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Alien Invasion: Biology of *Philornis* Flies Highlighting *Philornis downsi*, an Introduced Parasite of Galápagos Birds

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Abstract

The muscid genus *Philornis* comprises approximately 50 described species of flies, nearly all of which are obligate parasites of nestling birds. *Philornis* species are native to the Neotropics and widely distributed from Florida to Argentina. Most research on this group has focused on *P. downsi*, which was introduced to the Galápagos Islands in the late twentieth century. Although *Philornis* parasitism kills nestlings in several native host species, nowhere do the effects seem more severe than in *P. downsi* in the Galápagos. Here, we review studies of native and introduced *Philornis* in an attempt to identify factors that may influence virulence and consider implications for the conservation of hosts in the Galápagos.

INTRODUCTION

The introduced parasitic nest fly *Philornis downsi* (Diptera: Muscidae) is one of the most significant threats to birds in the Galápagos Islands. The larvae of this fly feed on nestling and adult birds and cause high nestling mortality in many endemic Galápagos species (64). *P. downsi* has already been implicated in the decline of two critically endangered species, the mangrove finch (*Camarhynchus heliobates*) and the medium tree finch (*C. pauper*) (79, 100). Moreover, mathematical models suggest that *P. downsi* has the potential to drive even common species locally extinct (74). Why *P. downsi* is so virulent in the Galápagos is a pressing question in the fields of disease ecology and conservation biology.

P. downsi is one of approximately 50 species in the genus *Philornis*, all but two of which are obligate parasites of nestling birds. The goal of this article is to review the current knowledge of *P. downsi* and its congeneric relatives. We begin with a background overview of the biology of *Philornis*. Then, we examine the effects of *Philornis* flies on native and nonnative hosts at both the individual and population levels. Finally, we evaluate mechanisms of host defense against *Philornis* and discuss management options for the control of *P. downsi* in the Galápagos.

BACKGROUND

In this section, we review the systematics, distribution, life cycle, and hosts of *Philornis* flies. We also discuss the arrival, hosts, and distribution of *P. downsi* in the Galápagos Islands.

Systematics and Biogeography

Philornis Meinert (1890) is a genus of New World muscid flies (27, 64, 115). *Philornis* includes species originally described in the genera *Aricia* Macquart (1853), *Hylemyia* Loew (82), and *Mydaea* Jannicke (1867) (2, 92). The genus *Philornis* was expanded with the description of several *Philornis* species from Trinidad in the 1960s and subsequent work in South America in the 1980s (22, 32, 33).

Early work placed *Philornis* in the family Calliphoridae, which includes ecologically similar parasites of birds. However, subsequent taxonomic revisions transferred *Philornis* to the Muscidae (2, 24). Taxonomic relationships among *Philornis* species are largely based on the morphology of adult specimens (25). The latest phylogeny, based on the morphology of 41 *Philornis* species, identified three distinct clades: the *aitkeni*, *falsificus*, and *angustifrons* groups (25). *P. downsi* is sister to the *angustifrons* group, which includes most of the described species. New molecular data suggest cryptic species within the genus, which prompts calls for more extensive molecular phylogenetic analysis of the group (105). Populations of *Philornis* have been found in the United States (104), the Caribbean (34, 118), Mexico (54, 123), Costa Rica, (120), Panama (9), Peru (101, 114), Brazil (57, 85, 102), Argentina (10, 21, 28, 89, 92, 94, 106, 111), Venezuela (116), and mainland Ecuador (13). Specimens are rare in collections (25) and generally reared from pupae and larvae collected from birds' nests. The lack of historical specimens and scant information on population genetics make determining the provenance of *Philornis* populations difficult. Outside of the Galápagos, *Philornis* populations are assumed to be native. However, it is possible that humans had a role in establishing *Philornis* populations on other islands (see the sidebar Did *Philornis* Also Invade Puerto Rico?).

Natural History

Information on the life cycle exists for only approximately half of the described *Philornis* species (115). The larvae of these species of *Philornis* are obligate associates of nestling birds, and all but two are parasites (24). *Philornis* and the related genus *Passeromyia* (which comprises five

DID PHILORNIS ALSO INVADE PUERTO RICO?

Philornis is a common parasite of Puerto Rico birds such as Pearly-eyed thrashers (*Margarops fuscatus*), Puerto Rican parrots (*Amazona vittata*), and sharp-shinned hawks (*Accipiter striatus venator*) (5, 6, 30). Although the specific identity of *Philornis* in Puerto Rico is unclear (6), it is associated with high nestling mortality in all three hosts (5, 6, 30). The high prevalence and virulence of *Philornis* in Puerto Rico are more similar to those of *Philornis* in the Galápagos than to those of native *Philornis* spp. in other parts of the world. Moreover, widespread parasitoids of *Philornis*, such as *Conura annulifera* and *Brachymeria subrugosa*, are not reported from Puerto Rico (12, 95). These data suggest that as in the Galápagos, *Philornis* may have invaded Puerto Rico relatively recently. Work on the systematics and biogeography of *Philornis* in the Caribbean is needed to test this hypothesis.

