Adaptive divergence, genetic connectivity, and post-parasitism morbidity in Darwin’s small ground finch, *Geospiza fuliginosa*, on the island of Santa Cruz, Galápagos Archipelago.

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A thesis submitted in fulfilment of the requirements for the

Degree of Doctor of Philosophy

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I dedicate this work first to my beautiful Zonnetje, my family, and my friends – all of whom understand why I did it; and second to all the small ground finches – all of which will never understand why I did it.

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.

Toby H Galligan

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10th January 2011

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THESIS SUMMARY

Speciation is arguably the most important problem in evolutionary biology. Following the biological species concept, speciation is the process by which populations of one species reduce inter-population mating – that is, gene flow – to the point where they become two reproductively isolated species. Gene flow can be reduced more or less incidentally by geographical isolation (i.e., allopatry), or by strong divergent selection on intrinsic barriers (e.g. immigrant inviability, divergent mate preference, or divergent mate recognition) in the same (symparty) or adjacent (parapatry) locations. In birds, the beak is used for foraging and mate recognition (e.g. song production); thereby, divergent niches or habitats can directly select for adaptive divergence in beak dimensions, while indirectly selecting for divergence in mate recognition. The significance of allopatric divergence has been long appreciated; however, the significance of sympatric and parapatric divergence remains debated (particularly in birds). Darwin's finches of the Galápagos Archipelago are a model system in which to study evolution in nature. On the island of Santa Cruz, Darwin's small ground finch *G. fuliginosa* has recently expanded its range from the arid lowlands into the humid highlands; the ecological contrast between these zones providing strong disruptive selection. Previous studies have shown evidence for adaptive divergence in this system (i.e., morphological clines along the ecological cline, environment-phenotype matching at the extreme zones, and more resightings across years of individuals with predicted trait values for each zone). My thesis has expanded on this work in five ways. First, I have used neutral molecular data to show high gene flow among all ecological zones on Santa Cruz; rejecting non-adaptive divergence in this system (Chapter 2). Second, I have shown the predicted breakdown of morphological clines under relaxed selection in a "benign" high rainfall year; which infers a central role for alternating strong and weak selection against immigrants as a mechanism of divergence in this system (Chapter 3). Third, I have revealed a loss of assortative pairing within highland-colonist *G. fuliginosa* in response to ecological opportunities and reduced interspecific competition that have followed range expansion (Chapter 4). Fourth, I have demonstrated the importance of ecological contrasts in the formation of barriers to gene flow, by showing greater divergence in song and song discrimination between lowland and highland zones, than between localities within each

zone, while controlling for geographical distance (Chapter 5). Fifth, I have shown that the introduced parasitic botfly *P. downsi*, which is causes high nestling mortality in Darwin's finches, also causes beak malformations that may significantly influence adaptation, mate recognition, and divergence in this system and this group of birds as a whole (Chapter 6). In synthesising my findings, I conclude while strong divergent selection exists between lowland and highland zones, intrinsic aspects of *G. fuliginosa* (e.g. high mobility) and Santa Cruz (e.g. no physical barriers between zones) can permit high levels of active dispersal, and probably gene flow, between zones (Chapter 3). In low rainfall periods, divergent selection and adaptive divergence is predicted to be strongest; whereas, in high rainfall years divergent selection is weakest and immigration of otherwise ill-adapted individuals is high, effectively reshuffling phenotypes among zones (Chapter 3). The long-term product of these counter processes requires further research. Yet, song discrimination in lowland *G. fuliginosa* in a high rainfall year suggests that partial barriers to gene flow may have arisen (Chapter 5).

STATEMENT OF AUTHORSHIP AND ACKNOWLEDGEMENT

This thesis represents original and independent research. I have performed all significant aspects of the research design, analysis, and interpretation.

