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Taxonomic Shifts in *Philornis* Larval Behaviour and Rapid Changes in *Philornis downsi* Dodge & Aitken (Diptera: Muscidae): An Invasive Avian Parasite on the Galápagos Islands

Lauren K. Common, Rachael Y. Dudaniec,
Diane Colombelli-Négrel and Sonia Kleindorfer

Abstract

The parasitic larvae of *Philornis downsi* Dodge & Aitken (Diptera: Muscidae) were first discovered in Darwin's finch nests on the Galápagos Islands in 1997. Larvae of *P. downsi* consume the blood and tissue of developing birds, causing high in-nest mortality in their Galápagos hosts. The fly has been spreading across the archipelago and is considered the biggest threat to the survival of Galápagos land birds. Here, we review (1) *Philornis* systematics and taxonomy, (2) discuss shifts in feeding habits across *Philornis* species comparing basal to more recently evolved groups, (3) report on differences in the ontogeny of wild and captive *P. downsi* larvae, (4) describe what is known about adult *P. downsi* behaviour, and (5) discuss changes in *P. downsi* behaviour since its discovery on the Galápagos Islands. From 1997 to 2010, *P. downsi* larvae have been rarely detected in Darwin's finch nests with eggs. Since 2012, *P. downsi* larvae have regularly been found in the nests of incubating Darwin's finches. Exploring *P. downsi* ontogeny and behaviour in the larger context of taxonomic relationships provides clues about the breadth of behavioural flexibility that may facilitate successful colonisation.

Keywords: *Protocalliphora*, *Passeromyia*, *Philornis*, nest larvae, hematophagous, subcutaneous, Darwin's finches, Passeriformes

1. Introduction

Three genera of flies within the order Diptera have larvae that parasitise avian hosts: *Protocalliphora* Hough (Calliphoridae), as well as *Passeromyia* Rodhain & Villeneuve (Muscidae) and *Philornis* Meinert (Muscidae). The adult flies in these genera are free-living and do not parasitise birds, but their larvae develop in the nests of altricial birds, feed on their avian hosts, and exhibit feeding behaviours

from hematophagy to coprophagy [1, 2]. Most larval infestations have been documented in host nests of the order Passeriformes, but larvae have also been found in nests of Accipitriformes, Apodiformes, Strigiformes and other avian taxa (*Protophormia*: [3]; *Passeromyia*: [4]; *Philornis*: [5, 6]). The effect of these parasitic fly larvae on host survival can be severe to mild, depending on many factors including host population size, body size, nesting density and the presence of behavioural or immunological defence mechanisms [6–8].

Protophormia is widely distributed throughout the Holarctic and contains 40+ species with obligate avian parasitic larvae [3]. Within Muscidae, only *Passeromyia* and *Philornis* larvae parasitise birds [4, 9, 10]. Both *Passeromyia* and *Philornis* are members of the subfamily Cyrtoneurinae, however their complete evolutionary relationships have yet to be resolved [11, 12]. Due to the similarities between *Passeromyia* and *Philornis*, many workers regarded the two genera as close relatives, including Skidmore [9], who stated that their similarities could not be based on convergent evolution alone. The five *Passeromyia* species include *P. steini* (Pont), *P. heterochaeta* (Villeneuve), *P. indecora* (Walker), *P. longicornis* (Macquart) and *P. veitchi* (Bezzi), and are distributed throughout Europe, Africa, Asia and Australasia [4, 13]. *Passeromyia* species differ in their larval habits. For example, *P. steini* larvae scavenge nests for organic matter and *P. indecora* larvae consume host resources as subcutaneous parasites. The 52 *Philornis* species are distributed primarily in Neotropical South America and southern North America [1, 2, 10]. *Philornis* species also show a wide range of feeding habits, including free-living coprophagous larvae, free-living semi-hematophagous larvae, and subcutaneous hematophagous larvae (Table 1). One species, *P. downsi*, is a recently discovered invasive species on the Galápagos Islands [14, 15]. Its semi-hematophagous larvae cause significant in-nest host mortality in their novel Galápagos land bird hosts [16]. Cladistics and molecular phylogenetic analyses suggest that the parasitic larval habits of *Passeromyia* and *Philornis* evolved independently [10, 12] despite the similarities between both genera including cocoon-wrapped puparia, life history, and clade.

The Galápagos Islands have been listed as a World Heritage site in 1978. Given a suite of threats, including introduced species, the archipelago was added to the ‘List of the World Heritage in Danger’ in 2007 and then removed from this list in 2010 because of actions by the Government of Ecuador to reduce invasions [17, 18]. Biological invasion is considered the greatest threat to biodiversity in the Galápagos Islands [19]. Currently, 543 terrestrial species have been introduced, of which 55 are considered harmful or potentially harmful to native biodiversity [17].

