REVIEW

Additive negative effects of *Philornis* nest parasitism on small and declining Neotropical bird populations

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Summary

The declining-population paradigm holds that small populations are particularly vulnerable to anthropogenic influences such as habitat destruction, pollution and species introductions. While the effects of particular stressors, such as parasitism, may be unimportant in a large, healthy population, they can be serious and even devastating in situations characterized by a restricted geographic range, or by fragmented or reduced population sizes. We apply this idea to nest parasitism of threatened Neotropical bird species that exist in small populations, focusing on dipteran nest parasites in the genus *Philornis*. We review the literature on *Philornis* parasitism exerting negative pressure on bird populations that have become small and isolated due to human actions and present a new case of *Philornis* parasitism of a threatened hummingbird species. Our aim is to raise awareness about the exacerbating effect that nest parasites can have on small and declining bird populations; especially when biological information is scarce. The five reviewed cases involve two species of Darwin's Finches in the Galápagos Islands attacked by the invasive *P. downsi*, two species of hawks on islands in the Caribbean attacked by the native *P. pici* and *P. obscura*, and the Yellow Cardinal (*Gubernatrix cristata*) in southern South America attacked by an unknown *Philornis* species. We also present new documentation of parasitism of a threatened hummingbird species in mainland Ecuador by an unidentified *Philornis* species. We recommend more field studies to determine the presence of nest parasites in bird populations worldwide to improve understanding how nest parasites affect bird fitness and population viability and to allow time to act in advance if needed. Parasitism by *Philornis* may represent a severe mortality factor in most already threatened bird species, putting them at greater risk of extinction. Therefore, parasitism management should be included in all threatened species recovery plans.

Keywords: avian nest parasites, host-parasite interactions, Neotropics, *Philornis*.

Resumen

El paradigma de las poblaciones en disminución afirma que las poblaciones pequeñas son particularmente vulnerables a las influencias antropogénicas tales como la destrucción de hábitat, la contaminación y la introducción de especies. Mientras los efectos de estresores particulares, tales como el parasitismo, pueden no ser importantes en poblaciones grandes y saludables, éstos podrían ser devastadores en poblaciones que tienen un rango geográfico restricto, un tamaño reducido o que están fragmentadas. Aquí se aplica esta idea al parasitismo de nido en especies de aves Neotropicales amenazadas con poblaciones pequeñas, enfocándonos en los parásitos de nido del género *Philornis*. Revisamos casos en la literatura acerca del parasitismo de *Philornis* ejerciendo una presión negativa en poblaciones de aves que presentan un tamaño poblacional reducido o están aisladas debido a la acción humana y presentamos un nuevo caso de parasitismo de *Philornis* en una especie de colibrí en peligro de extinción. Nuestro objetivo es poner en relieve el efecto agravatorio que los parásitos de nidos pueden tener en poblaciones de aves reducidas y en disminución numérica, especialmente cuando la información biológica es escasa. Los cinco casos examinados incluyen dos especies de Pinzones de Darwin en las Islas Galápagos que son atacadas por la mosca invasora *P. downsi*, dos especies de gavilanes en islas del Caribe que son atacadas por las moscas nativas *P. pici* y *P. obscura* y el Cardenal Amarillo (*Gubernatrix cristata*) en el Sur de Sudamérica que es parasitado por una especie de *Philornis* desconocida. Además, presentamos nueva información de parasitismo en una especie de colibrí en peligro en Ecuador que es atacada por una especie de *Philornis* no identificada.

Recomendamos más estudios de campo a nivel mundial para determinar la presencia de parásitos de nido en poblaciones de aves con el objetivo de entender cómo estos parásitos afectan el fitness de las aves y la viabilidad de la población para actuar a tiempo de ser necesario. El parasitismo de *Philornis* puede representar un factor de mortalidad significativo que pone en mayor riesgo de extinción especies de aves que ya se encuentran en peligro. Por lo tanto, sugerimos que el manejo de parásitos sea incluido en todos los planes de recuperación de dichas especies.

Palabras claves: parásitos de nido, interacciones de huéspedes y sus parásitos, Neotrópico, *Philornis*

Introduction

Numerous species worldwide exist in small populations. In some cases this is a natural phenomenon that occurs in populations adapted to scarce or fragmented habitats. The small-population paradigm holds that these populations are at risk of extinction due to rareness or smallness as such (Caughley 1994). The effects of inbreeding depression, genetic drift and demographic stochasticity acting alone or together can reduce reproduction and increase mortality resulting in even lower population sizes which in turn leads to more inbreeding and greater effects of genetic drift, a process also known as the extinction vortex (Gilpin and Soulé 1986). Examples of naturally occurring small populations include the Lord Howe Woodhen (*Hypotaenidia sylvestris*), restricted to Lord Howe Island; the Straight-billed Reedhaunter (*Limnoctites rectirostris*), a furnariid that occurs in extreme south Brazil, south Uruguay and east Argentina in small marshes and swales, as well as short trees and shrubs bordering wet areas (Ridgely and Tudor 2009); and the South Georgia Pipit

(*Anthus antarcticus*), a bird that is endemic to the sub-Antarctic island of South Georgia. Another scenario, called the declining-population paradigm (Caughley 1994) posits that a population is in decline because something external to it has been modified. Low population sizes are often a consequence of anthropogenic influence such as habitat destruction, pollution, and invasive species, among others. Examples of the declining-population paradigm include the Critically Endangered Kakapo (*Strigops habroptila*), a parrot known to survive in only three small offshore New Zealand islands (Clout and Merton 1998). There were no land mammals in New Zealand prior to human settlement, except for bats. The combination of flightlessness, solo parentage, nocturnal behaviour, altricial young, and ground-nesting made Kakapo an easy target for mammalian predators which drove the species to the brink of extinction (Lloyd and Powlesland 1994, Clout and Merton 1998). Another example is the California Condor (*Gymnogyps californianus*), a species that in 1982 had a world population of 22 individuals (Snyder and Snyder 2000). The main threats to condors are persecution (shooting and poisoning), unintentional lead poisoning and loss of wildlands (Finkelstein *et al*. 2012). A third example is the North Island Brown Kiwi (*Apteryx australis mantelli*) which only remains scattered in small islands of forest and scrub left after large-scale forest clearance for farmland use in New Zealand's North Island (Potter 1990).