I have presented this thesis as a series of manuscripts that are either published or "in preparation" for publication in scientific journals. Each chapter represents a separate manuscript. Published chapters are formatted according to the author guidelines for the journal of submission; bar tables and figures, which are imbedded in the text for ease of reading. The journal of submission for each manuscript is given on chapter title pages, where I have also acknowledged my collaborators as co-authors. Further acknowledgements are made at the end of each chapter. The contribution of collaborators is as follows:

Sonia Kleindorfer, my primary supervisor, instructed me in evolutionary ecology research theory, field techniques for the collection of data, and desk-top data analysis. Sonia contributed data collected prior to 2008, financial support for data collection in 2008, and comments on all manuscript drafts. Further, this research would not have been possible without Sonia's established connections with the Charles Darwin Research Station and Galápagos National Park in Ecuador.

Steve C. Donnellan, my secondary supervisor, instructed me in molecular genetics research theory, and field and laboratory techniques used to collect and analyse molecular data. Steve contributed comments to manuscript drafts were I have acknowledged him as co-author.

Frank J. Sulloway instructed me in evolutionary ecology research theory, experimental design, and statistical analysis for morphological and genetic data. Frank contributed comments to manuscript drafts were I have acknowledged him as co-author.

Terry Bertozzi and Alison J. Fitch instructed me in techniques used to collect and analyse molecular genetic data. Terry and Alison contributed comments to manuscript drafts were I have acknowledged them as co-authors.

Finally, the work represented by this thesis has adhered to the legal and ethical requirements of the Government of Australia, the Government of Ecuador, Charles Darwin Research Station (Ecuador), and Flinders University (Australia).

CHAPTER ONE

Introduction

Speciation

Speciation is arguably the most important problem in the study of evolutionary biology (Coyne and Orr 2004; Dieckmann *et al.* 2004; Grant and Grant 2008a; Price 2008). Speciation refers to the process by which a new species arises; this can occur if two or more populations of one species diverge in phenotype and/or genotype to an extent where they become reproductively isolated, cease exchanging genes freely, and thereby form two or more new species. Tens of millions of extant species and hundreds of millions of extinct species are proof of the significant influence speciation has on life. Speciation is the link between the occurrence of evolution (i.e., microevolution – genetic change within and between populations) and the vastness of diversity (i.e., macroevolution – genetic distinctness and disparity in higher taxa). As such, an enhanced understanding of the mechanisms for speciation is essential to an enhanced understanding of biodiversity and how best to conserve it.

Divergence with Gene Flow

It has long been appreciated that reproductive isolation can be achieved by completely restricting gene flow between populations by means of a physical structure in the landscape (Dobzhansky 1937; Mayr 1942, 1947). This is referred to as the *allopatric* mode of speciation, of which there are many examples that can be inferred in nature (reviewed in Coyne and Orr 2004). A good example of allopatric speciation would be two sister species each inhabiting different islands where expanses of water prevents interisland dispersal, and thereby, prevents gene flow (Mayr and Diamond 2001). In reality, many scenarios where allopatric speciation has been invoked, gene flow between divergent populations is likely to have been ongoing, but at potentially negligible levels (for example, dispersal between islands is not likely to be a singular event; *sensu* Petren *et al.* 2005). This raises two obvious questions: (1) *can speciation occur between populations where gene flow is not prevented by a physical structure in the landscape?* (2) *And if so, how significant is speciation with gene flow?* The answers are: (1) yes – speciation *can* occur between populations where gene flow is not prevented by a physical structure in the landscape; and (2) unknown – the significance of speciation with gene flow remains unknown (reviewed in Coyne and Orr 2004; see also Nosil 2008).

We refer to modes of speciation with gene flow as *parapatric* – if populations inhabit separate geographical locations – or *sympatric* – if populations inhabit the same geographical location. For these modes, it is adaptation to differing habitats (parapatric), niches (sympatric), or sexual preferences (parapatric and sympatric) that drive divergence between populations, reducing gene flow over time, and results in reproductive isolation. More recently, the parapatric and sympatric modes are often referred to together as divergence with gene flow, which serves to highlight the key difference between these modes and the allopatric mode. Another key differences is that parapatric and sympatric speciation, unlike allopatric speciation that can be driven by non-adaptive processes (i.e., genetic drift, founder effects, and inbreeding), more often represent true ecological (Schluter 2000, 2001; Rundle and Nosil 2005) and adaptive (Dieckmann *et al.* 2004) speciation; where selection for adaptive divergence overrides the homogenising effect of gene flow.