In this chapter, we consider changes in the development and behaviour of the accidentally introduced fly *P. downsi* Dodge and Aitken (Diptera: Muscidae), that is now considered the biggest threat to the survival of Galápagos land birds [20]. The first *P. downsi* larvae were collected from Galápagos land bird nests on Santa Cruz Island in 1997 [21]. From examination of museum specimens collected in 1899 (during the Stanford University Expedition led by Robert Snodgrass and Edmund Heller), in 1905–1906 and 1932 (during expeditions sponsored by the California Academy of Sciences), and in 1962 (by Robert Bowman) on Floreana Island, there is no current evidence to suggest *P. downsi* was present or abundant on the Galápagos Islands prior to 1964, though this is possible [22, 23]. By collating information from a range of researchers investigating *Philornis* in general and *P. downsi* in particular, we aim to improve our understanding of the ontogeny and behaviour of an invasive *Philornis* species within the larger context of Dipteran parasites of birds. We review *Philornis* systematics and taxonomy, discuss feeding habits across *Philornis* species, report on differences in the ontogeny of wild and captive *P. downsi* larvae, report on adult *P. downsi* behaviour, and describe changes in *P. downsi* behaviour since its discovery on the Galápagos Islands.

Aitkeni group	Larval habits	Falsificus group	Larval habits	Angustifrons group	Larval habits
<i>P. fasciventris</i> [37]	FLC	<i>P. fumicosta</i>		<i>P. downsi</i> [30]	FLSH
<i>P. schildi</i>		<i>P. univittatus</i>		<i>P. niger</i> [1, 30]	SubH
<i>P. amazonensis</i>		<i>P. grandis</i>		<i>P. porteri</i> ¹ [43]	SubH
<i>P. lopesi</i>		<i>P. sabroskyi</i>		<i>P. mimicola</i> ² [40]	SubH
<i>P. aikteni</i> [30]	FLC	<i>P. falsificus</i> [1, 30]	FLSH	<i>P. sperophilus</i> [1]	SubH
<i>P. zeteki</i>				<i>P. carinatus</i> [47]	SubH
<i>P. rufoscutellaris</i> [36]	FLC			<i>P. deceptiva</i> [48, 49]	SubH
<i>P. rettenmeyeri</i>				<i>P. trinitensis</i> [30]	SubH
<i>P. setinervis</i>				<i>P. glaucinis</i> [30]	SubH
				<i>P. pici</i> [24]	SubH
				<i>P. vespodicola</i> ³ [2]	SubH
				<i>P. medianus</i> [33]	SubH
				<i>P. vulgaris</i> [1]	SubH
				<i>P. masoni</i>	SubH
				<i>P. diminutus</i> [1]	SubH
				<i>P. querulus</i> [30]	SubH
				<i>P. albuquerquei</i>	
				<i>P. frontalis</i> [1]	SubH
				<i>P. gagnei</i> [33]	SubH
				<i>P. insularis</i> [33]	SubH
				<i>P. obscurinervis</i>	
				<i>P. petersoni</i>	
				<i>P. torquans</i> [1]	SubH
				<i>P. angustifrons</i> [30]	SubH
				<i>P. bellus</i> [2]	SubH
				<i>P. sanguinis</i> [30]	SubH
				<i>P. seguyi</i> ⁴ [50, 51]	SubH

¹Some *P. porteri* larvae found in ear canals and nares of nestlings; some later instars found feeding externally on abdomen and wings [41, 43].
²*P. mimicola* larvae found in the nasal cavity of owls, mainly subcutaneous on body [40].
³Only known specimens of *P. vespodicola* collected from nests of the wasp *Paracharitopus frontalis* (Hymenoptera: Vespidae) [2, 29].
⁴*P. nielsenii* proposed synonym of *P. seguyi* [34].

Table 1.
Philornis species ordered according to taxonomy, from the most basal ‘aitkeni-group’ to the most recently evolved ‘angustifrons-group’ (groups from [33]). Larval feeding habits are shown where known and abbreviated as follows: free-living coprophagous larvae (FLC), free-living semi-hematophagous larvae (FLSH), subcutaneous hematophagous larvae (SubH). The following nine species are not included in the list as they are currently not assigned to a taxonomic group [33] given insufficient information: *P. molesta*, *P. nielsenii*, *P. blanchardi*, *P. cinnamomina*, *P. convexus*, *P. mima*, *P. obscurus*, *P. steini*, *P. umanani*.

2. *Philornis* systematics and taxonomy

Macquart [24] provided the first description of *Philornis* larvae when he described *Aricia pici*; a subcutaneous larval parasite found on an adult Hispaniolan woodpecker (*Melanerpes striatus*; previously *Picus striatus*) Muller (Piciformes: Picidae). Meinert [25] erected the genus *Philornis* for the single species, *P. molesta*,

based on larvae with distinctive posterior spiracles found parasitising nestlings. At this time, *Philornis* was suggested to be a synonym for *Protocalliphora* and assigned to the family Calliphoridae [26]. In 1921, Malloch [27] proposed the genus *Neomusca* based on adult specimens, whereas the genus *Philornis* was based on larval characters. Aldrich [28] revised this group and synonymized *Neomusca* with *Philornis* as independent genera, assigning both within the family Muscidae (Anthomyiidae at the time). This revision was supported by further work on *Philornis* species, as new and previously described species were transferred from other genera including *Hylemyia*, *Mesembrina*, *Neomusca* and *Mydaea* [9, 28–31]. *Philornis* adults are distinguished from other muscid genera by the presence of hair on the anepimeron and the postalar wall [1, 32].