Once populations become smaller and more fragmented, interactions with other species such as predation, mutualism or parasitism can more strongly influence population trajectories and community structure (Bennet and Saunders 2010). A growing number of studies have focused on how a change in species abundance or the loss of a species can impact ecological processes in fragmented habitats. For example, fragmentation of habitats increases the amount of forest edge, which in turn, can change predator-prey relationships as these edges allow generalist predators access to birds that nest in these fragments (Andrén 1992, Flaspohler *et al.* 2001). Other effects of population declines include disruption in seed dispersal of large-seeded plants after reduction of frugivorous bird and bat species in subtropical rainforest fragments (Moran *et al.* 2009) and increased aggressive competition in bird communities in landscapes fragmented due to human activity (Maron and Kennedy 2007). Each situation is particular to region, taxa and context, which is why the effect of fragmentation cannot be easily generalized (Bennet and Saunders 2010).

Here we focus on the effect of *Philornis* nest parasitism on Neotropical bird species that are already present at low population sizes. Because parasitism exerts extra pressure on already small or declining populations, we call it an additive negative effect of parasitism, in agreement with Delannoy and Cruz (1991). While in a large population the effects of nest parasitism may be negligible; in fragmented and small size populations, its effects could be devastating. However, field studies focusing on the detrimental effects of parasitism on small and declining bird populations are few and scattered. We review five examples that illustrate this and include a new case not previously discussed in the literature. The six cases fit into the declining-population paradigm since for all cases, population sizes are extremely low. First, we discuss the introduction of *Philornis downsi* into the Galápagos Islands, emphasizing its effects on Mangrove Finch (*Camarhynchus heliobates*) and Medium Tree Finch (*C. pauper*) populations. Second, we discuss the case of *P. pici* parasitizing Ridgway's Hawk (*Buteo ridgwayi*) in the Dominican Republic. Third, we discuss the status of Sharp-shinned Hawk (*Accipiter striatus vennator*) populations in Puerto Rico parasitized by *P. pici* and *P. obscura*. Fourth, we discuss the Yellow Cardinal (*Gubernatrix cristata*) being attacked by an unidentified *Philornis* species in Argentina. There are other reports of unidentified *Philornis* species attacking rare or threatened bird species, including the parrot

Amazona vitatta in Puerto Rico (Snyder *et al.* 1987 cited by Delannoy and Cruz 1991) and the Choco Screech Owl (*Megascops guatemalae centralis*) in Ecuador (Reyes and Astudillo-Sánchez 2017) but we focus here on the published cases that present the most information (Table 1). Lastly, we include a newly reported case of *Philornis* parasitism on the endemic and rare Esmeraldas Woodstar (*Chaetocercus berlepschi*) of western Ecuador whose effects on host fledging rates are currently unknown (Fig. 1). The goal of this review is to raise awareness of the additional negative effects that nest parasites can bring upon bird populations that are small and declining, by accelerating the population decline.

Biology of Philornis *flies*

The genus *Philornis* is comprised of ~50 species of Neotropical muscid flies (Couri *et al.* 2007). Some information on the ecology and life cycle is known for about half of these, all of which are intimately associated with bird nests (Couri 1999, Teixeira 1999, Dudaniec and Kleindorfer 2006, Fessl *et al*. 2006a, Kleindorfer and Dudaniec 2016). While adult *Philornis* are free-living their larvae complete development within bird nests. The larvae of most species are parasites on nestlings, but at least two are coprophagous, feeding on excrement and other material within nests. The larvae of most of the parasitic species feed subcutaneously on nestlings, but in at least two species (*P. downsi* and *P. falsificus*) the late-stage larvae feed ectoparasitically on nestlings (Fig. 2). Collectively, *Philornis* species parasitize a broad range of landbird species in the Neotropical region that produce altricial young, but the host range can vary greatly among species (Dodge and Aitken 1968, Teixeira 1999, Dudaniec and Kleindorfer 2006, Löwenberg-Neto 2008, Bulgarella and Heimpel 2015).

Effects of Philornis *on host birds*

Philornis parasites can cause substantial levels of nestling mortality in host birds. The fitness effects imposed on bird populations varies greatly depending on which species of *Philornis* and host are involved (Dudaniec and Kleindorfer 2006, Kleindorfer and Dudaniec 2016, Manzoli *et al*. 2018). In addition, a number of ecological, demographic and behavioural factors determine the effects of *Philornis* parasitism on bird fitness. These include the per-nestling level of infestation (Arendt 1985, Fessl and Tebbich 2002, Fessl *et al*. 2006b, Koop *et al.* 2011, Knutie *et al.* 2016, Heimpel *et al.* 2017), the timing of nestling infestation (Arendt 2000, Kleindorfer *et al.* 2014a), parental provisioning in relation to parasite-weakened begging (O'Connor et al. 2014), sibling competition, *Philornis* spp. consumption by the birds (O'Connor et al. 2010a), and the availability of food for nestlings, which is itself often determined by environmental conditions (Arendt 2000, Dudaniec *et al.* 2007, Antoniazzi *et al.* 2011, Koop *et al.* 2013a, Manzoli *et al.* 2013, Cimadom *et al.* 2014).

Much of the information on *Philornis* effects on bird fitness has been gained from experimental field studies on *P. downsi* in the Galápagos Islands, where it is an invasive parasite of landbirds including Darwin's Finches (Kleindorfer and Dudaniec 2016; Fessl *et al.* 2018; McNew and Clayton 2018; see below). Larval feeding by *P. downsi* on Darwin's Finches can cause anaemia, beak scarring and death of infested nestlings (Dudaniec *et al.* 2006, Galligan and Kleindorfer 2009, Fessl *et al.* 2006b, Huber *et al.* 2010, Kleindorfer and Sulloway 2016). Mean nestling mortality is estimated at 55%, but it varies from 3% to 100% (reviewed by Kleindorfer and Dudaniec 2016). Population viability modelling has suggested that local or global extinction as a result of *P. downsi* infestation is a distinct possibility for some species of Darwin's Finches (Fessl *et al.* 2010a, Koop *et al.* 2016, see below).