described species) are the only known genera in the Muscidae whose larvae parasitize birds (24). The adult flies (Figure 1a), which are free-living, feed on decaying matter (17, 23) and lay their eggs in the nests of birds. The larvae (Figure 1b) are either free-living coprophages (*P. aitkeni* and *P. rufoscutellaris*) or hematophagous parasites of nestlings and occasionally adult birds (5, 23, 115). Most parasitic *Philornis* species have subcutaneous larvae that burrow under the host's skin, where they feed on blood and tissues (24, 39, 117) (Figure 2); however, two of the parasitic species (*P. downsi* and *P. falsifica*) have larvae that are nonsubcutaneous and attach externally to the host to feed. After completing the three larval instar stages, the larvae pupate in the host's nest (the subcutaneous larvae leave the host to pupate) (113, 117). *Philornis* species spin a characteristic frothy cocoon that encloses the puparium (24, 33, 46). The adult fly emerges from this puparium 5–20 days later (77, 107, 113).

The natural history of *P. downsi* is particularly well studied because of the parasite's threat to Galápagos birds. The first-instar larvae may live and feed in the nares (nostrils) or developing feather quills of nestling birds (46, 68) (Figure 3). However, the second- and third-instar larvae

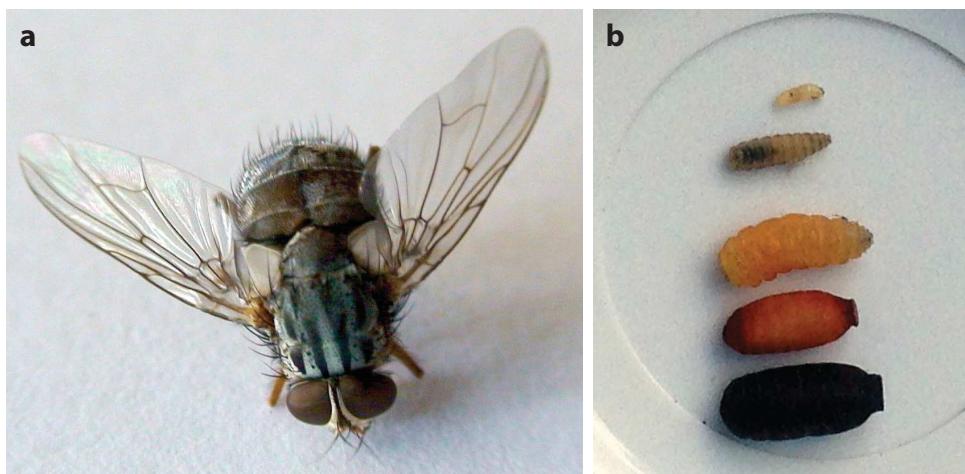


Figure 1

Philornis downsi life cycle: (a) adult stage and (b, top to bottom) three larval stages, a third-instar larva in the process of pupating, and a fully formed black pupa. Panel a courtesy of Jody O'Connor, and panel b courtesy of Sabrina McNew.



Figure 2

Twelve-day-old tropical mockingbird (*Mimus gilvus*) nestling in Tobago with a heavy infestation of approximately 70 subcutaneous *Philornis trinitensis* larvae. Photo courtesy of Jordan Herman, reprinted from Reference 69.



Figure 3

Medium ground finch (*Geospiza fortis*) nestling in the Galápagos with extensive damage to the nares (nostrils) from first-instar *Philornis downsi*. Photo courtesy of Sarah Huber.

live in the nest material (99). *In vitro*, *P. downsi* require 3 days for the eggs to hatch, 9–10 days to complete the larval stages, and another 9–10 days as pupae (77). Estimates from field-based studies suggest that the larvae might develop in as few as 4–7 days under natural conditions (66, 77). Thus, estimates of total time to develop from a newly laid egg to an adult fly average between 17 and 23 days (77).

Intensity: the number of individual parasites in an infested host

Host Use

Philornis flies are known to parasitize more than 150 species of birds (39, 115) (**Supplemental Table 1**). Most hosts are passerines (perching birds); however, *Philornis* larvae have also been found in the nests of hawks (Accipitriformes), hummingbirds (Apodiformes), motmots (Coraciiformes), cuckoos (Cuculiformes), doves (Columbiformes), falcons (Falconiformes), woodpeckers (Piciformes), parrots (Psittaciformes), and owls (Strigiformes) (29, 101, 102, 104, 115) (**Supplemental Table 1**).

Host specificity is difficult to evaluate in *Philornis* because many species are known from just one or a few records. A network analysis based on published host–parasite associations concluded that *Philornis* includes both specialist and generalist species (84). Within generalist species, however, there may still be variation in host use. A survey of *P. torquans* in a bird community in Argentina found that although *P. torquans* larvae were found on nestlings of 20 different bird species, the majority of larvae were found on nestlings of just two species, *Pitangus sulphuratus* and *Phacellodomus ruber* (3). More research is needed to evaluate how and why *Philornis* flies choose certain hosts to parasitize. Variation in host use may provide clues as to how *Philornis* find hosts and/or the defenses that hosts use to combat *Philornis*.