Using morphological and ecological data, *Philornis* can be divided into three phylogenetic groups: the ‘*aitkeni*-group’, the ‘*falsificus*-group’ and the ‘*angustifrons*-group’ [33]. Male characters (given few female specimens) generally define the most basal lineage of *Philornis*, the ‘*aitkeni*-group’, including enlarged upper eye facets in holotypic males [29, 33]. The members of this group display adult character states that are considered primitive among muscids (i.e., enlarged upper eye facets and presence of cilia on the surface of the wing vein R_{4+5}) [33]. This group includes *P. aitkeni* (Dodge), *P. rufoscutellaris* (Couri), and *P. fasciventris* (Wulp). The phylogeny of the *aitkeni*-group is not completely resolved because of missing information about life history and morphology, as female and larval specimens are not available for many species. The second group, the *falsificus*-group, is defined primarily by *P. falsificus* (Dodge and Aitken), whose larvae are free-living [9]. Common morphological characters include five scutellar marginal setae that also place *P. fumicosta* (Dodge), *P. univittatus* (Dodge), *P. grandis* (Couri) and *P. sabroskyi* (Albuquerque) within this group [33]; however, data on the ecology of these species are missing. More information on larval life history is necessary to confirm whether species other than *P. falsificus* belong in this lineage. Despite a similar life history to *P. falsificus*, *P. downsi* is not within the *falsificus*-group [1, 9, 33], but forms a sister-group to all species within the *angustifrons*-group for which larval habits have mostly been documented (Table 1). The *angustifrons*-group is the most recently evolved and largest of the three *Philornis* lineages and contains species with subcutaneous hematophagous larvae as well as *P. downsi* with semi-hematophagous larvae.

Comparative taxonomic analyses of *Philornis* species have been hampered by a lack of specimens and information [9]. For several species of *Philornis*, their morphological descriptions are based solely on one sex, generally males. In others, the holotype is missing or destroyed, and so other traits and ecological information are missing. *Philornis blanchardi* (Garcia) has been originally identified and described in Argentina from a single female specimen, which has since been lost [34]. This specimen may belong to a previously described species as it has not been captured and identified since, however the original description is considered sufficiently unique that it may be a separate species [34]. The single male holotype used to describe *P. umanani* (Garcia) has also been lost and due to the lack of detail provided in the original description, this species is deemed unrecognisable and is now considered a *nomen dubium* [34]. Evidence of a *Philornis* species complex within specimens of *P. seguyi* (Garcia) and *P. torquans* (Nielsen) in Argentina throws further doubt on the original taxonomic characterisation of many *Philornis* species [35]. These issues highlight the need for more extensive molecular and morphological analysis of currently recognised *Philornis* species to confirm species classifications and their evolutionary relationships.

3. Larval feeding habits across *Philornis* species

3.1 *Philornis* larval behaviour

Philornis species differ in their larval feeding habits, which include coprophagous and hematophagous diets (**Table 1**). Larval habits have been documented for 30 out of 52 described species (**Table 1**). The most basal group in the *Philornis* phylogeny (*aikteni*) have free-living coprophagous larvae [33]. These larvae parasitise cavity nesting host species that do not remove waste, such as the rufous-tailed jacamar (*Galbula ruficauda*) Cuvier (Piciformes: Galbulidae) and appear to be specific to this type of nest [2, 5, 30, 36, 37]. Free-living saprophagous larvae in the nest are regarded as the ancestral trait, evolving into coprophagous larvae, semi-hematophagous larvae and then subcutaneous larvae [9, 33]. This transition is also supported in *Passeromyia* where species show a similar order of descent [4, 10, 33]. Two documented species, *P. downsi* (*angustifrons*-group) and *P. falsificus* (*falsificus*-group), have free-living and semi-hematophagous larvae, although other undescribed species within the *falsificus*-group may also have free-living larvae [1, 30, 33].

