Conservation issues for Darwin's finches in the Galápagos Islands: invasive species and loss of genetic diversity

Jody Anne O'Connor

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School of Biological Sciences

Faculty of Science and Engineering

Flinders University

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Summary

This study examines the impacts of a novel host-parasite system for population dynamics in Darwin's finches on Floreana Island, Galápagos Archipelago. I focus in particular on the interaction between Darwin's finches and parasitic larvae of an introduced fly, *Philornis downsi*, which causes high nestling mortality. This is the first project to systematically study Darwin's finches on Floreana Island since the pioneering work of David Lack in the 1930s, and Robert Bowman in the 1960s. I provide the first descriptive study of the breeding biology of the locally endemic medium tree finch, *Camarhynchus pauper*, which – at the start of the study – was listed as "data deficient" on the IUCN RedList.

I begin with a study of the population status and population trends of finches on Floreana Island. The only population of Darwin's medium tree finches (*C. pauper*) had declined by 61% between 2004 and 2008 to ~1660 individuals. I also document evidence for lack of recruitment into the breeding population, given my finding that medium tree finches had an age-biased population, with few one year old or 5+ year old males. The survey reports on the lack of suitable habitat for highland birds. I devote several chapters to the study of the impacts of *P. downsi* on host mortality, and the potential for Darwin's finches to adapt to the negative impacts of this invasive parasite. *P. downsi* is unanimously considered the biggest threat to the survival of Galápagos landbirds, including Darwin's finches. The parasite caused 38-92% of nestling mortality across all five host species studied in this thesis. The impacts of this parasite are greatest for Darwin's tree finches (*Camarhynchus* spp) because parasite intensity is highest in their highland forest habitat. In particular, *P. downsi* is identified as the primary cause of nestling mortality in Darwin's medium tree finch. As a result of this research, the medium tree finch status

was reassessed from "vulnerable" to "critically endangered" on the IUCN RedList. Video surveillance of finch behaviour showed that parent and nestling finches now have a range of anti-parasite behaviours that can partially mitigate the impacts of the parasite, including preening and removal of larvae. Experimental studies using parasitised and parasite-free nests showed that finch parents increased food provisioning to parasitised nestlings, but did not compensate for the negative impacts of parasitism (*P. downsi* caused 92% of nestling mortality in 2010). Collectively, these findings indicate that *P. downsi* parasitism is a major conservation concern for the finches on Floreana Island. I also examine population genetic structure and gene flow between the three sympatric tree finch species on Floreana Island, and find evidence for the loss of genetic diversity in the sympatric tree finches. High levels of hybridisation were detected within the tree finch group, suggesting that the mechanism for loss of genetic diversity is via introgression with closely-related taxa, that is – "speciation in reverse".

This thesis represents a novel and multi-faceted approach to understanding the complex interactions of human impacts, introduced species, and endemic species decline in island birds. The results of this research will have immediate impacts on the development of *P*. *downsi* control programs, and highlight the need for focussed recovery plans for the medium tree finch.

Declaration

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Jody Anne O'Connor 30th September 2011

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Statement of Authorship

Chapters 1 & 8: J.O'C

Chapter 2:

Data collection: S.K. (2004), J.O'C (2008) Statistical analyses: J.O'C, F.S., S.K. Manuscript writing: J.O'C, S.K., F.S.

Chapter 3

Data collection: J.O'C Statistical analyses: F.S., J.O'C, S.K. Manuscript writing: J.O'C, S.K., F.S., J.R.

Chapter 4

Data collection: J.O'C, R.D., S.K. Statistical analyses: J.O'C, S.K. Manuscript writing: J.O'C, S.K., R.D.

Chapter 5

Data collection: J.O'C Statistical analyses: J.O'C, S.K. Manuscript writing: J.O'C, S.K., J.R.

Chapter 6

Data collection: J.O'C Statistical analyses: J.O'C, S.K. Manuscript writing: J.O'C, S.K., J.R.

Chapter 7

Data collection (field): J.O'C, S.K. Laboratory analysis of DNA samples: J.O'C Statistical analyses: J.O'C, S.M., R.D., S.K. Manuscript writing: J.O'C, S.K., R.D., S.M., F.S.