Host responses to Philornis

Little is known about behavioural or physiological defences mounted by bird hosts to *Philornis* parasitism. Removal of *Philornis* larvae by adult birds (a behavioural defence) has been observed in Galápagos (O'Connor *et al*. 2010a). However, in most *Philornis*-host associations, this behaviour is considered not to occur at meaningful levels (Fraga 1984, Koop *et al.* 2013b, Fessl *et al.* 2018). Also in Galápagos, adult birds have been observed probing the base of the nest to remove larvae and nestlings compete to stand on top of each other in order to avoid larvae on the nest base, as recorded on video: https://www.youtube.com/watch?v=YfkMFxBZSns (Kleindorfer and Dudaniec 2016). Another potential behavioural defence involves the use of repellent substances by host birds. Certain birds place green materials in their nests; these are not part of the nest structure, but they are placed on the inside or the edges of the nest (Wimberger 1984). The nest protection hypothesis states that green plants decrease nest parasites or pathogens through their secondary compounds, benefiting the nestlings (Wimberger 1984). Cimadom *et al.* (2016) have recently discovered that some species of Darwin's Finches rub their feathers with leaves of an endemic Galápagos plant that has repellent properties to *P. downsi* and mosquitoes. The extent to which this activity protects these birds from *Philornis* infection is not known. In terms of physiological defences, brooding females of Darwin's Finches have been shown to produce antibodies in response to *P. downsi* infection in some studies (Huber *et al.* 2010, Koop *et al.* 2013b) but not others (Knutie *et al.* 2016, 2017). However, even in cases where an immune response was detected, this response was not effective at helping nestlings survive (Koop *et al.* 2013b).

Other bird species, however, seem to tolerate *Philornis* parasitism more easily. Several mockingbird species are attacked by various *Philornis* species (Fraga 1984, Löwenberg-Neto 2008, Bulgarella and Heimpel 2015). A recent study showed that *Mimus* *parvulus* and *M. gilvus* exhibited high levels of tolerance to *P. downsi* and *P. trinitensis*, respectively (Knutie *et al.* 2016, 2017). Nestlings of these species can tolerate heavy *Philornis* parasitism without suffering decreased fledging rates or weights although parasitism by *P. trinitensis* did reduce the length of the primary feather and tarsus of *M. gilvus* fledglings (Knutie *et al.* 2017). In a study done on the Galápagos Mockingbird, *M. parvulus*, nestlings in parasitized nests exhibited enhanced begging behaviour and this resulted in increased parental feeding, which can likely compensate for blood lost to parasitism (Knutie *et al.* 2016). Another study in central Argentina compared the resistance and tolerance of three host bird species that have co-evolved with *Philornis torquans* under natural conditions. Great Kiskadees (*Pitangus sulphuratus*) showed no detectable effect of larval infestation on survival, exhibiting tolerance rather than resistance to parasitism. On the other hand, two species of thornbirds (*Phacellodomus ruber* and *P. sibilatrix*) mounted inflammatory responses that demonstrate investment in a resistance response to *P. torquans* parasitism (Manzoli *et al*. 2018). Of the two thornbird species, *P. sibilatrix* exhibited less tolerance and presented lower parasite loads leading to lower effects of *Philornis* on survival, growth and mean virulence in this species than on *P. ruber*, which presented much higher numbers of larvae (Manzoli *et al*. 2018). Despite this difference, virulence was relatively high for both thornbird species, leading to substantial levels of host mortality. This study showed how a tolerant *Philornis* host (the Great Kiskadee) can serve as a 'reservoir host' that puts less tolerant hosts (thornbirds) at increased risk of attack by producing high numbers of parasites. A similar argument has been made for *P. downsi* and *P. trinitensis* attacking both larger-bodied tolerant host species and smaller host species that suffer more negative fitness effects of parasitism (Knutie *et al*. 2016, 2017; Heimpel *et al*. 2017).

Philornis downsi in the Galápagos Islands

As noted above, *P. downsi* is invasive in the Galápagos Islands where it was introduced from its native range in mainland South America sometime before or during the 1960s (Causton *et al.* 2006, Bulgarella *et al.* 2015, Kleindorfer and Sulloway 2016, Fessl *et al.* 2018). This parasite is having a stronger effect on various species of Darwin's Finches in Galápagos than it does on birds in its native range, possibly because it has escaped enemies such as parasitoids and possibly ants (Bulgarella *et al.* 2015, 2017, Delvare *et al.* 2017, Knutie *et al.* 2017). However, using in-nest videos in Galápagos, researchers found one instance in which small ants removed *P. downsi* larvae from a Darwin's Finch nest during the daytime (O'Connor et al. 2010a). Of the 17 recognized species of Darwin's Finches in Galápagos, 11 have been documented as hosts for *P. downsi* (Fessl *et al.* 2018). Of these, two – the Mangrove Finch and the Medium Tree Finch – are Critically Endangered and *P. downsi* is implicated in their declines as we discuss below. *Philornis downsi* has also been suggested as a possible contributing factor for island-level extinctions or near-extinctions of the Warbler Finch (*Certhidea fusca*) and Vegetarian Finch (*Platyspiza crassirostris*) and the Vermilion Flycatcher (*Pyrocephalus nanus*) on Floreana Island (Grant *et al.* 2005, Dvorak *et al.* 2017, Peters and Kleindorfer 2017) and is implicated in a steep decline of a Warbler Finch (*Certhidea olivacea*) population in the highlands of Santa Cruz Island (Cimadom *et al.* 2014). In addition, population viability analyses suggest that populations of the abundant Medium Ground Finch (*Geospiza fortis*) may go extinct within the next 50–100 years depending upon ecological conditions (Koop *et al.* 2016). It is also worth noting that recent genetic analyses of the Vermillion Flycatcher have shown that the San Cristóbal endemic (*Pyrocephalus dubius*) went extinct on the island of San Cristóbal sometime before the 1980's (Carmi *et al.*

2016). *Philornis downsi* is known to attack a sister species, the Vermilion Flycatcher (Fessl and Tebbich 2002) and is present on San Cristóbal (Wiedenfeld *et al.* 2007) making it conceivable that it played a role in the extinction of the San Cristóbal Vermillion Flycatcher.