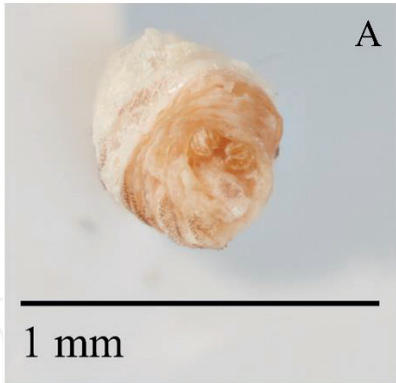
Most *Philornis* species (83%) have larvae with subcutaneous hematophagous feeding habits, which is also the primary larval strategy in the *angustifrons*-group. Within this group, only *P. downsi* has non-subcutaneous larvae. The semi-hematophagous *P. downsi* larvae may be similar to *P. falsificus* (*falsificus*-group), which is also suspected of having free-living semi-hematophagous larvae [33]—but not enough is known about the biology of the *falsificus*-group. While *P. falsificus* is considered a free-living ectoparasite [30], this assessment is limited by the observations to date of later instars and puparia [38, 39]. On the other hand, in two species with subcutaneous feeding habits in the *angustifrons*-group, a few *Philornis* larvae have been also observed in avian nares. Specifically, *P. mimicola* larvae have been found in the nares of ferruginous pygmy-owl nestlings (*Glaucidium brasilianum*) Gmelin (Strigiformes: Strigidae), but most larvae occurred subcutaneously [40]. Larvae of *P. porteri* (Dodge) have been found in the nares and ear canals of some nestlings [41, 42], and 3rd instar larvae observed to feed externally on the abdomen and wings of their hosts [41, 43]. In the semi-hematophagous *P. downsi* larvae, 1st instars regularly reside within the avian nares [44–46] and later instars move to the base of the nest where they emerge at dusk and dawn to feed externally on the blood and tissue of the developing birds [45, 46]. Lineages with free-living larvae have been far less studied than lineages with subcutaneous larvae (**Table 1**). Free-living larvae move freely within the host nest, detach from the host at various times and reside in the nest base during the day, making them less conspicuous to human observers [45, 46]. In contrast, subcutaneous larvae reside under the skin of the host and hence can be detected when nestlings are examined.

4. *Philornis downsi* larval development in the wild and in the laboratory

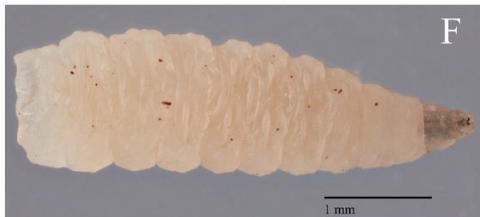
4.1 *Philornis downsi* larval instars

Philornis downsi larval development is split into three instar development stages. 1st instar larvae generally reside in the naris and ear canals of developing nestlings, but some have also been found moving freely within the nesting material [21, 52, 53]. First instars are commonly collected from 2 to 3 day old nestlings [43]. Late 2nd and 3rd instar larvae are generally free-living, residing within the base of the nest and feeding externally on nestlings at night [14, 45, 46]. These later instar larvae feed

1.1 First Instar



1.2 Second Instar



1.3 Third Instar

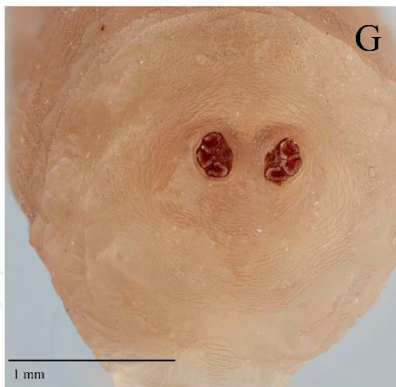


Figure 1. Three larval stages of *Philornis downsi*. (1) First instar: (A) posterior spiracles, (B) lateral view, (C) ventral view. (2) second instar: (D) posterior spiracles, (E) lateral view, (F) ventral view. (3) third instar: (G) posterior spiracles, (H) lateral view, (I) ventral view. Obtained by the authors from larvae collected on Floreana Island, Galápagos, Ecuador between 2010 and 2014. The photographs were taken using a visionary digital LK imaging system (dun, Inc) with a canon EOS 5DsR camera and capture one pro 11.3.1, phase one (Flinders University). Images were produced using Zerene stacker 1.04, Zerene systems LLC, software, and cropped and resized in Photoshop CS5.

on the blood and fluids of their host by penetrating the skin of the nestlings [2, 30]. Larval instar morphological descriptions are given by Fessl et al. [44]. The most distinct character between the instars is the posterior spiracles, which change in colour, shape and number of spiracular slits present throughout larval development [44].

Figure 1(1A) shows the posterior spiracles of a 1st instar *P. downsi* larva, characterised by their light pigmentation and two oval slits present [44]. The spiracles of a

1st instar larva are separated by slightly more than their diameter. First instar larvae lack anterior spiracles (**Figure 1(1B)**). The posterior spiracles of a 2nd instar larva are similarly round with two oval slits; however, the distance between them is two to three times of their diameter (**Figure 1(2D)**; [44]). Anterior spiracles are present during the 2nd instar, and semicircular in shape, lightly pigmented and visible in (**Figure 1(2E)**). 3rd instar posterior spiracular plates are darkly pigmented and round in shape, distinct C-shaped spiracular slits radiate from median ecdysial scar (**Figure 1(3G)**). Pigmentation of the median ecdysial scar is light in early 3rd instar larvae and becoming darkly pigmented later in the stage. Semi-circular anterior spiracles are retained in 3rd instar larvae (**Figure 1(3H)**). Cephaloskeleton morphology differs between instars as outlined in Fessl et al. [44]. Recent studies report a decrease in *P. downsi* puparia size across 2004–2014 [54]. Common et al. (unpublished data), and hence body size is certainly not a useful method to classify instars. In general, it is recommended to use a suite of morphological characters, including anterior and posterior spiracular morphology, to determine the larval instar.