Introduced *P. downsi* has been found in the nests of nearly all Galápagos passerines as well as the dark-billed cuckoo (*Coccyzus melacoryphus*) and the introduced smooth-billed ani (*Crotophaga ani*) (47, 64, 81). Larger host species tend to have more *P. downsi* per nest (36, 55, 63, 71). Intensity (the number of individual parasites in an infected host) may increase proportionally with the amount of host tissue when host species do not differ in their ability to resist infestation (e.g., 71). In some cases, however, intensity is not correlated with host size (19, 100). In a comparison of small, medium, and large tree finches (*Camarhynchus parvulus*, *C. pauper*, and *C. psittacula*), O'Connor et al. (100) found that intensity was highest in nests of the medium-sized tree finch (*C. pauper*). It is unclear whether *P. downsi* preferentially infests *C. pauper* or the other species are somehow more resistant to parasitism. In any case, the disproportionately heavier intensity of *P. downsi* in *C. pauper* may be partly responsible for the decline of this critically endangered host species.

▶ **Supplemental Material**

History of *Philornis downsi* in the Galápagos

Specimens of adult *P. downsi* were collected in the Galápagos in the 1960s; however, larvae were not observed in nests there until 1998 (16, 44). Historical data corroborate a late twentieth-century arrival and spread of *P. downsi* in the Galápagos: *P. downsi* causes characteristic deformities in finch nares that are not seen in museum specimens of birds collected before 1962 (68) (**Figure 3**). Specimen collecting has been highly restricted in the Galápagos, which limits finer-scale estimation of the timing of the *P. downsi* invasion using this method.

P. downsi has been found on nearly all islands in the Galápagos (62, 122). In the first and only systematic census of its distribution in the Galápagos, completed in 2005, *P. downsi* was found on 11 out of 13 main islands surveyed (122). Only Genovesa and Española were free of the parasite. Although these are small, outlying islands, Española and Genovesa are visited regularly by cruise ships, which could provide an avenue for the introduction of flies. An up-to-date careful census of

the islands is needed to further track the spread and abundance of *P. downsi* in the Galápagos. Such a census would include the remote islands Darwin and Wolf, which are approximately 150 km northeast of the main archipelago and have not been censused thoroughly for *P. downsi*.

Abundance: the number of individual parasites per host, including parasite-free hosts

Prevalence: the percent of parasitized individuals (or nests) in a host population

Microsatellite data revealed low levels of genetic variation in *P. downsi* in the Galápagos, which suggests that the founding population was small and/or the product of a small number of introductions (37). The most likely source of *P. downsi* in the Galápagos is mainland Ecuador, where *P. downsi* is known to be native (13). Most maritime and airplane traffic to the islands originates in mainland Ecuador, further suggesting it as the original source of colonization (8, 16).

POPULATION ECOLOGY OF *PHILORNIS*

Native *Philornis* spp. intensity is often positively correlated with rainfall and temperature (3, 6, 78, 86, 93). In some systems, prevalence (the proportion of hosts parasitized) and intensity increase over the breeding season (6, 106, 110), presumably as a result of the increase in available hosts as birds breed. One study evaluated whether *Philornis* intensity increases with habitat disturbance in the form of urbanization, but it did not find a significant association (80).

Philornis downsi in the Galápagos

P. downsi tends to be most prevalent on Galápagos islands with humid highland regions and less prevalent on arid islands (122). These patterns may reflect a higher abundance of food for adult flies on the more humid islands or better access to hosts, which are less likely to breed in dry conditions (75, 122). Within individual islands, there is some evidence that flies are more common in the humid highland regions than the arid lowlands. *P. downsi* intensity is higher in the humid highlands of Floreana than the more arid lowlands (96); however, this is not the case on Santa Cruz Island (36).

Populations of *P. downsi* may also be affected by climatic variation among years. Annual rainfall in the Galápagos varies by several orders of magnitude (51). The intensity of *P. downsi* typically increases in years of high rainfall (36, 47), when conditions for breeding hosts and adult flies are better. Oddly, *P. downsi* intensities do not appear to decrease in dry years on Santa Cruz Island (45, 46). Fly populations may be insulated from effects of dry years on Santa Cruz because permanently humid highland regions serve as a reservoir for adult flies (45, 46). Monitoring *P. downsi* population dynamics is difficult, partly due to challenges in developing attractants for trapping adult flies (17). A better understanding of the environmental factors influencing *P. downsi* population growth is key to developing management strategies (7).

Recent evidence suggests that *P. downsi* is increasing in overall prevalence and intensity (64, 66). Comparisons of finch nests on Floreana Island from 2004 to 2013 suggest that fly intensity has increased over time; in 2014, nests were infested earlier and nestling mortality was greater (66). The authors suggest that high abundance of *P. downsi* on Floreana may mean that competition among flies for host resources has selected for earlier infestation of nests by flies each year. Nests may be parasitized by several female flies (38); thus the fly eggs that are laid first have the most time to develop before the host dies.

EFFECTS OF *PHILORNIS* ON HOST FITNESS

In this section, we discuss the effects of *Philornis* on host survival and reproduction. Using data from published studies, we compare the effects of *P. downsi* to those of other *Philornis* species to identify factors associated with virulence.