Theoretically, divergence with gene flow is plausible (Endler 1977; Coyne and Orr 2004; Dieckmann *et al.* 2004; Gavrilets 2004; Von Doorn *et al.* 2009), but there is a scarcity of convincing examples in nature (reviews in Coyne and Orr 2004; Giraud *et al.* 2008; Price 2008; Rocha and Bowen 2008). This scarcity stems from the fact that in almost all scenarios where either parapatric or sympatric speciation can be invoked, so too can the more parsimonious allopatric speciation; for example, sister species with adjacent or overlapping distributions can be explained by secondary contact following speciation in allopatry (Coyne and Orr 2004). Therefore, the true significance of the parapatric and sympatric modes of speciation in nature remains unknown; particularly in groups like birds (reviewed in Price 2008).

Studying speciation in birds

Birds represent model organisms in which to study speciation (Mayr 1947, 1963; Lack 1947, 1976; Grant 1999; Grant and Grant 2008a; Price 2008). Birds are diverse (approximately 10,000 species), are easily identified in the field (by size, shape, plumage, vocalisations, and behaviours), and generally sampled with little difficulty (because they are generally diurnal, non-reclusive, easily detectable, commonly encountered, and lack dangerous weapons). This is particularly so for the Passerines (Passeriformes) – the small to medium sized birds commonly referred to as the *song birds* or *perching birds*. Passerines also represent the most diverse group of birds; accounting for approximately half of all species. Perhaps above all, the key characteristic that makes birds ideal model organisms for divergence with gene flow research are their beaks (more accurately *bills*, however in the literature on Darwin's finches *beak* is traditionally used and therefore I use this term throughout this thesis).

A bird's beak has both an ecological and reproductive function; and thereby, links the two. Ecologically, the beak is used to acquire, manipulate, and consume food. Reproductively, the beak is used to attract, recognise, and select mates, via audible (song) and visual (size, shape, and colouration) cues. Because a bird's beak links foraging and mating behaviour, divergence in one can lead to divergence in the other (Grant 1999; Schluter 2001; Rundle and Nosil 2005; Grant and Grant 2008a; Benkman 2009). For example, if two habitats within a species' range differ in the primary type of food available, say the size of seeds, then selection would favour divergence in beak size to best adapt to foraging on large seeds in one habitat and small seeds in the other habitat. It follows that audible and visual cues that are dependent on beak size would simultaneously diverge between habitats also. For example, larger-beaked birds in one habitat may be physically constrained to sing lower frequency songs with slower trill rates and smaller-beaked birds in the other habitat may be physically constrained to sing higher frequency songs with faster trill rates (Podos 2001). Selection would also favour assortative mating between these two populations – that is, larger-beaked males and larger-beaked females more often mate than larger-beaked males and smaller-beaked females, and vice versa – so that offspring inherit the beak size adaptation favoured by their local habitat (Huber and Podos 2006). This process can continue in a positive feedback loop, increasing divergence and reducing gene flow to the point of speciation (i.e., ecological speciation: Schluter 2001; Rundle and Nosil 2005; Price 2008; or adaptive speciation: Dieckmann *et al.* 2004). Thus, a bird's beak represents a "magic trait"– that is, a trait that can facilitate reproductive isolation as a by-product of ecological divergence (Gavrilets 2004).

Of course there exist a number of alternative ecological, social, and biological mechanisms through which reproductive isolation can occur in birds and organisms in general (see Coyne and Orr 2004; Price 2008; Van Doorn *et al.* 2009); and an evolutionary ornithologist needs to be mindful of them all. However, the *beak as a magic trait* hypothesis is predicted to be particularly important in some groups of birds; including the species which I have studied here.