4.2 Larval development

The developmental period of *Philornis* larvae is associated with the species' larval feeding habit. For example, time to pupation in coprophagous species takes up to 29 days, but only 4–8 days in subcutaneous species [2, 55]. Larval development periods in free-living species such as *P. downsi* are difficult to determine in the wild as the host nest needs to be dismantled to observe the larvae. Early studies of abandoned or failed nests found 1st instar larvae in nests with 1–3 day old nestlings, 2nd instars in nests with 3–6 day old nestlings and 3rd instars in nests with 3–10 day old nestlings [44]. Larval collections following the cessation of activity at host nests suggest that the minimum time for pupation in *P. downsi* is 4–7 days [54].

Compared with larval development times in the wild, larval development times under laboratory conditions are longer. First attempts to rear *P. downsi* larvae in the absence of a living host had a low success rate, with only three larvae out of 477 reaching the adult stage after a 36 day development time (mean 18 day larval development, 12 day pupation) [56]. As the diet for rearing larvae in captivity was refined, the success rate increased to 10% and larval development time decreased [57]. Development time in the laboratory ranged from 9 to 10 days from larva to pupa [57] with even faster development times occurring as the rearing conditions have improved [pers. comm. P. Lahuatte]. Egg hatch rates in captivity have been high (96%), with most mortality in 1st instar larvae (77%) [57]. Laboratory-based diets that have been developed in the absence of a bird host are primarily based on chicken blood, with more successful diets including hydrolysed protein and vitamin fortification [57]. The lack of keratin in the diet may be causing elevated 1st instar mortality, as 1st instars consume the keratin of the beak in which they reside [44], however the true cause is unknown.

5. *Philornis downsi* adult behaviour

The behaviour of adult *P. downsi* is much less understood than that of the larvae. The adult fly is vegetarian, feeding on decaying fruits and flowers, including the invasive blackberry (*Rubus niveus*) Thunb (Rosales: Rosaceae) [9, 15, 31]. *Philornis downsi* is commonly attracted to a mix of blended papaya and sugar, which is used to trap adult flies (developed by P. Lincango and C. Causton; used by [58], Causton et al. in review). This mix is particularly attractive to adult flies due to the presence of yeast and fermentation products such as ethanol and acetic acid [59].

A one-year study on Floreana Island found that male and female *P. downsi* display dimorphic flight patterns, with females more likely to be caught in high and low traps (2 m, most common at 6–7 m), and males more likely to be caught in traps of intermediate height (4–5 m) [58]. As the pattern of male and female abundance are quadratic opposites, this has tentatively been suggested to be an advantage for females to avoid male flies, as frequent mating in other Dipterans has been found to decrease female reproductive success and lifespan [60, 61]. This flight pattern may also explain why certain host species experience higher parasite intensities, such as the medium tree finch (*Camarhynchus pauper*) Ridgway (Passeriformes: Thraupidae) that has an average nest height of 6 m, thus making it more susceptible to being encountered by female *P. downsi* [58, 62, 63]. However, the factors that cause bird species to experience differing intensities of *P. downsi* are complicated and vary between years. Comparison of flight height in *P. downsi* on different islands is needed to test the generality of this pattern, which may be influenced by average tree height and/or other ecological variables.

5.1 Mating behaviour

The mating behaviour of *Philornis* in general is not well understood, though there are some insights into *P. downsi* mating patterns. While mating has not been observed at or inside the nest, multiple *P. downsi* flies have been video recorded to enter host nests concurrently [45, 64]. Analysis of offspring genetic relatedness has provided estimates of the re-mating frequency of *P. downsi* [65]. Evidence for multiple mating by females has been frequently detected, and each larval infrapopulation (i.e., within nests) is sired by 1–5 males (average ~1.9 males per female) [65]. How *P. downsi* adults find each other to initiate mating is unknown. Pheromones for attraction and aggregation in muscid flies have been identified and studied [66–68]. Cuticular compounds show promise for determining if *P. downsi* produces pheromones, as females and mature males showed distinct cuticular profiles and females respond to chemicals produced by males [69–71]. Cuticular profiles could be developed as an attractant to capture flies in the field [20, 72].

5.2 Oviposition behaviour

Studies into oviposition in the genus *Philornis* have revealed that species spanning diverse larval feeding habits are oviparous [1, 9, 31, 73, 74]. This current view has previously been hotly debated, in part because the majority of species remain unstudied. Laboratory rearing and field observation have confirmed that *P. downsi* is oviparous [45, 56, 57, 75]. *Philornis* flies enter and oviposit in nests regardless of nesting phase or nestling age but have not been observed to enter nests abandoned by the parent birds during the incubation phase [45, 47]. From in-nest video recordings, *P. downsi* flies have been observed entering nests throughout the day, but generally during dusk between 1500 and 1800, with visiting rates peaking around 1700 [45, 64]. Visit length averaged 1.3–1.5 min and occurred most commonly when the adult host is away from the nest and completed once the adult host returned [45, 64]. Eggs have been generally deposited on nesting material and the base of the nest [45, 57], however on one occasion, eggs have been also laid directly by the naris of a nestling [45]. A genetic study of *P. downsi* larvae estimated that 1–6 adult females (average ~3 females) oviposit within a single nest, supporting previous observations of different sized larval groups within nests and suggesting repeated nest infestations throughout the nestling period [7, 65].