Native *Philornis* spp.

Native *Philornis* parasitism is generally associated with negative effects on the growth rates and mass of nestlings (4, 94, 106, 110) (Figure 3). In some cases, parasitism causes significant nestling mortality (5, 6, 29, 35, 69, 106, 109, 110, 113, 117, 124) (Supplemental Table 2). In other cases, however, *Philornis* parasitism is associated with little or no nestling mortality (3, 20, 69, 83, 90, 93, 94).

▶ Supplemental Material

Intensity of *Philornis* in its native range is often correlated with nestling mortality (3, 69, 112). Timing of parasitism also influences mortality; infestation of hosts earlier in the nestling period is associated with higher mortality (4, 109). Infestation by *Philornis* spp. often varies within broods, with some nestlings experiencing higher intensity and mortality, whereas other nestlings fare better. In Puerto Rico, Arendt (6) found that the intensity of *Philornis* is higher in older than younger siblings within a brood, yet third- and fourth-born chicks died earlier than older siblings. This difference is attributed to size variation within the brood; because of asynchronous hatching, later-born nestlings are often the smallest and least able to tolerate parasitism.

Variation in the effects of *Philornis* parasitism occurs among host species in the same community. Knutie et al. (69) recently showed that *P. trinitensis* in Tobago causes high mortality in black-faced grassquit (*Tiaris bicolor*) nestlings but not tropical mockingbird (*Mimus gilvus*) nestlings. In the Galápagos, *P. downsi* causes high mortality in Darwin's finches (see below), which are sister taxa of grassquits but not Galápagos mockingbirds, which are congeners of tropical mockingbirds (71). Hence, in these studies, the effect of *Philornis* on nestling survival differed between finch and mockingbird species but not between native and naïve hosts. These results indicate that differences in host biology influence the ability of hosts to tolerate parasitism, independent of the evolutionary duration of the host–parasite association.

Closely related hosts are not necessarily affected similarly by *Philornis*. For example, in a study of sympatric congeneric flycatchers, the campo suiriri (*Suiriri affinis*) and chapada flycatcher (*S. islerorum*), apparent mortality due to *Philornis* was observed only in the chapada flycatcher (83).

Philornis downsi in the Galápagos

P. downsi parasitism is associated with high morbidity and mortality in almost all Galápagos hosts (19, 40, 45, 47, 58, 73, 76, 96) (Supplemental Table 2). Parasitized nestlings often have lower hemoglobin levels than unparasitized nestlings (40, 45, 71). Parasitized nestlings are also often smaller, based on measurements of overall body mass or other characteristics, such as tarsus length (45, 71). However, in cases where mortality of parasitized chicks is high and occurs early, growth rates between surviving parasitized and unparasitized chicks may not differ significantly (58, 73). First-instar *P. downsi* larvae can also deform the nares and beak, which may have implications for later-life song (50, 68) (Figure 2).

Effects of *P. downsi* on host fitness can be severe, sometimes leading to 100% mortality of parasitized nestlings (76, 98). Mortality often increases with higher parasite intensity (19, 40, 47, 58; but see 71, 99). *P. downsi* appears to have little or no effect on at least two species of birds in the Galápagos: the Galápagos mockingbird (*Mimus parvulus*) and the vegetarian finch (*Platyspiza crassirostris*) (55, 71). Notably, these two species are the largest-bodied hosts of *P. downsi* that have been monitored in the Galápagos. Although *P. downsi* generally increases in intensity with host size, larger-bodied species may be more tolerant of parasite damage (see the section titled Host Tolerance below).

Effects of *P. downsi* on host fitness also appear to be mediated by the environment, particularly seasonal rainfall. Cimadom et al. (19) hypothesized that low reproductive success in small tree finches and warbler finches (*Certhidea olivacea*) on Santa Cruz Island was the result of several interacting factors, including *P. downsi*, heavy rainfall, and habitat change. In contrast, higher

rainfall also leads to greater food abundance for breeding birds. Heimpel et al. (55) suggest that a short, intense rainy season increased food available to breeding vegetarian finches, which may have helped to mitigate potential negative effects of *P. downsi* on nestlings.

Finch reproductive success can be extremely low in dry years due to the combination of *P. downsi* and food limitation (45, 46, 75). Koop et al. (75) found that neither prevalence nor intensity of *P. downsi* in medium ground finch nests was diminished in an exceptionally dry year on Santa Cruz Island. Fledgling success in the few nests found that year did not differ significantly between fumigated and sham-fumigated nests. However, reproductive success for both treatments was extremely low, with just one chick in each treatment group fledgling successfully.

No evidence, to date, has suggested that *P. downsi* affects the condition or survival of adult hosts. In an experimental study, Knutie et al. (70) found that *P. downsi* did not affect corticosterone levels or condition of nesting female finches, suggesting that the mortality of nestlings associated with parasitism is not mediated by a stress response in mothers. It is not known whether *Philornis*' effects on host fitness are mediated by secondary infections. Aitken et al. (1) suggested that *Philornis* larvae might vector arboviruses, leading to disease in nestlings or their parents in addition to the direct negative effects of feeding larvae. However, pathogen transmission by dipteran larvae does not appear to be common, and this hypothesis has received little additional study.