Darwin's Finches and the Galápagos Archipelago

Darwin’s finches and the Galápagos Archipelago make arguably the finest system in which to study the dynamics of evolution in nature (Grant 1999; Schluter 2001; Grant and Grant 2008a). This statement is based on the following facts: (1) the Galápagos Archipelago is vastly isolated from other landmasses; (2) has a simple biotic community; and (3) is subject to an irregularly alternating wet and dry climate; and Darwin’s finches (4) have adaptively radiated in the archipelago; (5) maintain high adaptive potential (i.e., behavioural and morphological flexibility); and (6) possess a “magic trait” for diversification to act on (i.e., a beak; Grant and Grant 2008a).

Expanding on these points, Darwin’s finches represent 15 species of tanager (Thraupidae) belonging to the subfamily Tholospiza (Burns 2002). All are derived from a single common ancestor that arrived in the archipelago approximately two to three million years ago, and rapidly diversified in response to ecological opportunities and a lack of inter-specific competition (Lack 1947; Grant 1999; Grant and Grant 2008a). All but one species are endemic to the Galápagos Archipelago. Phenotypically, species differ greatest in the size and shape of their beaks, with almost all having a unique set of beak dimensions that are suited for a unique niche. Notable examples are: the fine pointed warbler-like beak of the insectivorous warbler finches *Certhidea* spp.; the large curved parrot-like beak of the folivorous vegetarian finch *Platyspiza crassirostris*; and the increasingly larger pyramidoid finch-like beaks of the granivorous small, medium, and large ground finches *Geospiza fuliginosa*, *Geospiza fortis*, and *Geospiza magnrostris* (respectively). However, considerable variation in beak dimensions can occur within species as well, which is best exemplified by populations of *Geospiza conirostris* and *Geospiza difficilis* inhabiting different islands (Grant and Grant 2008a).

The Galápagos Archipelago lies on the Equator approximately 1,000 km west of continental South America. Volcanic in origin, these islands first emerged from the Pacific Ocean approximately 10 million years ago (Christie *et al.* 1992; Sinton *et al.* 1996). The archipelago’s isolation has restricted the diversity of organisms (particularly terrestrial ones) that have colonised it. Despite straddling the Equator, the Galápagos Archipelago is subject to a bi-seasonal climate influenced by ocean currents: specifically, a hot and wet season between January and May; and a cool and dry season for the rest of the year. In addition, climate in the Galápagos Archipelago is affected by the *El Niño*-Southern Oscillation, which irregularly brings brief high rainfall *El Niño* periods (spanning 1-2 years) to typically low rainfall *La Niña* periods (spanning 2-11 years) in the eastern Pacific Ocean (Snell and Rae 1999; see Chapter 3 [Fig. 2]).

Combined, the seasonal and annual climate in the Galápagos Archipelago is one of unpredictable extremes. As a result, the majority of organisms inhabiting these islands follow a boom-bust pattern of phenology. In the hot and wet season the islands' receive most of their annual rainfall and boom into life with mass plant growth and seeding, and subsequent mass reproduction in animals. In the cool and dry season the islands' receive no or very little rainfall and food production largely ceases, supply decreases, competition increases, and mortality among species increases. Alternating through *El Niño* and *La Niña* periods, this same bust-boom pattern observed annually is magnified across decades with dramatic effect on life in the Galápagos Archipelago (interestingly, what I have just described is only true for the terrestrial environment, and the marine environment responds in exactly the opposite direction: boom in the cool and dry season and in a *La Niña* year; bust in the hot and wet season and in a *El Niño* year).

