



## Original research article

# Naris deformation in Darwin's finches: Experimental and historical evidence for a post-1960s arrival of the parasite *Philornis downsi*

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## ABSTRACT

The rate of evolution depends on the strength of selection, which may be particularly strong for introduced parasites and their naive hosts. Because natural selection acts on phenotypes and because parasites can alter host phenotype, one fruitful starting point to measure the impact of novel pathogens is to quantify parasite-induced changes to host phenotype. Our study system is Darwin's finches on Floreana Island, Galápagos Archipelago, and the virulent fly larvae of *Philornis downsi* that were first discovered in Darwin's finch nests in 1997. We use an experimental approach and measure host phenotype in parasitized and parasite-free chicks in Darwin's small ground finch (*Geospiza fuliginosa*). Beak size did not differ between the two treatment groups, but naris size was 106% larger in parasitized chicks (~3.3 mm) versus parasite-free chicks (~1.6 mm). To test if *P. downsi* was present prior to the 1960s, we compared naris size in historical (1899–1962) and contemporary birds (2004–2014) on Floreana Island in small ground finches (*G. fuliginosa*) and medium tree finches (*Camarhynchus pauper*). Contemporary Darwin's finches had significantly larger naris size (including extreme deformation), whereas historical naris size was both smaller and less variable. These findings provide the first longitudinal analysis for the extent of *P. downsi*-induced change to host naris size and show that Darwin's finches, prior to the 1960s, were not malformed. Thus natural selection on altered host phenotype as a consequence of *P. downsi* parasitism appears to be contemporary and novel.

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## 1. Introduction

Natural selection acts on phenotypes (Endler, 1986; Mayr, 1963), and parasites may alter the phenotype of their hosts (Moore, 2002; Poulin, 2011). For these reasons, parasites can drive population divergence of hosts and increase the rate of evolution among host populations whenever parasites alter host phenotypes (Karvonen and Seehausen, 2012; Maan and Seehausen, 2011; Miura et al., 2006; Schmid-Hempel, 2011). To understand the mutual evolutionary impact of parasites and hosts, it is necessary to measure phenotypic change in hosts and parasites as the outcome of the association. A growing number of examples showcase the remarkable capacity of parasites to change host morphology, host behavior, and host microhabitat selection—presumably to increase parasite fitness (Barber et al., 2000; Bass and Weis, 1999; Combes, 1991; Poulin, 2010; Seppälä et al., 2005; Thomas et al., 2010). But few studies have provided compelling evidence that the

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parasite is the sole cause of the altered host phenotype or measured changes in parasite fitness due to changes in host phenotype (Poulin, 1995). Phylogenetic and detailed species-level insights from host–parasite associations are limited due to the unknown onset of most host–parasite associations in the wild. Clearly, a temporal framework of known host–parasite association would provide a useful benchmark to test evolutionary patterns in hosts and parasites (Blanquart et al., 2013; Kaltz and Shykoff, 1998). Studies with known onset of host–parasite association combined with experimental approaches to identify parasite-induced changes in host phenotype will allow quantification of natural selection on parasite-altered host phenotype (Carius et al., 2001; Clayton et al., 1999; Fessl et al., 2006a).

By definition, parasites consume resources from a host at a fitness cost to the host (Loye and Zuk, 1991). It can be difficult to measure the fitness cost of parasites under conditions of age-specific parasitism, because some effects of parasites may persist in hosts for the short-term while others result in permanent change (Galligan and Kleindorfer, 2009). Parasites can cause short-term deformation in the host, such as tissue damage (which can subsequently heal) and/or long-term malformation caused by parasite-induced developmental instability (Møller, 1996). Hence, depending on parasite-induced deformation or malformation, different host phenotypes are expressed at different developmental stages and for different periods of time (Galligan and Kleindorfer, 2009; Møller, 2006). In order to quantify phenotypic changes in hosts with age-specific parasitism, it is important to distinguish between deformation, which is generally an extrinsic process, and malformation, which is an intrinsic and developmental process, although it may be triggered by extrinsic influences, including initial deformation by a parasite. When malformation has been identified, selection can be measured at different life stages as the malformation persists across an individuals' lifespan after the organism has survived earlier parasitism (Galligan and Kleindorfer, 2009; Goodman and Johnson, 2011; Johnson et al., 2002).