The Mangrove Finch and the Medium Tree Finch in the Galápagos Islands

The Mangrove Finch (*Camarhynchus heliobates*) is one of the rarest bird species in the world, with an estimated population size of approximately 80 to 100 individuals (Dvorak *et al.* 2004, Fessl *et al.* 2010a, Cunninghame *et al.* 2017). It is classified as Critically Endangered on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species (henceforth IUCN Red List) (BirdLife International 2017). The Mangrove Finch is a habitat–mangrove forest–specialist (Young *et al.* 2013) with a historical small population, fitting in the small-population paradigm. The species distribution used to include mangrove forests on the islands of Fernandina and Isabela, however, it disappeared from Fernandina sometime in the 1990s (Grant and Grant 1997). The remaining Mangrove Finch population is currently restricted to two coastal mangrove forests on northwestern Isabela Island.

Both human-induced and natural causes have led to the decline of the Mangrove Finch. Among the human-induced factors, invasive species have been perhaps the most important, and this includes effects of Ship Rats (*Rattus rattus*) that are predatory upon the eggs and nestlings, the Yellow Paper Wasp (*Polistes versicolor*) that competes for food (Grant and Grant 1997), and critically, the fly *Philornis downsi* that produces high nestling mortality (Fessl *et al.* 2010a, Lawson *et al.* 2017). Grant and Grant (1997) also noted that cutting mangroves may have been particularly detrimental, especially in the Villamil area of southern Isabela, which is now devoid of Mangrove Finches. Natural causes include habitat alteration due to volcanic uplift and hybridization with the closely related Woodpecker Finch (*C. pallidus*, classified as Vulnerable by the IUCN Red List) (Lawson *et al.* 2017). These and other causes have all contributed to pushing this species to the brink of extinction (Lawson *et al.* 2017).

A recovery plan for the Mangrove Finch was developed in 2010 (Fessl *et al.* 2010b). Conservation management since has included successful rat control within the Mangrove Finch range and a trial translocation, where nine birds were relocated to an area previously occupied by the species in May 2010, in an attempt to increase its geographic range. Unfortunately, four of the birds returned to the source population and none have been sighted in the translocation area since November 2010 (Cunninghame *et al.* 2013). By 2011, with successful rat control adopted as a management technique, parasitism by *P. downsi* was identified as the main factor responsible for causing nest failures. A more intensive conservation approach, head-starting, started in 2014 aimed at keeping the population buoyant and viable in the short term (Cunninghame *et al.* 2015). In brief, this technique consists of collecting eggs and/or nestlings from wild nests, artificially incubating eggs and hand-rearing chicks in captivity followed by the release of the juvenile birds back into the wild (Cristinacce *et al.* 2008, Cunninghame *et al.* 2015, Fessl *et al.* 2018), effectively circumventing the critical nesting period when *P. downsi* larvae feed on nestlings. Over four seasons of head-starting, from 2014 to 2017, a total of 39 juvenile Mangrove Finches have been released back into the wild. Captive-reared individuals have been observed surviving into the following breeding season and breeding with wild-reared Mangrove Finches, which demonstrates the success of the technique (F. Cunninghame pers. comm.). However due to the remote location of the remaining Mangrove Finch population, head starting is expensive and logistically challenging, thus a long term and financially sustainable solution to control *P. downsi* in the Galápagos archipelago is urgently needed.

Another of Darwin's Finches in steep decline is the Medium Tree Finch (*Camarhynchus pauper*) also classified as Critically Endangered and restricted to fragmented forest patches in the humid highlands of Floreana Island (Lack 1947, Grant 1999, Dvorak *et al.* 2017, Peters and Kleindorfer 2017). Its estimated population size is approximately 3,900–4,700 individuals (Fessl *et al.* 2018). The Floreana Island *Camarhynchus* species have been studied almost annually since 2004, representing a long-term field study carried out in the Cerro Pajas region of Floreana from 2004 to 2016. Since 2004, 561 active nests have been monitored, of which 196 belong to Medium Tree Finch nests (Kleindorfer et al. 2014a). Therefore, an excellent record for this species is available. *Camarhynchus pauper* declined 52% between 2004 and 2013, with 10% increase since 2008. In 2013, an estimated total of ~419 males remained in the Scalesia forest habitat and ~2537 males on the entire highland habitat of Floreana Island (Peters and Kleindorfer 2017). The main concerns for this species include habitat degradation, predation and *Philornis* parasitism (O'Connor *et al.* 2010b). Floreana Island has the longest history of human habitation within the archipelago. Consequently, extensive clearance of the highland areas for agriculture left only fragmented and invaded habitats for mid-to-high elevation birds (O'Connor *et al.* 2010c). In addition, these habitats experienced invasion by introduced plants and predators and high levels of nest parasitism (O'Connor *et al.* 2010b). In one season, *P. downsi* parasitism was responsible for 41% mortality of Medium Tree Finch nestlings (O'Connor *et al.* 2010b). This species presents the highest *P. downsi* number per nest than any other bird species on Floreana Island. Medium Tree Finches presented significantly higher parasite intensity (54.7 ± 5.4) when compared with the more common species, Small Tree Finches (*C. parvulus*, 28.7

± 2.4) and Small Ground Finches (*Geospiza fuliginosa*, 31.0 ± 2.1) (Kleindorfer et al. 2014a). A 10-year study carried out from 2004 to 2013, demonstrated a decrease in host age at death from ~11 to ~5 day-old, an increase in parasite intensity from ~28 to ~48 parasites per nest, and an increase in host mortality from ~50% to ~90% (Kleindorfer et al. 2014a). Interestingly, nesting height was shown to predict *P. downsi* intensity in tree finch species on Floreana Island (Kleindorfer *et al.* 2016). The Medium Tree Finch presents the highest nesting height at the approximate altitude where traps catch the largest number of *P. downsi* flies, which suggests that the high number of parasites found on this species might be related to the parasite flight behaviour rather than specific host attributes *per se* (Kleindorfer *et al.* 2016).

