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Invasive Parasites and the Fate of Darwin's Finches in the Galapagos Islands: The Case of the Vegetarian Finch (*Platyspiza crassirostris*)

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ABSTRACT.—The Vegetarian Finch, *Platyspiza crassirostris* is a relatively unstudied Darwin's finch that appears to be in decline in the Galápagos Islands. We monitored 11 nests of Vegetarian Finches during 2013 and 2014 on Santa Cruz Island, Galápagos, and found that 10 of these were infested with an invasive parasitic fly, *Philornis downsi*. This is the first report of *P. downsi* attacking this bird species. The number of *P. downsi* in nests of Vegetarian Finches was higher than for other Darwin's finch species, but nestling mortality was relatively low. We hypothesize that both of these trends may be related to fact that the Vegetarian Finch is one of the largest-bodied species of Darwin's finches. We also consider the conservation implications of *P. downsi* parasitism for populations of vegetarian finches and other Darwin's finch species in the Galápagos Islands. *Received 11 April 2016. Accepted 16 September 2016.*

Key words: Darwin's Finches, Galápagos Islands, *Philornis downsi*, *Platyspiza crassirostris*, Vegetarian Finch.

Invasive species can have devastating effects on island avifauna and in some cases can lead to extinctions of endemic species (Warner 1968, Diamond and Veitch 1981). The Galapagos Islands are celebrated for their high level of bird endemism, with no species-level, human-mediated bird extinctions documented to date. Unfortunately, some species of Darwin's finches are now experiencing substantial population declines (Grant et al. 2005, O'Connor et al. 2010b, Dvorak et al. 2012, Cimadom et al. 2014, Kleindorfer et al. 2014). The most critically endangered bird species in the Galapagos—the Mangrove Finch, *Camarhynchus heliobates*—has been reduced to a population of <100 individuals, partly because of the parasitic fly *Philornis downsi* (Fessl et al. 2010). Another species, the Medium Tree Finch, *Camarhynchus pauper*, is also critically endangered, also partly as a result of the fly (O'Connor et al. 2010c). A recent population viability analysis suggests that even abundant species of Darwin's finches may suffer local extinction within the next century because of *P. downsi* (Koop et al. 2016).

Philornis downsi (Insecta: Diptera: *Muscidae*) is an avian nest parasite that is native to mainland South America (Bulgarella et al. 2015). In recent decades, it was inadvertently introduced to the Galapagos Islands, where it parasitizes most landbird species, including at least nine of the 13 species of Darwin's finches (Fessl and Tebbich 2002, O'Connor et al. 2010c). *P. downsi* females lay eggs in bird nests; upon hatching, the developing larvae feed primarily on nestlings, often killing them (Fessl et al. 2006b, Koop et al. 2011, Lincango et al. 2015). For all species of Darwin's finches that have been studied, a majority of nests are infested with *P. downsi*, and the average number of larvae per nest usually exceeds 20 (e.g., Cimadom et al. 2014, Kleindorfer et al. 2014). The level of infestation—both in terms of the proportion of nests attacked and the number of larvae per nest—is much higher than that found in the native range of the fly (Bulgarella et al. 2015).

Prior to this study, the following four species of Darwin's finches had not been investigated for parasitism by *P. downsi*—the Vegetarian Finch, *Platyspiza crassirostris*, the Large Ground Finch, *Geospiza magnirostris*, the Sharp-beaked Ground Finch, *G. difficilis*, and the Large Cactus Finch, *G. conirostris*. The lack of information on the Vegetarian Finch is noteworthy since this species

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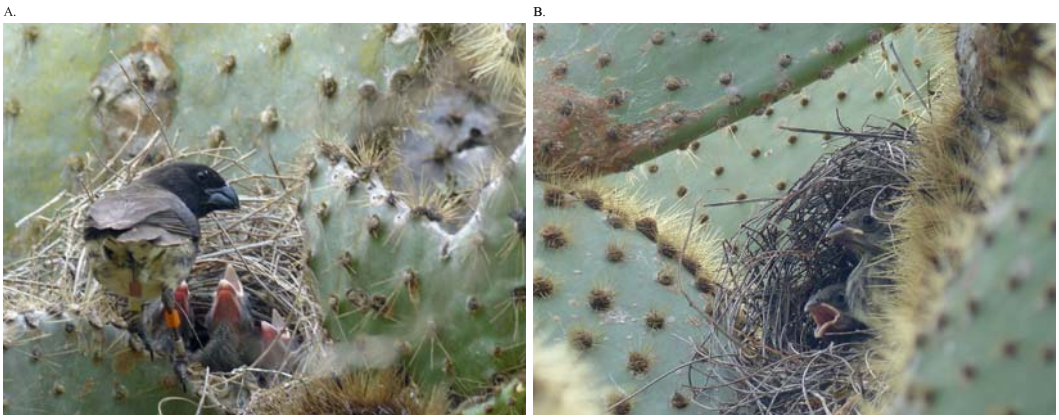

