested nests are chosen more frequently.

[§]Years with higher probability of fledging from infested nests are chosen more frequently.

years with the lowest probability of fledging were chosen more frequently) and (iii) weighted towards good years, in which we used the probability weightings 3/15, 2/15, 1/15, 4/15 and 5/15 for 2008, 2009, 2010, 2012 or 2013, respectively (the weightings were ranked in order of increasing probability of fledging from an infested nest, such that years with the highest probability of fledging were chosen more frequently).

Results

Under stable circumstances, a population growth rate of $r \geq 1$ indicates a steady state or growing population, increasing the likelihood for long-term survival. A population growth rate of $r < 1$ indicates a population in decline. In two of the three scenarios tested, our model predicted that medium ground finch populations on the island of Santa Cruz were declining and at risk of extinction within the next century (Table 3, Fig. 2). Under the scenario of equally weighted years, the population growth rate was

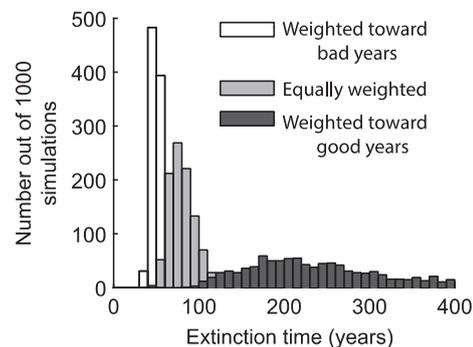


Fig. 2. Distribution of predicted extinction times over 1000 model simulations for medium ground finches on Santa Cruz Island. Parameters are estimated from data collected over 5 years of experimental study in the same population of medium ground finches (Table 2). The three scenarios correspond to the three scenarios described in the Materials and methods section and presented in Table 3.

$r = 0.86$, with a mean predicted time to extinction of 80 ± 15 years. Under the scenario of weighting towards bad years, the population growth rate indicated more rapid decline ($r = 0.78$) with a mean predicted time to extinction of 50 ± 7 years. Only under the third scenario, which weighted towards good years, were the population growth rate ($r = 0.96$) and predicted time to extinction (244 ± 90 years) sufficient to expect long-term population-level stability.

To determine the relative effects of each parameter on model behaviour, we independently varied parameters p_n , c_n , m_n^i , q_n , K , r_n^U , r_n^I , S_n^F , S_n^A by plus or minus 25% of their estimated value (Table 4) and ran model simulations to estimate population growth rates. (We did not allow the probability of breeding, p_n , nor the probability of infestation, q_n , to exceed 100%.) Predicted population growth rates varied with every parameter tested except population carrying capacity, K (Table 4).

In the interest of identifying manageable parameters for conservation efforts, we further explored the effects of the

probability of infestation, q_n , on population growth estimates. We tested the model with hypothetical probabilities of infestation (parasite prevalence) ranging from 0% to 100% (Fig. 3). As the probability of infestation decreased, predicted time to extinction (Fig. 3a) and population growth rate (Fig. 3b) increased dramatically.

Discussion

The main purpose of our model was to generate predictions of finch population viability relative to *P. downsi* infestation. Model parameters were estimated using 5 years of experimental data and other published literature, when available. Estimates of population growth rate and extinction risk were used to predict long-term population viability for medium ground finches on the island of Santa Cruz. We tested the model under three scenarios in which each of our study years were either weighted equally, weighted towards better years (years with higher reproductive success) or weighted towards bad years (years with lower reproductive success). Under two of the three scenarios tested, the model predicted that medium ground finches are at risk of local extinction within the next century. Our model highlights the potential negative

population-level effect of *P. downsi* on medium ground finches and demonstrates the need for continued vigilance and research on the impact of this invasive parasite on host populations.

A secondary goal in creating this model was to identify parameters that have a significant effect on extinction risk outcomes in an unbiased manner. Identifying these parameters may help to guide conservation efforts aimed at protecting vulnerable host populations and identify gaps in our knowledge of the system. Under the scenario of equally weighted years, our sensitivity analyses indicated that the probability of breeding, the probability of infestation, the maximum number of fledglings produced per clutch, the average number of clutches per year, annual fledgling survival and annual adult survival all influence predictions of extinction risk.