5.3 Effects of host species on *Philornis* behaviour and microbiome

Philornis downsi is one of the most generalist species within the genus, known to infest 38 host species across avian taxa [5, 6, 76]. However, this high host number may reflect the large number of studies focused on *P. downsi* due to its invasive status on the Galápagos Islands [15, 16].

It is currently unclear how *Philornis* species in general or *P. downsi* in particular find their hosts. Preliminary studies into the role of semiochemicals and volatiles in host nests as an attractant for *P. downsi* have produced inconclusive results [70]. Long-term ornithological field studies have provided some hints that the intensity of host cues may be relevant for *P. downsi* search behaviour, or alternatively that the density of host nests influences *P. downsi* oviposition behaviour. Aggregated host nests may attract *P. downsi* females due to an increase in olfactory or visual cues. These aggregated nests also provide a greater opportunity for *P. downsi* females to infest multiple nests. Indeed, small tree finch nests (*Camarhynchus parvulus*) Gould (Passeriformes: Thraupidae) with close neighbours contained more *P. downsi* larvae compared to solitary, more isolated nests [16]. Nests in areas of lower nesting density (i.e., lowlands) have been more likely to contain the offspring of a single *P. downsi* female than nests in areas of higher nesting density (i.e., highlands) that are more likely to contain the offspring of many *P. downsi* females [65]. Video recordings of adult *P. downsi* have been made inside the nests of the small ground finch (*Geospiza fuliginosa*) Gould (Passeriformes: Thraupidae), medium ground finch (*G. fortis*) Gould (Passeriformes: Thraupidae), small tree finch (*C. parvulus*) and Galápagos flycatcher (*Myiarchus magnirostris*) Gould (Passeriformes: Tyrannidae) [45, 64] (Pike et al. in prep). However, despite a combination of video recorders inside or outside the nest across studies, the recordings did not reveal information about *P. downsi* search behaviour from its flight behaviour.

A metagenomic study into *P. downsi* larval microbiome sampled from different host species found an effect of host diet on the gut bacterial community of *P. downsi* larvae [77]. Larvae retrieved from strictly insectivorous warbler finch (*Certhidea olivacea*) Gould (Passeriformes: Thraupidae) nests have a different microbiome structure compared with larvae parasitising hosts with broader dietary preferences (ground and tree finches, *Geospiza* and *Camarhynchus* sp., respectively) [77]. The gut microbiome also differed between *P. downsi* larvae (blood diet) and adults (plant diet), supporting the hypothesis that *P. downsi* microbiome changes during development and according to diet [77]. Further behavioural, biochemical and genetic studies are needed to understand *P. downsi* oviposition across host species, host locating behaviour and host specificity.

6. Changes in *P. downsi* behaviour since colonising the Galápagos Islands

6.1 Age of larval cohort in host nests

There is evidence that the oviposition behaviour of female *P. downsi* has changed since its discovery on the Galápagos archipelago. *Philornis downsi* flies are now known to oviposit during any stage of the nesting cycle [45]. In the first decades following initial discovery of *P. downsi* in Darwin's finch nests, changes in the proportions of instar classes among *P. downsi* have been observed, with evidence that oviposition occurred earlier and more synchronously in the nesting phase in the later years of the study [54]. Synchronisation in oviposition date may lead to an increase in larval competition for host resources, and as a consequence result in increased virulence for nestlings that must contend with a greater number of large,

mature larvae at a younger age [16]. The fitness consequences of female oviposition behaviour are further supported by observations in other *Philornis* systems. Host nests that are infested later in the nesting cycle are more likely to have higher fledging success than nests parasitized early in the nesting cycle [50, 78].

6.2 Larval feeding on adult birds

Philornis larvae are generally exclusive parasites of developing nestlings, whether they be subcutaneous or free-living semi-hematophagous species. Infestation of host nests can happen quickly and is often observed within 24 h of the first nestling hatching [41, 43, 50, 79]. Many studies on *Philornis* species in their native range found no evidence of larvae present during incubation [47, 48, 80, 81]. There have been a few cases of larvae feeding on adults in subcutaneous species [82–84], however these reports are rare, with generally only a few larvae per adult. For this reason, larval feeding on adults is generally regarded as opportunistic [2]. More data are needed to examine the oviposition behaviour of *Philornis* species to determine whether larvae are present during the incubation phase.