Furthermore, Medium Tree Finch females preferentially pair with Small Tree Finch males (*C. parvulus*) driving asymmetrical introgression (Kleindorfer *et al.* 2014b, Peters *et al*. 2017). Interestingly, these hybrids had fewer *P. downsi* parasites per nest than pure Medium Tree Finch (Kleindorfer *et al.* 2014b). These studies suggest that hybridization may be favoured by natural selection if the hybrids present higher reproductive success due to lower parasitism. As a result, the Medium Tree Finch as a species could disappear through reproductive absorption (Kleindorfer *et al.* 2014b, Peters *et al*. 2017).

A recent study reported significant differences on the microbiome of *P. downsi* sampled from several host birds from the Galápagos Islands (Ben-Yosef *et al*. 2017). The *P. downsi* microbiome differed between the life stages (larval vs. adults) and according to the feeding guild of the host bird species. The microbiome of the insectivorous Green Warbler Finch, *Certhidea olivacea*, was significantly different from the microbiome of other Darwin's Finch species (including the Medium Tree Finch) whose diet presents varying levels of omnivory. It seems that currently, Medium Tree Finches are exposed to the same *P. downsi* microbiome as other sympatric host species. These findings could inform effective control strategies for this parasite and have implications for understanding novel evolutionary pressures on small host populations (Ben-Yosef *et al*. 2017).

Ridgway's Hawk in the Dominican Republic

Ridgway's Hawk (*Buteo ridgwayi*) is an endemic species that historically occurred only in Haiti and the Dominican Republic (Wiley and Wiley 1981, BirdLife International 2000). This hawk is presently extinct in Haiti (Keith *et al.* 2003). With an estimated population of ~200 breeding pairs (McClure *et al.* 2017), it is classified as Critically Endangered (BirdLife International 2017). Historically, Ridgway's Hawks inhabited a wide variety of habitats, being more common in mature secondary forest and small agricultural plots at elevations from sea level to 1,800 m (Wiley and Wiley 1981, Thorstrom *et al.* 2007, Woolaver *et al.* 2013). More than 90% of the original forest cover present in the Dominican Republic has been destroyed by the practice of slash-and-burn agriculture (Harcourt and Ottenwalder 1996). The combined effects of forest loss and human persecution including activities such as intentional killing of adults and nestlings as well as the disturbance of nests have restricted the hawk's distributional range to Los Haitises National Park and surrounding areas in the north-eastern Dominican Republic leading to inbreeding and a recent population bottleneck (Woolaver *et al.* 2013, 2015). A five-year-study (2005–2009) conducted at Los Haitises National Park monitored the breeding biology of this hawk species and reported human disturbance as the main cause of nest failure (43%), with parasitism by the native *Philornis pici* mentioned among other causes of nest failure (Woolaver *et al.* 2015).

Philornis pici was first described from Santo Domingo in the Dominican Republic by Macquart (1854). Its larvae feed subcutaneously and until recently little was known about its effect on bird fitness. It parasitizes bird host species in the orders Passeriformes, Columbiformes, Piciformes and Psittaciformes (Teixeira 1999). A study reported that *P. pici* parasitism reduced the fledging success of this hawk by 179% over one breeding season (Hayes *et al*. *In press*). Further monitoring and potential management options for this parasite are desperately needed. A recent translocation of 104 juvenile birds from Los Haitises to Punta Cana has been successful in increasing the geographic range of Ridgway's Hawk, with hopes this program will increase overall population sizes (McClure *et al.* 2017). A *Philornis*-contingent recovery plan should be put in place to ensure the continued survival of the Ridgway's Hawk as a species.

Sharp-shinned Hawk in Puerto Rico

The Puerto Rican Sharp-shinned Hawk (*Accipiter striatus vennator*) is an endemic subspecies of the North American Sharp-shinned Hawk, occurring only in Puerto Rico. It is a small hawk mainly restricted to mature and secondary forests in a few isolated areas of the main island of Puerto Rico. This subspecies has suffered a 40% population decline between 1985 and 1991 with an estimated population size of approximately 150 birds as of 1997 (Delannoy and Cruz 1991, Delannoy 1992, Bildstein and Meyer 2000, Fergurson-Lees and Christie 2001), leading to its classification as Endangered by the U.S. Fish and Wildlife Service (USFWS 1997). Several factors have contributed to its rapid decline, including road construction, logging activities, predation of eggs and nestlings by Pearly-eyed Thrashers (*Margarops fuscatus*) and parasitism by the Puerto Rican native parasites *P. pici* and *P. obscura* (Wiley 1986, Wiley and Wunderle 1993, Delannoy 1997).

A long-term study carried out at the Maricao Commonwealth Forest (from 1979 to 1983 and in 1985) determined prevalence, parasite load and impact of *Philornis* parasitism on Sharp-shinned Hawk nestling survival (Delannoy and Cruz 1991). Thirty nests were investigated over the study, 20 of which contained at least one *Philornis*-infested nestling. Just over half of the 75 nestlings in the study were infested and the average parasite load per nestling was ten larvae. Fledgling mortality was nearly four times higher in parasitized versus non-parasitized nestlings (61% vs. 18%, respectively) resulting in a significant effect of parasitism on fledging success. Delannoy and Cruz (1991) concluded that parasitism by *Philornis* constitutes an additive mortality source for the Puerto Rican Sharp-shinned Hawk and therefore it contributes to population declines of this subspecies (Delannoy and Cruz 1991). In fact, intensive population censuses conducted at the Maricao Commonwealth Forest between 2012 and 2014 reported no more than seven hawk individuals, suggesting that the Puerto Rican Sharp-shinned Hawk has basically disappeared from its known distributional range (Gallardo and Villela 2014). However, no new information on the *Philornis*-Sharp-shinned Hawk system is available since the 1980's and 1990's studies (Gallardo and Villela 2014). It is imperative to produce updated information on the effects of *Philornis* parasitism and establish a *Philornis*-specific management plan if needed to warrant successful population recovery.