1 General Introduction

1.1 Island birds and vulnerability to extinction

Understanding and managing the causes of species decline is fundamental to the conservation of biodiversity. This study aims to identify the processes and causal mechanisms behind bird population declines in the Galápagos Islands. Endemic island birds typically exist in small populations within restricted and specialised habitat (Simberloff, 1995), where they are 40 times more likely to go extinct than continental species (Johnson and Stattersfield, 1990). Since 1800, 90% of all bird extinctions have been island taxa (Banko and Banko, 2009), and very few island systems retain their full suite of avian inhabitants. For example, habitat degradation and the introduction of predators and pathogens following human settlement has caused the extinction of 90% of Hawaiian birds (Pimm et al., 1995, Banko and Banko, 2009) and 73% of land birds on Guam (Pregill and Steadman, 2009). One in eight species of birds are at risk of becoming extinct by the year 2100 (BirdLife, 2000), and most of these threatened species are tropical forest birds on islands (Johnson and Stattersfield, 1990, Banko and Banko, 2009). The ominous history and predicted continuation of island bird extinctions has provided the impetus for this study of Darwin's finches on the Galápagos Islands. So far, no species of bird on the Galápagos has become extinct, and the archipelago retains 95% of its original biodiversity. However, there is only a small window of opportunity to identify and mitigate the threats to Darwin's finches as we are already witnessing the first local extinctions (Grant et al., 2005) and population declines across the archipelago (Curry, 1986, Dvorak et al., 2004, Fessl et al., 2010, Dvorak et al., in press). This thesis is mainly focused on conservation issues for birds on Floreana Island (Figures 1.1 & 1.2), because the island has the longest history of human settlement, has the worst record for local bird

extirpations and is home to the only population of Darwin's medium tree finch. Current population sizes and recruitment processes for Floreana birds are unknown (Chapter 2).

1.2 Darwin's finches in the Galápagos Islands

The 14 species of Darwin's finches in the Galápagos Islands are textbook examples of evolution in action. They are internationally recognized as prime examples of natural selection and adaptive radiation in a unique natural laboratory (Grant, 1999, Schluter, 2001, Grant and Grant, 2008). The ancestors of Darwin's finches traversed over >1000km of ocean to colonise the volcanic islands about 2.3 million years ago (Sato et al., 2001), where they have since evolved into a diverse and endemic group in isolation from humans, pathogens, and with few predators. Charles Darwin himself noted that: 'The natural history of this archipelago is very remarkable: it seems to be a little world within itself" (Darwin, 1839). But since Darwin's famous voyage through the Galápagos in 1835, the islands have undergone intense and rapid degradation as a result of increasing human settlement and tourism (Steadman et al., 1991, Mauchamp, 1997). In fact the most pivotal Galápagos species for the development of Darwin's theory of evolution, the Floreana Mockingbird, is now critically endangered and only persists on two small islets after being extirpated from it's main habitat on Floreana (Curry, 1986, Deem et al., 2011). Darwin's finches are now under threat as their habitat is cleared for agriculture and introduced predators and parasites consume their nestlings (Curry, 1986, Steadman, 1986, Fessl and Tebbich, 2002, Grant et al., 2005, Chapters 2-5). In particular, the accidental introduction of the parasitic fly, Philornis downsi, to the Galápagos Islands is considered the most severe and imminent threat to the survival of endemic birds. P. *downsi* has been given the highest risk ranking for invasive organisms that threaten biodiversity in the Galápagos (Causton et al., 2006).

1.3 Philornis downsi parasitism causes endemic finch declines.

Parasites have such a strong impact on bird hosts they are 'likely to play a role in practically every aspect of (avian) evolutionary biology' (Price, 1991) Although Darwin's finches are famous for rapid evolution, they have certainly met their match in the new host-parasite relationship with *P. downsi*. Adult *P. downsi* flies are vegetarian but have three free-ranging parasitic larval instar stages, which feed on the blood and flesh of nestling birds (Fessl et al., 2006b)(Figure 1.3). Parasitism results in reduced haemoglobin concentration (Dudaniec et al., 2006), multiple body wounds and infections, substantial blood loss (18-55%) (Fessl et al., 2006a, Fessl et al., 2006b), reduced growth rates (Fessl et al., 2006a), grossly deformed nasal cavities of nestlings (Fessl et al., 2006b) and deformed beaks of fledglings that survive into adulthood (Galligan and Kleindorfer, 2009). Consequently, it is not surprising that *P. downsi* parasitism was found to cause 19-76% of Darwin's finch nestling mortality across years, when studied between 1998 and 2005 (Fessl et al., 2006b)(Figure 1.3).

The detrimental impacts of *P. downsi* on Darwin's finches are well documented, but because larval parasitism occurs within finch nests at night (Fessl et al., 2006a), we have very few observations of the host-parasite interaction in the wild. Developing effective control methods requires a more detailed understanding of within-nest activity such as the fly's reproductive characteristics, larval feeding strategies, and finch antiparasite defences. This thesis represents the first study to use in-nest surveillance footage to examine real-time host-parasite interactions between Darwin's finches and *P. downsi* parasites (Chapters 5&6). Behavioural and nesting studies are used to examine the potential for Darwin's finches to adapt to parasitism, for example by showing antiparasite behaviour and altering the expression of key life history variables such as clutch size and parental care (Chapters 3-6). I quantify fledging success and causes of brood

mortality across species, habitats, and islands to examine the vulnerability of Darwin's finch species to the effects of introduced parasites and rodent predators (Chapters 3-6).