On the Galápagos Islands between 1998 and 2005, there have been no reported cases of *P. downsi* larvae present in host nests with eggs that would suggest that larvae also feed on incubating females. Two studies during this time period specifically stated that no *P. downsi* larvae have been found during host incubation (**Table 2**) [21, 85]. On Santa Cruz Island during 1998–2010, published studies report findings for 38 nests with eggs that have been inspected for the presence of *P. downsi* and found no larvae (**Table 2**) [21, 85]. In 2012, Cimadom and colleagues first observed *P. downsi* larvae in host nests during incubation where larvae have been found present in 17 of the 26 nests inspected [85]. Since this initial observation, the prevalence of *P. downsi* in host nests with eggs has increased to 80% in some species and years on Santa Cruz Island, with larvae and puparia found in 70 of 177 nests inspected with eggs [86]. Concurrently across this time period, brooding Darwin's finch females have *P. downsi* antibodies that are associated with decreased *P. downsi* intensity, but not increased fledging success [87, 88]. This suggests that *P. downsi* larvae on the Galápagos Islands may have switched to feed on adult finches at some stage [87]. On Floreana Island, inspection of nests that failed during incubation during 2006 and 2016 found *P. downsi* larvae in 4 of 72 (5.6%) nests with host eggs (**Table 2**). In 2006, three medium ground finch (*G. fortis*) nests with eggs in the arid lowlands have *P. downsi* larvae and puparia, and in 2010 one highland small tree finch (*C. parvulus*) has *P. downsi* larvae during the egg stage. During a period of intense drought from 2003 until 2006 with less than 300 mm of rain per year in the lowlands, there were very few active host nests available for oviposition, which may be an explanation for a shift in *P. downsi* female oviposition and larval feeding on incubating females at the end of the drought during 2006. Notably, smaller larvae and eggs are not easily visible in nests and it is possible that *P. downsi* is present, but not detected during incubation in the early years of study.

In laboratory trials, *P. downsi* hatching success is found to be the same in nests with host eggs and nests with finch hatchlings (*Lonchura striata domestica*) Linnaeus (Passeriformes: Estrildidae) [89]. In these trials, there is even a fitness benefit for *P. downsi* that hatched during incubation and hence earlier during the host cycle, as they survived for longer [89]. Other than *P. downsi*, there is one report of an unidentified *Philornis* species parasitising adults in the pearly-eyed thrasher (*Margarops fuscatus*) Vieillot (Passeriformes: Mimidae) studied in Puerto Rico [49]. About 46% of incubating and brooding females and 13% of attending adult males sustained subcutaneous *Philornis* [49]. It has been suggested that this *Philornis* species may have invaded Puerto Rico, as the patterns of prevalence and host

Ref #	Year (s) of study	Island	Host species	Total no. of nests examined/no. inspected during egg phase	<i>P. downsi</i> larvae during the egg phase	Comments
[21]	1998, 2000	SC	ST, LT, SG, MG, WF, WP, CF, SBA, YW, VF, DBC, GM	105/17	No	Larvae not found in 17 SG, ST, WF and WP nests that failed during incubation
[85]	1998–2010	SC	ST, WF	na/21	No	Larvae not found in 21 ST and WF nests abandoned during incubation (reported as part of a study during 2012–2015 listed below [86])
[90]	2004	SC, FL, IS	SG	24/na		
[91]	2000, 2004	SC	SG, MG	27/na		Larvae not found in SG and MG nests depredated shortly after host hatch
[44]	2000, 2004, 2005	SC	SG, MF, CF	63/na		
[92]	1998, 2000, 2001, 2002, 2004, 2005	SC	SG, MG, ST, LT, WP, WF	249/na		
[93]	1998, 2000, 2003, 2004, 2005	13 islands incl. SC and FL		515/na		
[87]	2004, 2005, 2006	SC	MG	63/na		
[94]	2000, 2001, 2002, 2004	SC	ST, LT, SG, WF, WP	43/na		
[87]	2008	SC, DMj	MG			Brooding female MG had <i>P. downsi</i> -specific antibodies, suggesting nesting females are parasitised
[45]	2008	FL	ST, SG, MG	11/5	No	Larvae not found in 4 SG and 1 ST nests abandoned with eggs
[62]	2006, 2008	FL	ST, MT	63/2	No	Larvae not found in 2 MT nests depredated during egg phase
[95]	2004, 2005, 2006	FL	SG	71/na		
Kleindorfer (unpubl. data)	2006	FL	MT, SG, MG	129/27	Yes	Larvae and puparia found in 3 MGF nests abandoned with eggs in the arid lowlands
Kleindorfer (unpubl. data)	2010	FL	ST, MT, SG	153/38	Yes	Larvae found in 1 ST nest depredated with eggs in the highlands
[96]	2008	SC	MG	48/na		

Ref #	Year (s) of study	Island	Host species	Total no. of nests examined/no. inspected during egg phase	<i>P. downsi</i> larvae during the egg phase	Comments
[97]	2009	SC	MG	61/na		
[88]	2010	SC	MG	43/na		Female MG in parasitised nests had more <i>P. downsi</i> antibodies and spent more time standing upright when brooding than non-parasitised nests
[98]	2010	SC	MG	30/na		
[63]	2005–2010	FL	ST, MT	43/na		
[54]	2004, 2006, 2008, 2010, 2012, 2013	FL	ST, MT, SG	561/na		Evidence that <i>P. downsi</i> oviposition behaviour occurred more synchronously and earlier in nesting phase in later years of the study
[99]	2013	SC	ST, SG, MG, VGF	26/na		
[46]	2010	FL	SG	14/na		
[57]	2014	SC	GF	1/na		
[100]	2012, 2013	SC	MG, GM	127/na		
[58]	2004, 2005, 2006, 2008, 2010, 2012, 2013, 2014	FL	ST, MT, SG	254/na		
[101]	2013, 2014	SC	VGF	11/na		
[64]	2015	SC	GF	2/na		
[102]	2013	SC	MG, GM	37/na		
[86]	2012, 2014, 2015, 2016, 2017	SC	ST, WF	850/177	Yes	Larvae and puparia found in 18/72 ST nests and 52/105 WF nests that failed during egg phase; range in prevalence across species and years was 0–80% of nests
[103]	2012, 2013, 2015, 2016	SC	GM	131/na		
[104]	2010, 2013, 2014	FL	ST, MT	27/na		