FIG. 1. (A) A male Vegetarian Finch, *Platyspiza crassirostris*, feeds a brood of chicks. (B) Two nestling Vegetarian Finches within 1 day of fledging. All of these nestlings shown here fledged successfully despite having supported 81 and 56 *P. downsi* larvae per nest, respectively. Photos: G. E. Heimpel.

has a historically wide distribution across the Galapagos archipelago (Grant 1986) and appears to be diminishing on some islands (Grant et al. 2005, O'Connor et al 2010b, Dvorak et al. 2012). The Vegetarian Finch is also one of the largest-bodied Darwin's finch species, and thus may support more fly larvae per chick than other species (Dudaniec et al. 2007, O'Connor et al. 2010c, Knutie et al. 2016). This, in turn, could contribute to higher population sizes of the fly in regions where Vegetarian Finches are abundant. Understanding the full range of hosts parasitized by *P. downsi* can provide a more complete picture of the risk to endemic birds in the Galapagos. It will also enable a greater understanding of potential parasite-mediated indirect interactions among the bird species.

METHODS

We monitored 11 nests of Vegetarian Finches at two lowland (arid) sites on Santa Cruz Island during the 2013 and 2014 breeding seasons. One site was adjacent to the Charles Darwin Research Station on the southern coast of the island ('El Barranco'; 0° 44′ 14.0" S 90° 18′ 4.1" W). The other site was relatively isolated on the south-eastern coast of the island ('El Garrapatero'; 0° 40′ 41.8" S 90° 13′ 29.7" W) (Knutie et al. 2014). We monitored three nests at El Garrapatero during 2013 and eight at El Barranco during 2014. Most nests had been constructed among pads of the endemic Galapagos tree cactus, *Opuntia echios giganteum*, and all were constructed as typical Darwin's finch dome nests (see Fig. 1). All but two nests were encountered in the egg or early nestling stage. We checked the status of active nests every two to three days to determine the number of eggs and/or nestlings present using an endoscopic fiber-optic camera with wireless monitor (shaft diameter 17 mm diameter, fiber-optic cable length 91 cm) mounted on a pole. Once nestlings appeared to be close to fledging age, nests were checked daily in order to record the date of fledging. When nests were empty, we scanned the area near the nest for fledglings and the area under the nesting site for dead nestlings (parents of some Darwin's finches sometimes discard dead nestlings; O'Connor et al. 2010a). At that time, we also collected the empty nests and placed them individually into plastic bags for transport to the laboratory. Since Darwin's finches do not re-use nests (Grant 1986), this procedure does not affect finch reproductive behavior. Nests were inspected at the Charles Darwin Research Station within 8 hrs of collection. Specifically, nests were dissected and dead nestlings and *P. downsi* were counted. *P. downsi* were categorized into three life stages, second instars, third instars, and puparia. Puparia were categorized as emerged or unemerged. The sum of the individuals from these life stages was used as a measure of abundance of *P. downsi*.

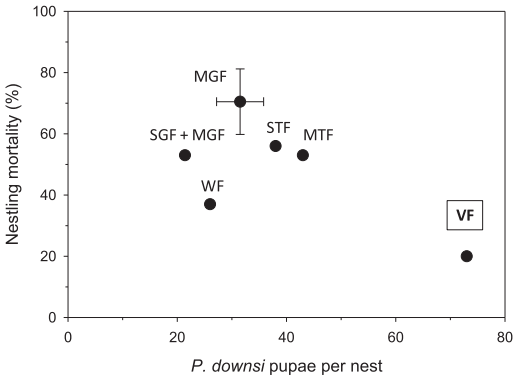

FIG. 2. Pupal number of *Philornis downsi* per nest and nestling mortality from studies of six species of Darwin's finches, including our own data from the Vegetarian Finch (VG). Other finch species are as follows. SGF: Small Ground Finch, *Geospiza fuliginosa*; MGF: Medium Ground Finch, *G. fortis*; WF: Warbler Finch, *Certhidea olivacea*, SGF: Small Tree Finch, *Camarhynchus parvulus*; MTF: Medium Tree Finch, *C. pauper*. Data on the Medium Ground Finch were averaged (+ S. E.) from five data sets contained in four studies (Koop et al. 2011, 2013a, b, 2016) and other data sets are from Fessl et al. (2006a), O'Connor et al. (2010c), and Cimadom et al. (2014).