***Philornis downsi* Versus Other *Philornis* Species**

The effects of *P. downsi* on Galápagos hosts appear to be more severe than the effects of *Philornis* spp. on native hosts. To test this hypothesis explicitly, we compared data on the effects of introduced *P. downsi* in the Galápagos to data on the effects of native *Philornis* spp. in other regions of the world. We defined cost of parasitism as the difference in fledgling success between parasitized and unparasitized nestlings. We used linear mixed effect models to evaluate the impact of parasite prevalence, intensity, and host mass on the cost of parasitism (see **Supplemental Tables 3** and **4** for detailed methods).

Our results show that the cost of *P. downsi* parasitism is indeed higher than that of native *Philornis* spp. [linear mixed model (LMM) estimates: *P. downsi* = 43.8%, native *Philornis* spp. = 23.8%; $p = 0.03$]. Prevalence of *P. downsi* in the Galápagos is higher than that of native *Philornis* spp. (LMM estimates: *P. downsi* = 96.7%, native *Philornis* spp. = 49.16%; $p < 0.001$). Surprisingly, however, mean intensity per nestling does not differ significantly between *P. downsi* and other *Philornis* species (LMM estimates: *P. downsi* = 19.5, native *Philornis* spp. = 13.8; $p = 0.42$).

In every study of *P. downsi* in the Galápagos, prevalence has exceeded 85% (**Figure 4**). Despite the lack of variation in this parameter, prevalence is a significant predictor of the cost of parasitism in the Galápagos (**Figure 4**) (**Supplemental Table 3b**). In contrast, prevalence does not predict the cost of native *Philornis* spp. to hosts in other locations (**Figure 4**) (**Supplemental Table 3c**). There is a marginally significant negative correlation between the cost of *P. downsi* parasitism and host mass in the Galápagos but not in native *Philornis* spp. (**Figure 5**) (**Supplemental Table 4b,c**).

In general, both the prevalence and effects of *P. downsi* in Galápagos hosts are higher than those of other *Philornis* species (**Figure 4**). However, there are two noteworthy exceptions: native *Philornis* spp. in European starlings in Argentina (*Sturnus vulgaris*) and *Philornis* spp. in several bird species in Puerto Rico (6, 61). In the case of Argentina, although the *Philornis* spp. are native, the host-parasite interaction is a relatively new one (starlings were first seen in Argentina in 1987) (61). It is important to note, however, that the fledgling success of the few unparasitized chicks in the Argentina study was also low, so controlled experimental work is needed to rigorously test the effects of *Philornis* on this species. In Puerto Rico, both the prevalence and effects on endemic hosts are much more similar to those seen in the Galápagos than those seen in other native hosts.

Supplemental Material

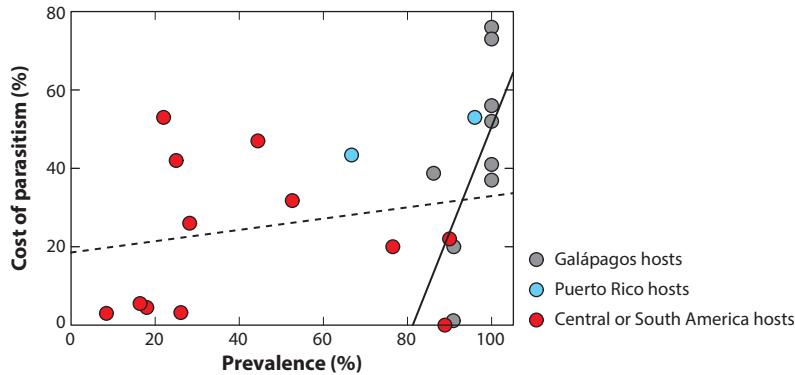


Figure 4

Relationship between *Philornis* prevalence (percentage of nests infested) and the cost of parasitism (percentage reduction in fledging success of parasitized nestlings compared to unparasitized nestlings). Each point represents data for a single host species. Shown are hosts of *P. downsi* in the Galápagos (gray points), of *Philornis* spp. in Puerto Rico (light blue points), and of *Philornis* spp. in Central or South America (red points). The regression line for Galápagos hosts (solid line) and the (nonsignificant) regression line for native hosts (dashed line) are also indicated. The cost of parasitism increases significantly with prevalence in Galápagos hosts but not native hosts [linear mixed model (LMM) estimates: Galápagos $p < 0.0001$ and native $p = 0.441$ (Supplemental Tables 3b and 3c, respectively)]. Readers are referred to Supplemental Table 3a for details of methods and analyses.