1.4 Genetic diversity and hybridisation in Darwin's finches

The evolution of Darwin's finches has been greatly influenced by the isolation of the archipelago, extreme climatic variation, and limited opportunities for dispersal (Grant, 1999, Grant and Grant, 2008). These conditions created a unique environment, which promoted rapid adaptive radiation facilitated by niche competition and character divergence between species (Grant, 1999, Grant and Grant, 2008). But human-induced landscape changes such as the introduction of new food resources, predators and pathogens can alter the evolutionary trajectory of closely-related taxa, and should be considered when evaluating modern drivers of hybridisation, speciation and extinction (Hendry et al., 2006, Taylor et al., 2006, De León et al., 2011). To date, most field research about Darwin's finches has come from long term studies of the ground finches (Geospizinae), while remarkably little is known about any aspect of the tree finches (Camarhynchus spp), including speciation scenarios, temporal and spatial patterns of hybridisation, and population genetic structure. This is the first study to systematically examine species boundaries, genetic diversity and divergence in three sympatric species of Darwin's tree finches on Floreana Island: the small, medium, and large tree finch (C. *parvulus, pauper* and *psittacula*)(Chapter 7). Notably, the medium tree finch is endemic to Floreana Island and at the time of commencing this research in 2006, the species was listed as "vulnerable" but "data deficient" on the IUCN redlist of threatened species. I studied gene flow between the three sympatric tree finch species on Floreana Island and contrasted patterns of gene flow between study years with low and high rainfall (Chapter 7). Previous research by Peter and Rosemary Grant has shown that Darwin's ground

finches are likely to hybridise during high rainfall years (Grant and Grant 1992). This finding is significant because hybridisation can result in extinction when declining taxa are genetically overwhelmed by introgression from closely-related species (Dabrowski and Fraser, 2005, Hendry et al., 2006, Taylor et al., 2006, De León et al., 2011), and this process is predicted to become increasingly prevalent as species' distributions are altered by human-induced changes (Dabrowski and Fraser, 2005, De León et al., 2011). Understanding patterns of hybridisation is therefore important for the effective conservation of sympatric populations of Darwin's tree finches that may be threatened by interspecific genetic interactions (Chapter 7).

1.5 Thesis scope and objectives

The chapters of this thesis examine the effects of bio-ecology of invasive species as well as an assessment of genetic processes that will affect the persistence of common and threatened Darwin's finch species. This information is integral to the development of control programs for invasive species and conservation management guidelines for threatened birds and habitats.

Specifically the aims of this study are to:

- Survey population numbers of Darwin's finches in the degraded highland forest of Floreana island.
- Identify the major cause of population decline in the critically endangered Darwin's medium tree finch.
- 3. Identify variation in *P. downsi* impacts and prevalence across species, years, habitats and islands.
- 4. Examine the impacts of nest predation and parasitism on the life history strategies of Darwin's small ground finch across two distinct habitats (arid lowlands and forest highlands).
- 5. Examine host-parasite interactions inside finch nests to increase our understanding of the life-cycle of *P. downsi* and the development of anti-parasite behavior in host birds.

- 6. Use experimental techniques to examine the role of parasitism on chick begging behavior and parental food compensation.
- Use molecular techniques to test the idea that hybridisation will change in frequency across years that differ in rainfall, and will affect genetic diversity in Darwin's tree finches.

1.6 Organisation of this thesis

The thesis is presented as a series of manuscripts that are either published, submitted or in preparation for publication in peer-reviewed, scientific journals. The thesis is comprised of four published papers (Chapters 2-5), one paper that is submitted and "in review"(Chapter 6), and the final paper is in preparation (Chapter 7). A general discussion of the main findings of this research and suggestions for future work is included at the end of the research chapters.



Figure 1.1 Map of the Galápagos Islands (northern islands of Darwin and Wolf not pictured). The archipelago is located 1000km west of mainland Ecuador.



Figure 1.2 Floreana Island, Galápagos. Photo shows the island's largest volcano: Cerro Pajas (around the base of which lies the highland forest zone).



Figure 1.3 a) Adult *Philornis downsi* fly, b) small ground finch (*Geospiza fuliginosa*) nestling with signs of *P. downsi* larval feeding (body wounds and enlarged nares), c) dead medium tree finch (*Camarhynchus pauper*) nestling, d) dead medium tree finch nestlings with signs of parasitism along with 2nd and 3rd instar *P. downsi* larvae collected from the same nest