The recently discovered host–parasite association between Darwin's finches and parasitic larvae of *Philornis downsi* on the Galápagos Archipelago provides a timely case study to measure parasite-induced changes in host phenotype on the one hand, and on the other hand, to use this information to assess whether the parasite was present on the Galápagos Islands prior to the 1960s. We focus on this date because the first known *P. downsi* sample is from an insect collection made on Santa Cruz Island in 1964 (Causton et al., 2006; Dudaniec and Kleindorfer, 2006). Given ample historical collections of Darwin's finch species by the Stanford University expedition led by Robert Snodgrass and Edmund Heller (1898–1899), the expedition of the California Academy of Sciences (1899, 1905–1906, 1932), and later by Robert Bowman (in the 1950s and 1960s), one can access historical specimens against which to compare contemporary host phenotype. If historical specimens do not contain *P. downsi*-induced changes in host phenotype, we can conclude that *P. downsi* was introduced post-1960s. Determining the decade of introduction of *P. downsi* is crucial to modeling the strength of selection and rates of evolution in host–parasite associations across Galápagos species and islands in order to predict trajectories for population extinctions and/or local host–parasite adaptedness (Boyer, 2008; Fessl et al., 2010; Jarvi et al., 2001; Kaltz and Shykoff, 1998; Koop et al., 2015).

In 1997, larvae of *P. downsi* were first discovered in Darwin's finch nests on Santa Cruz Island (Fessl et al., 2001), though the adult fly was retrospectively found in insect collections from this same island in 1964 (Causton et al., 2006, 2013). Our study site, Floreana, lies 50 km to the south of Santa Cruz. Both islands have settlements that have long been interconnected by boat travel. Floreana was first settled in 1832, three years before Darwin's historic visit with H.M.S. *Beagle*, and Santa Cruz was colonized in the 1920s, when a group of Norwegians established a fishing cannery on the island (Latorre, 1999). During and after World War II, fishermen and supply vessels were increasingly frequent visitors to these two islands, as well as to settlements located on two other islands. *Philornis* has recently been detected on the Ecuadorian mainland, and it probably arrived from the mainland on a cargo vessel (Bulgarella, 1999). Once introduced – most likely to Santa Cruz Island – this insect would easily have dispersed throughout the archipelago, either by active flight, wind, or conveyance on ships. Two wasp species (*Polistes versicolor* and *Brachygastra lecheguana*) and a species of black fly (*Simulium bipunctatum*) are known to have arrived in the Galápagos in the 1980s and 1990s, and all three species spread from their initial point of introduction to other islands in less than a decade (Heraty and Abedrabbo, 1992; Roque-Albelo and Causton, 1999). *Philornis* is now known to be present on 13 of the 16 major islands in the Galápagos group (Causton et al., 2013).

The *P. downsi* larvae consume the blood and tissue of developing birds and are considered the biggest risk to survival among all Galápagos land birds (Causton et al., 2013; O'Connor et al., 2010d). Among Darwin's finches, in-nest chick mortality due to *P. downsi* has been 3%–100% across years (Cimadom et al., 2014; Dudaniec and Kleindorfer, 2006; Dudaniec et al., 2007; Fessl et al., 2010; Huber, 2008; Kleindorfer et al., 2014b; Knutie et al., 2014; O'Connor et al., 2010d). From previous study, including experimental manipulation and in-nest video cameras, we know that 1st instar larvae reside inside the nares of developing birds where they feed on the soft keratinous tissue (Fessl et al., 2006a,b; O'Connor et al., 2010b, 2014). The 2nd and 3rd instar larvae feed on chicks internally and externally, and they subsequently pupate inside the nest base before emerging as adult flies after 10–14 days (Fessl et al., 2006a,b). The few surviving Darwin's finch chicks fledge with varying levels of naris deformation (enclosed with pupae, normal, or empty and enlarged) that persists into adulthood as varying degrees of naris malformation (Galligan and Kleindorfer, 2009).

In this study of small ground finch (*Geospiza fuliginosa*) and medium tree finch (*Camarhynchus pauper*) on Floreana Island, Galápagos Archipelago, we have two main aims. (1) We use an experimental approach to test the magnitude of naris deformation in developing *G. fuliginosa* chicks due to *P. downsi* parasitism. (2) We also examine naris size among adult *G. fuliginosa* and *C. pauper* across three time periods in order to compare patterns of parasite-induced host malformation across the past century. The historical samples, which are divided into two temporal subsamples, consist of collections made between 1899 and 1962. Contemporary samples are part of an ongoing long-term field study from 2004 to 2014. We test the

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