Interestingly, varying the probability of fledging from infested and uninfested nests had little effect on predictions of population growth rate. However, this result may be a reflection of how our sensitivity analyses were performed. For example, the probability of infestation is high for all 5 study years (>80%). Since so few nests remain uninfested, varying the probability of fledging from an uninfested nest would not be expected to have a large effect on the population growth rate. Similarly, the probability of fledging from an infested nest is quite low in four of the 5 study years. Therefore, varying this parameter, even in the positive direction, did not lead to major increases in the population growth rate. However, our sensitivity analyses were designed to isolate each parameter's impact on the model predictions. If the probability of fledging from an uninfested nest and an infested nest are varied simultaneously, the model predicts changes in population growth rates similar to that seen when varying the probability of infestation (discussed below). Thus, it is important to acknowledge that alternative methods for conducting sensitivity analyses could produce different results.

Table 4. Table of annual expected growth rate r under different parameters. Parameters were varied by increasing or decreasing the estimated values by 25%. Simulations were done using the equally weighted case in which every year is assumed to have an equal probability of being like years 2008, 2009, 2010, 2012 or 2013

Parameters	Up 25%	Down 25%
p_n, c_n, m_n^i, S_n^F	0.90	0.82
q_n	0.78	0.94
r_n^I	0.89	0.84
r_n^U	0.88	0.85
K	0.86	0.86
S_n^A	1.04	0.69

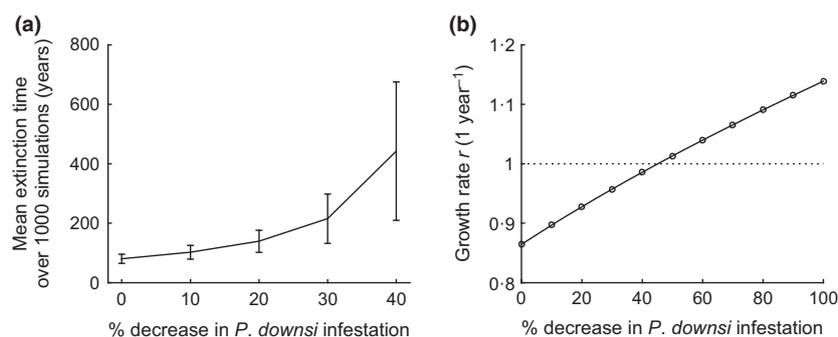


Fig. 3. Sensitivity of medium ground finch populations to changes in probability of infestation by *Philornis downsi*. Parameter estimates are shown in Table 2, and estimates are based on the model scenario of all years being weighed equally. (a) Mean extinction times (\pm standard deviation) over 1000 simulations as a function of percentage decrease in parasite infestation. Only, the results for decreases of up to 40% are shown. When infestation levels are reduced by more than 40%, simulated extinction times exceed 1000 years. (b) Annual finch population growth rate r as a function of percentage decrease in infestation.

Among year differences in fledging success of both infested and uninfested nests may be attributed, at least in part, to rainfall. Differences in annual rainfall and the effects of rainfall on finch survival have been well-documented in this system (Grant 1999). The second year of our study, 2009, was the driest of all 5 years. While fledging success did not differ significantly between treatments that year, overall breeding attempts were very few in number compared to wetter years (Koop, Le Bohec & Clayton 2013). Recent work has also shown that periods of extremely heavy rainfall can also reduce finch reproductive success (Cimadam *et al.* 2014). Further study is needed to better understand the relationship between annual rainfall and the effects of *P. downsi* on finch reproductive success. The inclusion of additional data collected in years with low, moderate and heavy rainfalls will better inform future iterations of the model.

Altering estimates of adult survival probability had the most variable effects on estimates of population growth rate. Interestingly, a 25% increase, from $S_n^A = 0.69$ to 0.86, resulted in a promising population growth rate estimate of $r = 1.04$. A 25% decrease, from $S_n^A = 0.69$ to 0.52, resulted in a population growth rate estimate of $r = 0.69$. Quantifying adult survivorship in our focal population was outside the scope of our field work. Thus, our estimate for this parameter was based on a study by Gibbs & Grant (1987) that quantified adult survivorship among seven cohorts of medium ground finches on Daphne Major. However, there are several differences between our population of finches and the population observed on Daphne Major that must be considered in interpreting this parameter's effect on model predictions. First, finch nests on Daphne Major are apparently free of *P. downsi* (Fessl & Tebbich 2002). Secondly, some populations of finches on Santa Cruz suffer from habitat loss and invasive predators in addition to parasitism by *P. downsi*. Together, these factors may challenge our assumption that adult survival is similar between Santa Cruz and Daphne Major. The influence of adult survivorship on the model's predictions thus warrants additional field work aimed at measuring adult survivorship in and beyond our focal population.