Yellow Cardinal in Argentina

The Yellow Cardinal (*Gubernatrix cristata*) is a passerine endemic to southern South America. This species was historically found throughout Uruguay, southern Brazil and the espinal region (thorny deciduous shrubland forests) of central Argentina (Ridgely and Tudor 2009, Domínguez *et al.* 2015). However, for over a century extensive poaching of male

Yellow Cardinals for the illegal pet trade (Pessino and Titarelli 2006) combined with the destruction of its habitat for agriculture and cattle pasture (Domínguez *et al.* 2016) have severely affected this species. Yellow Cardinals are now very rare in Brazil; less than 300 individuals are believed to remain in Uruguay and the populations in Argentina are discontinuous and reduced in size (Domínguez *et al.* 2015). Thus, this species is currently classified as Endangered on the IUCN Red List (BirdLife International 2017) with an estimated population size of about 1,500–3,000 individuals. In addition, the Yellow Cardinal is also subjected to brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*) (Domínguez *et al.* 2015) and hybridization with its sister species, the Common Diuca Finch (*Diuca diuca*) in Argentina (Bertonatti and López Guerra 1997). Furthermore, in a study carried out during the 2011 and 2012 breeding seasons in the northern Argentinian province of Corrientes, four out of 18 nests (22%) examined presented parasitism by an unidentified subcutaneous species of *Philornis*. Of the four nests, only two fledged nestlings successfully (Domínguez *et al.* 2015). This study was the first to report *Philornis* parasitism on Yellow Cardinals. We recommend examining Yellow Cardinal nests throughout its distributional range to determine whether *Philornis* parasitism is ubiquitous or it only occurs in the Argentinian province of Corrientes.

Esmeraldas Woodstar in Ecuador

The Esmeraldas Woodstar (*Chaetocercus berlepschi*) is a rare hummingbird species endemic to lowland and foothill garúa forest in western Ecuador (Harris *et al.* 2009). Its distribution is small, restricted, and severely fragmented. The lowland humid forest habitat in western Ecuador is fast disappearing through clearing for agriculture and ranching (Becker and López Lanús 1997). For these reasons, the Esmeraldas Woodstar has been classified as

Endangered on the IUCN Red List. Population size is estimated to be ~250–299 individuals (BirdLife International 2017). Recently, we presented the first record of *Philornis* parasitism on the Esmeraldas Woodstar (Bulgarella *et al.* 2017).

During our studies in mainland Ecuador, we sampled previously used, wild bird nests once the breeding season finished at the Reserva Ecológica Loma Alta (1.85694 °S, 80.59938 °W), 17 km inland from the Pacific Ocean in Santa Elena province. A field technician for a different research project monitored a wild Esmeraldas Woodstar nest during the 2015 breeding season. After the fledglings left, the nest was collected on 24 May 2015. When disassembled and inspected a total of six fly puparia were found; no dead nestlings were found in the nest. Five of these puparia produced adult flies that had emerged prior to nest collection and the other puparium had an unemerged, unidentified parasitoid species inside. Photographs of the empty puparia were sent to Dr Brad J. Sinclair who confirmed that, based on the spiracular plates, these puparia belonged to a *Philornis* species (Fig. 3). Because we do not have the adult fly specimens we are not able to determine the *Philornis* species as the only taxonomic key is based on adult morphology (Couri 1999). Although nothing is known of the effects and/or prevalence of *Philornis* parasitism on the Esmeraldas Woodstar, we strongly recommend further field studies that follow nests of this unique species to make sure that nest parasitism is not interfering with successful breeding and intended population recovery.

Discussion

Additive versus compensatory mortality effects on hosts

Bird population sizes are limited by available habitat and food, and by the prevalence of natural enemies including predators, parasites and diseases (Gill 2007). The effects of dipteran nest parasites, including *Philornis*, has long been neglected in avian conservation efforts (Loye and Carroll 1995, 1998, Williams *et al.* 2012). To determine the effects of a parasite on a host population, it is important to know whether the parasite-induced mortality is additive or compensatory. This distinction matters because they have different consequences for the host populations. With compensatory mortality, the host population is not reduced by parasitism; whereas with additive mortality, the host population is reduced at a lower level in the presence of the parasite than in the absence of parasitism (Combes 2001). Some of the examples reviewed here are illustrative of the additive effects of *Philornis* parasitism on small and declining Neotropical bird populations, i.e., the mortality induced by *Philornis* reduces the bird population size below parasite-free levels. Of the six bird species or subspecies discussed in this review as case studies, additive rather than compensatory effects has been demonstrated for four species (Mangrove Finch, MediumTree Finch, Ridgway's Hawk, and Puerto Rican Sharp-shinned Hawk). The data available are not sufficient to distinguish between additive and compensatory mortality due to *Philornis* parasitism for the remaining two species (Yellow Cardinal and Esmeraldas Woodstar).

Direct and indirect effects of Philornis parasitism

The effects of *Philornis* parasitism are not restricted to reduced nestling growth and survival (Antoniazzi *et al*. 2011, Quiroga and Reboreda 2012, Rabufetti and Reboreda 2007, see Kleindorfer and Dudaniec 2016 for a summary of mortality rates in the Galápagos Islands). Birds that survive and fledge a nest infested by *Philornis* are still affected by parasitism.

Detrimental consequences during the nestling phase include reduced haemoglobin and hematocrit levels (Fessl *et al*. 2006b, Dudaniec *et al.* 2006), reduced red blood cell counts and boosted white blood cell counts in infected nestlings when compared to nestlings whose larvae were experimentally removed (Manzoli *et al*. 2018), lower body mass (Fessl *et al*. 2006b) and reduced feather and tarsus length (Koop *et al.* 2011). Therefore, infested nestlings might be less able to compete with siblings and beg for food which might contribute to early mortality and lower reproductive success (Koop *et al.* 2011).