▶ **Supplemental Material**

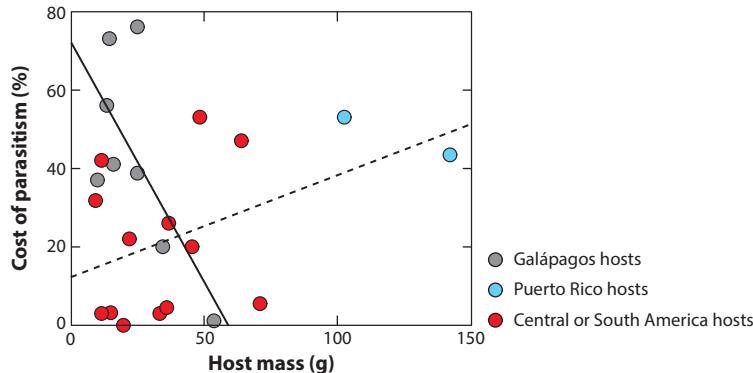


Figure 5

Relationship between host species' mass and the cost of parasitism. Each point represents data for a single host species. Shown are hosts of *Philornis downsi* in the Galápagos (gray points), of *Philornis* spp. in Puerto Rico (light blue points), and of *Philornis* spp. in Central or South America (red points). The regression line for Galápagos hosts (solid line) and the (nonsignificant) regression line for native hosts (dashed line) are also indicated. Larger species of hosts in the Galápagos show a marginally significant decrease in the cost of parasitism, whereas larger native hosts show a marginally significant increase in the cost of parasitism [linear mixed model (LMM) estimates: Galápagos $p = 0.056$ and native $p = 0.066$ (Supplemental Tables 4b and 4c, respectively)]. Readers are referred to Supplemental Table 4a for details of methods and analyses.

(see the sidebar titled Did *Philornis* Also Invade Puerto Rico?). As with *Philornis* in the Galápagos, *Philornis* may be a recent arrival to Puerto Rico. These two case studies further suggest that the virulence of *Philornis* is higher in new hosts.

HOST DEFENSES AGAINST PHILORNIS

Several studies have tested for defenses by hosts against *Philornis* parasitism. The first line of defense includes mechanisms for avoiding parasitism in the first place. Once parasitized, however, hosts can try to tolerate or resist the parasites (108). Tolerance and resistance differ in their mechanisms and implications for host–parasite coevolution (108).

Avoidance

Some native hosts appear to alter their nesting behavior in response to *Philornis*. White-throated magpie-jays in Costa Rica (*Calocitta formosa*) breed over an extended 7-month period that spans the dry and wet seasons (78). The magpie-jays initiate their first broods during the dry season, which is surprising given that arthropod food resources are scarce at this time of year. However, *Philornis*, which causes significant nestling mortality in magpie-jays, increases in prevalence during the wet season. Thus, magpie-jays may avoid *Philornis* by breeding earlier than would be predicted by arthropod food availability alone.

Spatial positioning of nests, such as height and distance to other nests, might also influence encounter rates with flies. For example, Kleindorfer et al. (67) found that the trapping frequency of female *P. downsi* and larval intensity per nest increased with trap height and nest height. Intensity of *P. downsi* also increases with host density (63). Differences in nest site preferences may therefore help explain why some species are parasitized at higher intensities than others. Nestlings in highly parasitized nests sometimes crawl on top of other nestmates to avoid parasitism (97).

Immune Resistance

Nesting female medium ground finches (*Geospiza fortis*) mount an immune response when parasitized (76). The strength of the female's immune response is inversely proportional to the number of parasites in her nest; thus, the immune response may help to reduce fly intensity in the nest (76). However, as Koop et al. (76) point out, the inverse correlation of immune response and parasite intensity may actually reflect the inability of highly parasitized birds to mount strong immune responses. Moreover, the immune response was not correlated with nestling survival, because 100% of parasitized nestlings died; thus, even if it was a response to parasitism, it was not an effective defense strategy. There is no evidence that immune responses to *P. downsi* are mounted by nestlings of Darwin's finches or Galápagos mockingbirds during their brief time in the nest (71, 76). Similarly, related native hosts (black-faced grassquits and tropical mockingbirds) do not mount an immune response when parasitized by *P. trinitensis* (69). These results suggest that the high cost of *P. downsi* to Galápagos nestling survival is not due to Galápagos hosts lacking the immune defenses found in native hosts.

Tolerance: a defense mechanism that maintains host health by compensating for damage done by the parasite without decreasing parasite load

Resistance: a defense mechanism that maintains host health by reducing parasite load

Behavioral Resistance

Antiparasite behavior, such as preening, is often the first line of defense against external parasites (52, 119). However, behavioral defenses are not common against *P. downsi* in Darwin's finches. O'Conner et al. (97) reported a single observation of a nestling finch preening off and consuming a fly larva. An adult female finch in that same study was observed picking at a nestling's nares

(nostrils). *P. downsi* feeds mainly at night and hides in the nest material during the day, which may help it to avoid host detection (97). Some studies of native *Philornis* spp. report hosts removing larvae from nestlings by preening (49, 112), but this behavior does not appear to be widespread.

Behavioral responses of female finches may actually exacerbate the effects of *P. downsi*. Observational studies find that females spend less time brooding and more time standing when nests are heavily parasitized, presumably to avoid being fed on by larvae themselves (71, 76). This behavior may disrupt thermoregulation of the nest and contribute to nestling mortality.