Variation in parasite prevalence (probability of infestation) had a significant effect on predictions of extinction risk and is therefore important from a management perspective. Small reductions in parasite prevalence substantially reduced the risk of local host extinction (Fig. 3). Therefore, our model confirms that reducing the prevalence of *P. downsi* should be a management priority. Several methods for controlling *P. downsi* populations are currently being considered or tested (Causton, Cunningham & Tapia 2013). Traps designed to capture adult flies offer a low-cost, low-maintenance option for reducing populations. However, attempts to capture adult flies using bait (e.g. fruits, water and syrups) have had limited success (Causton, Cunningham & Tapia 2013). A sterile insect programme, in which gravid females are exposed to

experimentally sterilized males, has the potential to eradicate *P. downsi*, as in other pest systems (Hendrichs *et al.* 2005). Unfortunately, this approach is both labour-intensive and expensive. Augmentative biological control with natural parasites of *P. downsi* may also provide a long-term solution because this method can be used over a large area. One drawback of this method is that it may take more than a decade to release an effective, ecologically safe parasite of *P. downsi* in the Galápagos (Alvarez *et al.* 2012). Direct application of permethrin to nests can also eliminate *P. downsi*; however, this method is labour-intensive and therefore limited in potential scope. Another interesting stop gap method is self-fumigation, in which finches are allowed to fumigate nests themselves with permethrin-treated cotton materials (Knutie *et al.* 2014).

In an effort to keep our model simple, we assumed that all populations of medium ground finches on the island of Santa Cruz are affected similarly by *P. downsi*. This assumption may be an oversimplification and continued research on the effects of *P. downsi* across populations and species is necessary to understand the level of variation in virulence that may be present in this system. To date, there are no reports of populations of finches on Santa Cruz that are not parasitized by *P. downsi*. The only other experimental study performed on the island of Santa Cruz also found a nearly two-fold increase in fledging success when *P. downsi* abundance was reduced in the nests of medium and small ground finches *Geospiza fuliginosa* (Fessl, Kleindorfer & Tebbich 2006). This study, which was performed a short distance (~13 km) from our study site, suggests that the impact of *P. downsi* may be similar across populations.

Our model indirectly assumed that reservoir hosts may contribute to the persistence of *P. downsi* in the environment, despite declines of vulnerable finch hosts. Such reservoir hosts may be relatively unaffected by the parasite and therefore can maintain large numbers of the parasite in the environment independent of any single host. *P. downsi* parasitizes most land bird species in the Galápagos (Fessl & Tebbich 2002; Wiedenfeld *et al.* 2007); these species vary in body size, feeding ecology and nesting biology, which may affect their ability to defend themselves against *P. downsi*. For example, *P. downsi* has been shown to have no detrimental effect on the reproductive success of Galápagos mockingbirds *Mimus parvulus*, despite that fact that the density of flies in mockingbird and medium ground finch nests did not differ significantly (Knutie *et al.* 2015). In summary, reservoir hosts may amplify the effect of *P. downsi* on medium ground finches, increasing the risk of local extinction (McCallum & Dobson 1995).

In conclusion, our model suggests that while *P. downsi* is a threat to populations of even abundant finch species, conservation efforts that succeed in reducing fly prevalence may be an effective management strategy. While our model highlights the potential effect of *P. downsi* on host populations, it does not consider possible evolutionary

adaptations by the host or parasite. Kleindorfer *et al.* (2014) found that over the past 9 years, *P. downsi* intensity increased, host mortality due to parasitism increased and the age of hosts at death decreased. Furthermore, our model does not consider every threat currently facing these birds. Additional factors, such as introduced predatory rats and cats, habitat degradation and agricultural chemicals, may also contribute to host mortality and may increase extinction risk for certain populations or species of Darwin's finches (Cimadom *et al.* 2014). Thus, it is important to note that while our model is a useful tool, its simulations must be interpreted with caution. Encompassing the dynamic and complex interactions that occur in this, or any other natural system, will require continued research and collaboration by field, mathematical and conservation biologists (Beissinger *et al.* 2006).

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Data accessibility

MATLAB scripts and raw data: uploaded as online Supporting Information and to Dryad Digital Repository doi:10.5061/dryad.vs4d3 (Koop *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Model parameter estimation methods and calculations of population growth rate.

Fig. S1. Histogram of the number of nestlings hatched per clutch in each study year.