Darwin's finches and the Galápagos Archipelago have enhanced our understanding of the interplay between evolution, ecology, and biology possibly more than any other system. This has been achieved through the work of many ingenious and determined researchers – David Lack, Peter Bowman, Peter Grant, Rosemary Grant, Ian Abbot, Lynette Abbott, Peter Boag, Lisle Gibbs, Laurene Ratcliffe, Dolph Schluter, Trevor Price, Ken Petren, Sonia Kleindorfer, Jeffery Podos, Andrew Hendry, Akie Sato, Lukas Keller, Sabine Tebbich, and Arhat Abzhanov: to name a few (their contributions are largely reviewed in Grant and Grant 2008a). Darwin's finches demonstrate how natural selection shapes populations (Price *et al.* 1984; Gibbs and Grant 1987; Grant and Grant 1989; Grant and Grant 2002); how one species can adaptively radiate (speciate) into many others (Lack 1947; Grant 1999; Grant and Grant 2008a); and how speciation is a process, not an event (Grant and Grant 2008a). Work in this group has shown the central importance of character displacement and release (Boag and Grant 1984; Schluter *et al.* 1985; Grant and Grant 2006, 2010; Hendry *et al.* 2009); introgressive hybridisation (Grant 1993; Grant and Grant 1992, 1994, 1996, 2008b; Grant *et al.* 2005); and underlying genes (Abzhanov *et al.* 2004, 2006) for speciation. In addition, the link between ecological adaptation and reproduction isolation via beak morphology is apparent in Darwin's finches (Ratcliffe and Grant 1983, 1985; Christensen *et al.* 2006; Huber and Podos 2006; Podos 2001, 2010).

Darwin's finches and the Galápagos Archipelago have also been central to the divergence with gene flow debate. Traditionally, adaptive radiation of Darwin's finches has been regarded a text book example of allopatric speciation: where species largely diverged on separate islands and then established their present distributions (Lack 1947; Grant 1999;

Grant and Grant 2008). However, in the last half of this decade, evidence has emerged that rejects a strict allopatric model – specifically, considerable gene flow between island populations (Petren *et al.* 2005) and species in sympatry (Grant *et al.* 2005); and suggest a potential important influence of within-island divergence – namely, adaptive divergence in a sympatric population of medium ground finch *G. fortis* (reviewed in de Leon 2010) and a parapatric population of small ground finch *G. fuliginosa* (reviewed in Kleindorfer and Mitchell 2009) both of which inhabit the central island of Santa Cruz.

Darwin's Small Ground Finch* Geospiza fuliginosa *on the island of Santa Cruz

Darwin's small ground *Geospiza fuliginosa* (Fig. 1), as its name suggests, is one of the smallest species of Darwin's finches (approximate mean weight = 14 g) and predominately forages close to or on the ground using the base of its beak to crush small seeds. *Geospiza fuliginosa* is the most abundant and widely distributed of Darwin's finches; the most recently split, evolutionarily (sister species to the medium ground finch *Geospiza fortis*; Petren *et al.* 1999); and the most generalist species, displaying a variety of foraging behaviours and consuming a diversity of prey (Bowman 1961; Kleindorfer *et al.* 2006).

Figure 1: Darwin’s small ground finch *Geospiza fuliginosa* (male aged 3-4 years). Photograph by Frank J. Sulloway.

The island of Santa Cruz is the second largest (986 km^2) and highest island (850 m a.s.l.) in the Galápagos Archipelago. It is roughly circular in shape with its highest points in the centre (see Chapter 2 [Fig. 1]); it is also middle aged for the islands in the archipelago, with no obvious crater and a considerable deposit of soil in the highlands. Rainfall (and precipitation from sea mists) increases with altitude on Santa Cruz; supporting four main ecological zones on the southern side of the island: running from the lowlands to the highlands they are the arid zone, transitional zone, agricultural zone, and humid zone. On the northern side of the island, the agricultural zone is absent, and the humid and transitional zones reduced due to southern prevailing winds and a rain shadow cast by the central peaks (at any given altitude the northern side receives less rainfall than the southern side). The extremes of the ecological gradient on Santa Cruz contrasts dramatically: dry-deciduous open forest and woodland in the arid zone; evergreen closed forest and shrubland in the humid zone. In addition, the biotic community and food productivity between these zones differs markedly; yet, *G. fuliginosa* forages and breeds in both. Therefore, *G. fuliginosa* is subjected to strong divergent natural selection within Santa Cruz.