Another recent study suggested the possibility that Darwin's finches use self-medicating behavior to deter *Philornis*. Cimadom et al. (18) observed members of four different finch species (*Geospiza fortis*, *G. fuliginosa*, *Certhida olivacea*, and *Camarhynchus parvulus*) rubbing leaves of the endemic Galápagos guava or guayabillo tree (*Psidium galapaeum*) on their feathers. This leaf has insect-repellent properties; thus, the behavior may help birds repel *P. downsi*. More work is needed to test this interesting hypothesis.

Host Tolerance

Behavioral data from Galápagos mockingbirds suggest that increased provisioning of nestlings by parents allows nestlings to tolerate *P. downsi* with no ultimate reduction in fitness (71). In an experimental study, Knutie et al. (71) found that parasitized mockingbird nestlings begged more than unparasitized chicks and that their parents responded to this cue by increasing provisioning. By contrast, there was no effect of *P. downsi* on the begging or provisioning rates of the medium ground finch. Thus, larger-bodied hosts, such as mockingbirds, may be better able to withstand fly larvae feeding on them at night. Smaller hosts, such as Darwin's finches, may simply be too weak in the morning to signal their parents that they need extra provisioning (98). Because the mechanism of tolerance is increased provisioning, host tolerance of *P. downsi* may be condition-dependent. Galápagos mockingbird tolerance ultimately could have consequences for other host species in the community. Because tolerant hosts survive parasitism without reducing parasite populations, they may serve as reservoir hosts that contribute to the size of *P. downsi* populations, thus exacerbating the risk to smaller, more vulnerable hosts (53, 71).

Tolerance to *Philornis* may be widespread among native hosts. Clutch sizes in most Neotropical birds are smaller than those of temperate relatives, a difference that may be an adaptive response to greater parasite pressure in the Neotropics (87, 88, 103). Moss & Camin (91) showed that purple martins (*Progne subis*) hatch fewer eggs in a colony heavily infested with martin mites (*Dermanyssus prognophilus*) compared to a fumigated colony. Moreover, in large broods, parasitized martin nestlings weighed less than unparasitized nestlings, presumably because the parents were unable to provision all of the chicks. These experimental data indicate that the added burden of nest parasites may limit the number of chicks that parents can rear.

Darwin's finches have large clutch sizes compared to most other Neotropical passerines (51), possibly due to the absence of native parasites and predators. However, the introduction of *P. downsi* together with introduced predators such as rats and cats may mean that finch parents can no longer provision four or five chicks at once. If so, then it is possible that *P. downsi* will contribute to the evolution of smaller clutch sizes in Darwin's finches over time.

EFFECTS OF *PHILORNIS DOWNSI* ON HOST POPULATION DYNAMICS

P. downsi is a significant threat to the survival of several finch species in the Galápagos, such as the critically endangered medium tree finch and the mangrove finch (48, 74, 79, 99, 100). The situation for the mangrove finch is especially dire, with fewer than 100 individuals of this species known to exist (79). Although rat control efforts in the past 5 years have significantly decreased the risk of

Parasite burden:

a general term encompassing the more precise measures of prevalence, intensity, and abundance; also known as parasite load

predation of nestlings, *P. downsi* remains a significant threat to the species (48, 79). The current management strategy developed by the Charles Darwin Research Station, Galápagos National Park, and San Diego Zoo includes hand-rearing chicks in the laboratory to avoid parasitism (26).

Even common finch species may be vulnerable to local extinction due to *P. downsi*. A recent population viability model suggests that *P. downsi* has the potential to cause local extinction of medium ground finch populations on Santa Cruz Island within 100 years (74). Fortunately, however, the model suggests that even a modest decrease in *P. downsi* prevalence (30–40%) will reduce the threat considerably. Thus, reducing populations of *P. downsi* in the Galápagos should benefit host populations, even if *P. downsi* is not completely eradicated (see below).

Paradoxically, populations of the medium ground finch appear to be stable or even increasing, despite the effect of *P. downsi* on reproductive success (41). In the lowlands of Santa Cruz Island, the prevalence of *P. downsi* in nests is close to 100%, with the number of successful fledglings per parasitized nest ranging from zero to approximately 1.7 (74). What explains the resilience of the population in the presence of *P. downsi*? The answer may lie in the fact that Darwin's finches are relatively long-lived species and have large clutches for tropical birds (51). A prolific finch can hatch 45 nestlings over the course of her lifetime (51)! As a result, species such as the medium ground finch may be able to maintain reproductive rates greater than 1, even if fledging success in any particular clutch is low.

Kleindorfer et al. (65) suggest that Darwin's finch populations are evolving in response to selection by *P. downsi*. They report an apparent increase in hybridization between small and medium tree finches on Floreana Island, with fewer *P. downsi* in the nests of hybrids. Additional research is needed to explore the relationship between host hybridization and resistance and/or tolerance to *P. downsi*.

WHY IS *PHILORNIS DOWNSI* SO VIRULENT IN THE GALÁPAGOS?