No studies on the long-term effects of *Philornis* on nestlings that survive parasitism have been conducted for *Philornis* species with subcutaneous larvae. Studies of longer-term consequences on surviving birds are rare and mostly specific to the Galápagos birds-*P. downsi* system. As explained above, *P. downsi* is an ectoparasite but the first instar larvae feed inside the nestling nares. This feeding causes changes in beak structure such as enlarged nares and deformed/crossed beaks (Galligan and Kleindorfer 2009, Kleindorfer and Sulloway 2016). Overall fitness will be negatively impacted in birds with deformed beaks (Kleindorfer and Sulloway 2016) as these birds may have problems feeding, preening and singing. Darwin's Finches are songbirds and beak shape is associated with song characteristics and assortative mating (Christensen *et al*. 2006). Thus a change of naris size due to parasitism could have carry-over mate choice effects with possible individual- and population-level effects (Custance 2015).

Birds worldwide are vulnerable to nest parasitism

We focused on the effects of *Philornis* on small and declining populations of Neotropical birds but parasitic nest flies occur worldwide. Other dipterans whose larvae are obligate parasites on nestling birds include members of the families Calliphoridae (*Protocalliphora*), Muscidae (*Passeromyia*) and Neottiophilidae (*Neottiophilum*). The genus *Protocalliphora* has a Holarctic distribution that includes North America, Nearctic Mexico, Palearctic Europe, North Africa and temperate Asia, with 26 described species (Sabrosky *et al.* 1989). The genus *Passeromyia* occurs in Asia, South Africa, Australia, and the West Pacific (Pont 1974), and includes five species (Couri and Carvalho 2003). The genus *Neottiophilum* is Palearctic, with *Neottiophilum praestum* being the only described member of the family (Owen 1957). While these nest parasites collectively attack a variety of host species, the majority of host records are within the Passeriformes (Little 2008).

Two Canadian studies evaluated the effect of human-induced land disturbance on parasitism of Tree Swallows (*Tachycineta bicolor*) by *Protocalliphora* flies and are therefore relevant to our discussion. The first study compared the prevalence and intensity of *Protocalliphora sialia*, *P. bennetti* and *P. braueri* parasitism on Tree Swallows in a site disturbed due to oil sand mining in Alberta versus a control (undisturbed) site. Nests built on the disturbed wetlands were more heavily parasitized (harboured 60 to 72% more larvae) than control nests and infected nestlings presented reduced growth on the oil-sands-impacted wetlands than in the control site (Gentes *et al.* 2007). This case study shows how habitat destruction resulted in higher parasite infestation of nestlings by *Protocalliphora* spp. The second study followed the tri-trophic interactions among the same Tree Swallow species, its *Protocalliphora* parasites and their *Nasonia* parasitoid wasps along a gradient of agricultural intensification. The number of swallow fledglings, the abundance of *P. sialia*, and the level of *Nasonia* wasp parasitism were all negatively affected by the habitat loss, fragmentation and degradation associated with the intensification of agricultural practices (Daoust *et al.* 2012). In this case however, lower fledging rate in the presence of human disturbance could not be attributed to nest parasitism.

The effect of *Passeromyia* flies on rare bird hosts was investigated in Tasmania, where the endemic and Endangered Forty-spotted Pardalotes (*Pardalotus quadragintus*) are restricted to isolated populations, with approximately 1,500 individuals left in the wild due to past forest clearing and fragmentation (BirdLife International 2017). This species inhabits second-growth forest where nesting cavities are limited and individuals are thus forced to compete aggressively with the Striated Pardalote (*P. substriatus*) for cavities (Edworthy 2016a). In 2012, larvae of the endemic *Passeromyia longicornis* were found parasitizing both pardalote species. Prevalence of *P. longicornis* in nests of Forty-spotted Pardalotes was 87% during a study spanning three breeding seasons. Nestling mortality in nests harbouring *P. longicornis* larvae was 85%, highlighting the detrimental effect of this fly on the already low Forty-spotted Pardalote population (Edworthy 2016b).

Long-term management plans for bird populations subjected to nest parasitism

For bird species fitting into the declining-population paradigm that are under stress by habitat destruction or modification, the lack of high-quality nesting sites might influence offspring survival as the birds are forced to either build nests in sub-optimal habitats, increasing exposure to predators and/or parasites (as in the Tree Swallow example) or to fight for nest sites (as discussed for the Forty-spotted Pardalote), or a combination of both. Vertical habitat availability may be another key factor in species persistence, especially in range-restricted ones impacted by habitat loss at a horizontal scale. Intensive agriculture in the highlands of Floreana Island in Galápagos leads to shorter-statured *Scalesia* trees than those on Santa Cruz Island where agricultural practices do not occur directly in *Scalesia* habitat. The highest nesting bird species in the *Scalesia* forest of Floreana Island (the Medium Tree Finch) sustained the most *P. downsi* larvae, but such a pattern was not observed on the highest nesting bird species on Santa Cruz Island (Peters and Kleindorfer 2015). One study in central Argentina determined the drivers of *Philornis* parasite abundance at the microhabitat and community levels. In this case nest height had no effect on brood infection but there was a strong reduction in mean larval abundance as the average forest height increased (except in forests dominated by exotic species). These findings suggest that for *Philornis torquans* in this case, what matters is not the height at which the hosts are but rather the microenvironment associated with differential forest height (Manzoli *et al*. 2013).

Still very little is known on how nest parasites locate hosts and how they survive dry seasons in highly seasonal habitats (Loye and Carroll 1998, Fessl *et al.* 2018). It is imperative that more field studies worldwide determine the presence of nest parasites in bird populations with some extinction risk in order to take action in time if needed. Nests of already small and declining bird populations should be examined first. Mitigating actions might include manually removing larvae from nestlings, applying a mild insecticide to nests to kill the fly larvae (Cristinacce *et al.* 2009, Knutie *et al.* 2014), and the head-starting technique (Cristinacce *et al.* 2008). For invasive nest parasites like *P. downsi* in Galápagos, the introduction of specialized biological control agents (Bulgarella *et al.* 2017, Boulton and Heimpel 2017, Delvare *et al.* 2017; Heimpel 2017; Boulton et al. *In press*) or sterile male release may be feasible management options (Dudaniec *et al.* 2010, Lahuatte *et al.* 2016; Fessl et al. 2018).