Not having been recorded in the highlands prior to the 1960s, the current patterns of divergence in *G. fuliginosa* is the product of a recent range expansion from the lowlands. Range expansion was presumably facilitated by the invasion of small-seeding weeds – for which *G. fuliginosa* is preadapted to forage – and the local extinction of the sharp beaked finch *Geospiza difficilis* – which may have excluded *G. fuliginosa*; both changes the result of an increase in agriculture on Santa Cruz in the latter half of the 19th century. Therefore, *G. fuliginosa* on Santa Cruz are possible at a very early stage of adaptive divergence; an uncommon scenario in nature and one worth examining further.

Kleindorfer *et al.* (2006), Kleindorfer (2007), and Sulloway and Kleindorfer (in review) have shown evidence for adaptive divergence in this system. First, highland *G. fuliginosa* had longer beaks and shorter feet, and more often gleaned insects from understory foliage; whereas, lowland *G. fuliginosa* had shorter beaks and longer feet, and more often picked seed from the ground (i.e., environment-phenotype matching: Kleindorfer *et al.* 2006). Second, clines in beak length, foot size, and other traits were found along the ecological cline on the southern side of Santa Cruz (Sulloway and Kleindorfer in review). Third, morphological divergence was maintained over a six year period (i.e., 2000-2005: Kleindorfer *et al.* 2006; Sulloway and Kleindorfer in review). Fourth, individuals with morphological trait values predicted for the arid and humid zone were more often re-sighted in subsequent sampling years (i.e., trait utility: Sulloway and Kleindorfer in review). Fifth, highland *G. fuliginosa* had smaller clutch sizes, shorter renesting intervals, and reduced behavioural conspicuousness in response to higher levels of depredation (Kleindorfer 2007).

However, the above evidence may not indicate *adaptation* in its classic sense – that is, a change in phenotype as a result of increased fitness on heritable traits. Phenotypic divergence between locations can also arise through phenotypic plasticity (i.e., an individual changes its phenotype to better match the environment) or matching habitat choice (i.e., an individual changes the environment to better match its phenotype; see Edelaar *et al.* 2008). While Phenotypic plasticity is unlikely because of the high heritability of morphological traits in Darwin's finches (e.g., bill length: Boag and Grant 1978; Boag 1983); matching habitat choice is a possible factor influencing phenotypic divergence in this system, particularly given the size of Santa Cruz and the dispersal ability of *G. fuliginosa*. Matching habitat choice can initiate and accelerate local adaptation, and may enable adaptive peak shifts (Edelaar *et al.* 2008; Holt and Barfield 2008); but it may also prevent classic adaptive divergence when selection against dispersal is negligible. Therefore, an enhanced understanding of divergence and dispersal in Santa Cruz's *G. fuliginosa* across space and time is required.

Darwin's finches and the introduced botfly Philornis downsi

A topic that impinges on all research in Darwin's finches is the impact of the introduced parasitic botfly *Philornis downsi* – identified as the greatest threat to the conservation of these birds (Causton *et al.* 2006). The larvae of *P. downsi* enter the nares of nestling and feed on blood and tissues. In some years, *P. downsi* is prevalent in 100 % of nests (Dudaniec *et al.* 2007) and causes 95 % nestling mortality (Fessl *et al.* 2006). Survivors of *P. downsi* parasitism are inflicted with nares and beak malformation; however, the implications for long-term survival and beak-centred divergence are presently unknown.

Objectives of my thesis

In my thesis, I will expand the examination of adaptive divergence, range expansion, and *P.downsi*-induced impact in *G. fuliginosa* on Santa Cruz. Specifically, I will:

1. Use neutral molecular data to examine population substructure and contemporary gene flow and validate adaptive divergence between ecological zones during periods of low rainfall;
2. Use morphological and neutral molecular data to examine dispersal behaviour across ecological zones, and the effect of dispersal on morphological clines in a "benign" high rainfall year;
3. Examine positive assortative pairing within lowland-source and highland-colonist populations for divergence in mating strategies following range expansion;

4. Examine song and response to song within and between lowland and highland zones for emerging barriers to gene flow;
5. Examine environmental predictors for *P. Downsi*-induced post-parasitism morbidity, and the effect of morbidity on beak dimensions, overall development, and foraging efficiency.

I will conclude my thesis with a synthesis of my findings and suggestions for future research.

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