It is commonly assumed that *P. downsi* is virulent in the Galápagos because naive hosts lack resistance and/or tolerance mechanisms (59). However, there is little evidence that native hosts are better defended against *Philornis* than Galápagos hosts. Although native hosts have occasionally been observed to remove larvae by preening (49, 112), mean intensities of *Philornis* from the nests of Galápagos and native hosts do not differ significantly across the studies we evaluated. These data suggest that once infested, native and nonnative hosts do not differ in their ability to reduce the parasite burden. Instead, some native hosts may be more tolerant to *Philornis* than Darwin's finches. Relatively low mortality from *Philornis* in native hosts indicates that some mechanism, such as reduced clutch size, may allow native hosts to compensate for effects of *Philornis*.

However, not all native hosts are tolerant to *Philornis*; a few studies document similar effects of *Philornis* in native and nonnative hosts (69). Prevalence of native *Philornis* populations is generally lower than in the Galápagos, potentially due to native enemies of *Philornis*, such as parasitoid wasps and ants, that are largely absent from the Galápagos (12, 31, 69). These enemies may serve as top-down controls on *Philornis* populations that then limit the effects of *Philornis* on native host populations. In summary, the high prevalence and virulence of *P. downsi* in the Galápagos may be a combination of enemy release from native predators and parasitoids that suppress native *Philornis* populations and a lack of tolerance in most endemic Galápagos hosts.

MANAGEMENT OF *PHILORNIS DOWNSI*

The development of effective control strategies for *P. downsi* is a major conservation priority in the Galápagos because of the threat this introduced parasite poses to endemic birds (14) (see the sidebar

THE *PHILORNIS* WORKING GROUP

Researchers from around the world are working to develop control strategies for *Philornis downsi* in the Galápagos. Efforts are coordinated through the *Philornis* Working Group, a collaboration of scientists from 15 institutions in eight countries, led by the Charles Darwin Foundation and Galápagos National Park. Workshops were conducted by this working group in 2012 and 2015 on Santa Cruz Island in the Galápagos. The workshops helped coordinate *P. downsi* research and highlight priorities for controlling *P. downsi* (7). Further information can be found at <http://www.darwinfoundation.org/en/science-research/invasive-species/philornis-downsi/>.

titled The *Philornis* Working Group). Although fumigation of nests with diluted permethrin has been used in several studies to experimentally reduce *P. downsi* abundance (45, 71, 76), broad-scale manual fumigation of nests is impractical. Knutie et al. (72) found that finches will readily incorporate permethrin-treated cotton into their nests and that treated cotton significantly reduces the intensity of *P. downsi*. The Charles Darwin Foundation and Galápagos National Park are investigating whether this self-fumigation technique can be used as a stopgap method to improve the reproductive success of the critically endangered mangrove finch. Although permethrin is considered to have extremely low toxicity for birds, its use carries at least some risk of inadvertent negative health effects for wildlife (including other native insects) as well as the evolution of resistance in *P. downsi* to permethrin (11, 15, 43, 60).

Trapping of *P. downsi* may also be an effective way to reduce fly populations in targeted areas (7, 14). Unfortunately, the efficacy of trapping has been limited by a lack of specific and attractive food baits (7). Two new volatile compounds derived from fermentative yeasts may improve trapping success in the future (17).

Other possible long-term control methods include sterile insect technique (SIT) or biological control of *P. downsi* (7, 14). SIT is a method in which sterilized males are released en masse as a form of birth control (42). This approach has been successful at eradicating screwworm (*Cochliomyia hominivorax*), another parasitic fly from North and Central America (42). The introduction of a biological control enemy of *P. downsi*, such as a parasitoid wasp, is also under consideration. A study of *Conura annulifera* (Hymenoptera: Chalcididae) suggested that this parasitoid wasp decreases *P. downsi* fitness and is fairly host-specific (12). However, both SIT and biological control require the rearing of significant numbers of *P. downsi* in culture, which is proving difficult (77, 121). Even if biological control proves viable, species introductions for biological control must be very carefully considered and monitored given the sensitivity of the Galápagos ecosystem (56).

SUMMARY POINTS

1. *Philornis* flies are widespread nest parasites of birds in the Americas.
2. Studies have explored the biology and effects of only approximately half of the 50 described species of *Philornis*.
3. *P. downsi* is an introduced parasite of land birds in the Galápagos Islands that poses a significant threat to populations of Darwin's finches and other endemic bird species.
4. The effects of *P. downsi* on Galápagos hosts are typically greater than those of native *Philornis* spp. on native hosts.

5. The severity of effects of *P. downsi* on Galápagos birds may be the result of enemy release, that is, a lack of *P. downsi* parasitoids or predators in the Galápagos.
6. Control measures for *P. downsi* are urgently needed to help endemic, endangered bird species such as the mangrove finch and medium tree finch.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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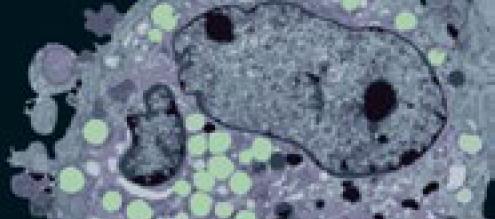
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