By focusing on these six cases of *Philornis* parasitism on small, declining or isolated bird populations in the Neotropics, we aimed at highlighting how sensitive these particular populations can be to dipteran nest parasites and how parasites can lead to imminent extinction. *Philornis* parasitism is just one case of nest parasites affecting bird species worldwide. For such reason, it is crucial to learn more about nest parasite-host behaviour, their general biology and their interactions before bird populations become at risk and incorporate this knowledge in bird conservation programs. It is our intention to make researchers that are directly or indirectly involved in bird conservation aware of the implications of any conservation policy on the general health of bird populations and to highlight that parasitism is one of the many determinants of population well-being (Scott 1988). Biodiversity research needs more boots on the ground (Wilson 2017).

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Table 1. Information on *Philornis* species with additive mortality effects on species (or subspecies) of Neotropical birds of conservation concern. Common names in bold refer to the (sub)species discussed in the text.

Host bird species	*Philornis* species	Locality where the parasitism was studied	*Philornis* species native or exotic	Anthropogenic factors responsible for population decline	Population size estimate	IUCN Red List status	*Philornis*-induced mortality compensatory or additive	Relevant references
Mangrove Finch *Camarhynchus heliobates*	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction	~100 individuals	Critically Endangered	Additive	Dvorak *et al*. (2004), Fessl *et al*. (2010a), Cunninghame *et al*. (2017)
Medium Tree Finch *Camarhynchus pauper*	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction, habitat destruction	~3,900–4,700 individuals	Critically Endangered	Additive	Grant (1999), Dvorak *et al*. (2017), Peters and Kleindorfer (2017)

Woodpecker Finch (*Camarhynchus pallidus*)	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction, habitat destruction	~12,000 singing males on Santa Cruz Is.	Vulnerable	Additive	Dvorak *et al*. (2012), BirdLife International (2017)
Large Tree Finch (*Camarhynchus psittacula*)	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction, habitat destruction, changes in insect availability	~8,900 singing males on Santa Cruz Is.	Vulnerable	Additive	Dvorak *et al*. (2012), BirdLife International (2017)
Little Vermillion Flycatcher (*Pyrocephalus nanus*)	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction, changes in land use and the application of pesticides	~2,500-10,000 mature individuals	Vulnerable	Additive	BirdLife International (2017), Carmi *et al*. (2016)

San Cristóbal Mockingbird (*Mimus melanotis*)	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction	~5,300 mature individuals	Endangered	Compensatory	BirdLife International (2017)
Floreana Mockingbird (*Mimus trifasciatus*)	*P. downsi*	Galápagos Islands, Ecuador	Exotic, introduced	Invasive species introduction, habitat degradation	~250–1,000 mature individuals	Endangered	Compensatory	BirdLife International (2017)
Ridgway's Hawk *Buteo ridgwayi*	*P. pici*	Dominican Republic	Native	Forest loss and human persecution (intentional killing of nestlings, nest disturbance)	~200 breeding pairs	Critically Endangered	Additive	Woolaver *et al*. (2015), McClure *et al*. (2017)
Sharp-shinned Hawk *Accipiter striatus venator*	*P. pici*, *P. obscura*	Puerto Rico	Native (both species)	Road construction, logging activities	~150 individuals	Endangered by USFWS (not	Additive	Wiley (1986), Wiley and Wunderle (1993),

						categorized by IUCN)		Delannoy and Cruz (1991), Delannoy (1992, 1997)
Puerto Rican Parrot (*Amazona vittata*)	*Philornis* sp.	Puerto Rico	Native	Habitat loss, hunting, cage-bird trade	~50–70 individuals	Critically Endangered	Additive	Snyder *et al*. (1987), White *et al*. (2012)
Esmeraldas Woodstar *Chaetocercus berlepschi*	*Philornis* sp.	Western Ecuador	Native	Habitat clearing for agriculture and ranching	~250–299 individuals	Endangered	Insufficient data	BirdLife International (2017), this study.
Choco Screech Owl (*Megascops guatemalae centralis*)	*Philornis* sp.	Western Ecuador	Native	Habitat clearing for agriculture and ranching	Unknown for the subspecies	Not categorized by IUCN. Subspecies is rare in Ecuador where parasitism	Insufficient data	Reyes and Astudillo-Sánchez (2017)

						was discovered		
Yellow Cardinal *Gubernatrix cristata*	*Philornis* sp.	Northern Argentina	Native	Illegal removal of males from the wild for pet trade, habitat destruction for agriculture and cattle pasture	~1,500–3,000 individuals	Endangered	Insufficient data	Domínguez *et al.* (2015)

List of Figures

Figure 1. Map showing the six species of small and declining bird populations suffering the additive effects of *Philornis* parasitism in the Neotropics. Note: Galápagos Islands are not to scale. Photo credits: Mangrove Finch by Francesca Cunninghame, Medium Tree Finch by Sonia Kleindorfer, Esmeraldas Woodstar by Berton Harris, Ridgway's Hawk by Thomas Hayes, Sharp-shinned Hawk by Julio C. Gallardo, and Yellow Cardinal by Mariana Bulgarella.

Figure 2. Life cycle of *Philornis downsi* from egg to adult. Photo credits: Egg, larvae and pupae photos by Mariana Bulgarella, adult fly photos by Dave Hansen.

Figure 3. Photographs of puparia of an unidentified *Philornis* species found in an Esmeraldas Woodstar nest on mainland Ecuador. The left panel shows the lateral view of the puparium and the right panel the posterior end of the pupa with the anal spiracles. Photo credits: Mariana Bulgarella.