The islands are abbreviated as Santa Cruz (SC), Floreana (FL), Isabela (IS), Daphne Major (DMj). The ‘total number of nests examined’ refers to all active nests monitored over the course of the study and ‘number inspected during egg phase’ is the sample size for the sub-set of nests examined during host incubation (usually following abandonment or predation) where ‘na’ denotes that nests have been not sampled during the egg phase. The column ‘*P. downsi* larvae during the egg phase’ states ‘yes/no’ referring only to nest inspections that occurred during the egg phase. Host species are abbreviated as small tree finch (ST), large tree finch (*Camarhynchus psittacula*) (LT), small ground finch (SG), medium ground finch (MG), woodpecker finch (*Cactospiza pallida*) (WP), warbler finch (*Certhidea olivacea*) (WF), cactus finch (*Geospiza scandens*) (CF), Galápagos mockingbird (GM), smooth billed ani (*Crotophaga ani*) (SBA), yellow warbler (*Dendroica petechia*) (YW), dark billed cuckoo (*Coccyzus melacoryphus*) (DBC), vermillion flycatcher (*Pyrocephalus rubinus*) (VF), vegetarian finch (*Platyspiza crassirostris*) (VGF), and Galápagos flycatcher (*Myiarchus magnirostris*) (GF).

Table 2.
Evidence of Philornis downsi larvae present in nests during incubation and before nestling hatching in studies on the Galápagos Islands.

mortality mirror that of the *P. downsi* invasion in the Galápagos Islands [6, 48, 49]. *Philornis* consumption of attending adult hosts may be an oviposition tactic that is more prevalent under conditions of resource limitation. Resource limitation could be influenced by resource termination such as early host death, resource availability when there is a limited supply of host nests (e.g., during drought), and resource accessibility, for example when competition within and between fly cohorts changes [54].

7. Conclusions

As one of three avian nest parasitic genera in Diptera, the genus *Philornis* provides a useful system to explore shifts in larval feeding behaviour in native and invasive species. *Philornis downsi* has been accidentally introduced to the Galápagos Islands and first observed in the nests of Galápagos land birds in 1997. In this chapter, we explored similarities and differences between *P. downsi* larval development and behaviour with what is known from the other 52 *Philornis* species. More basal *Philornis* (*aitkeni*-group) species have free-living coprophagous larvae and more recently evolved *Philornis* (*angustifrons*-group) tend to have subcutaneous hematophagous larvae with the exception of *P. downsi* that has free-living semi-hematophagous larvae. Since its introduction to the Galápagos Islands, there have been documented changes in the behaviour of *P. downsi*. During the early years after initial discovery of *P. downsi* on the Galápagos Islands, oviposition behaviour was asynchronous across the nesting cycle and larvae appeared to have fed exclusively on developing nestlings until 2005. In later years, *P. downsi* oviposition behaviour was earlier in the nesting cycle and more synchronous, and since 2006, larvae have also been recorded to feed on incubating females. The first records of *P. downsi* larvae in host nests with eggs rather than hatchlings occurred at the end of a four-year drought on the Galápagos in 2006. Since 2012, up to 80% of host nests with eggs may contain *P. downsi* larvae on Santa Cruz Island. Larval feeding by *P. downsi* on adult birds has been observed in laboratory finches and in one *Philornis* system (species unknown) in Puerto Rico. In light of changes in *P. downsi* larval feeding behaviour, we provided a description and photos of the larval instars for use in field identification. We compiled the observations to date of *Philornis* behaviour and ontogeny within a broad taxonomic framework and summarised patterns of change in the oviposition behaviour of *P. downsi* in its (presumably) novel habitat on the Galápagos Islands. By examining *P. downsi* in relation to other *Philornis* species, we provided a broad phylogenetic context for the potential behavioural repertoire of an invasive species under conditions of intense natural selection in a novel environment.

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Author details

Lauren K. Common¹, Rachael Y. Dudaniec², Diane Colombelli-Négrel¹
and Sonia Kleindorfer^{1,3*}

1 College of Science and Engineering, Flinders University, Adelaide, Australia

2 Department of Biological Sciences, Macquarie University, Sydney, Australia

3 Konrad Lorenz Research Center and Department of Behavioural Biology,
University of Vienna, Austria

*Address all correspondence to: sonia.kleindorfer@flinders.edu.au

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