RESULTS

Ten of the 11 nests that we monitored contained *P. downsi*; these included two of the three nests at El Garrapatero in 2013 and all eight nests at El Barranco in 2014. The mean abundance of *P. downsi* per nest was 71.3 + 12.1 (S.E.) individuals. The mean brood size was 2.8 + 0.3 chicks per nest, so each chick supported on average 26.1 *P. downsi* larvae (calculated across the 10 nests containing *P. downsi*). Although the number of parasites was high, the mortality of nestlings was relatively low. Out of 25 nestlings monitored over the course of the study, only five were found dead in the nests (20%), and these were all relatively small (estimated age <6 days) and exhibited substantial scarring from *P. downsi* (as in Fessl et al. 2006b). We observed fledged individuals from both of the infested nests at El Garrapatero, and two of the eight infested nests at El Barranco. We cannot exclude the possibility that dead nestlings were discarded by their parents from some of these nests (O'Connor et al. 2010a); however, this is unlikely because the 20 nestlings appeared healthy until the day before they were not seen in the nest (see Fig. 1B), and we did not find any dead nestlings on the ground near the nests. We suspect that instead we failed to locate some of the recently fledged birds.

DISCUSSION

Our study documents the first known cases of *P. downsi* parasitizing nests of Vegetarian Finches. This discovery adds another species to the list of Darwin's finches that are attacked by *P. downsi* (now 10/13 species). We found that *P. downsi* infested nests of Vegetarian Finches at two sites on Santa Cruz Island in the arid zone near the coast. The Vegetarian Finch is known to live in similar habitat on nine other Galapagos Islands (Grant 1986), and since *P. downsi* is found on those islands as well (Wiedenfeld et al. 2007), it is likely that Vegetarian Finches are parasitized throughout the archipelago.

Our results show a relatively high abundance of *P. downsi* coupled with relatively low nestling mortality. A comparison between our data set and those involving *P. downsi* attacking other Darwin's finch species shows that the Vegetarian Finch exhibits the highest number of parasites per nest, and the lowest nestling mortality out of the studies in which both of these quantities are published (Fig. 2). High numbers of *P. downsi* per nestling correlates with nestling mortality across other Darwin's finch species (Dudaniec et al. 2007) and here again, the effect of *P. downsi* on Vegetarian Finches appears to be relatively low. In other Darwin's finch species, nestling mortality is at least 45% with a range of 12–37 *P. downsi* per nestling (Dudaniec et al. 2007). In comparison, our values for the Vegetarian Finch were 20% nestling mortality and 26 *P. downsi* larvae per nestling. Together, these comparisons suggest a higher host tolerance of *P. downsi* in Vegetarian Finches compared to the other Darwin's finch species.

Higher abundance of *P. downsi* in nests of Vegetarian Finches compared to smaller finch species is consistent with the idea that larger birds support more *P. downsi* larvae (Dudaniec et al. 2007). Knutie et al. (2016) recently showed that *P. downsi* does not affect fledging success of Galápagos Mockingbirds (*Mimus parvulus*) despite relatively high numbers of *P. downsi*. The nestling mass of Galápagos Mockingbirds is approximately twice that of medium-sized ground finches (and greater than Vegetarian Finch nest-

lings); thus, the apparent tolerance of Galápagos Mockingbirds to *P. downsi* is hypothesized to relate to their larger body size (Knutie et al. 2016).

Mortality because of parasitism by *P. downsi* can be affected by a number of other variables in addition to body size, including the number of nestlings per nest, timing of parasitism, and food available to the foraging parents (Fessl and Tebbich 2002, Dudaniec et al. 2007, O'Connor et al. 2010c, Koop et al. 2013a, Cimadom et al. 2014, Knutie et al. 2016). Our study included a year (2014) with an intense but short rainy season, leading to unusually high insect availability (despite their name, Vegetarian Finches feed insects to their chicks). Increased nestling provisioning may have allowed parents to compensate for energy lost through blood feeding of the parasite, which has been shown in Galapagos Mockingbirds infested with *P. downsi* (Knutie et al. 2016).

Our observations have implications for the threat of *P. downsi* to the endemic avifauna of the Galapagos for two main reasons. First, our study shows that the Vegetarian Finch is a suitable host for *P. downsi* and may be under threat from the parasite. While the mortality imposed on Vegetarian Finches by *P. downsi* is lower than what is experienced by other species of Darwin's finches, it is still substantial at 20%. As noted, food availability appeared to be particularly high during one of the years of our study, and this may have contributed to lower-than-usual mortality of nestlings. Vegetarian Finches are declining on at least two Galapagos Islands that support a high incidence of *P. downsi* – Santa Cruz and Floreana (Grant et al. 2005, O'Connor et al 2010b, Dvorak et al. 2012). Our study suggests that parasitism by *P. downsi* should be considered a possible contributor to these declines. Second, our study shows that nests of Vegetarian Finches appear to support a higher number of *P. downsi* larvae than the nests of other Darwin's finch species. Vegetarian Finches could therefore act as reservoir hosts for *P. downsi*, putting disproportionate indirect pressure on co-occurring hosts of *P. downsi* through parasite-mediated apparent competition (Hatcher et al. 2006). Just such a scenario has recently been suggested by Knutie et al. (2016) for Galapagos Mockingbirds, which appear to suffer no negative consequences from infection by *P. downsi*. The 11 nests of Vegetarian Finches that we monitored in our study alone produced over 700 *P. downsi* larvae, illustrating the potential contribution of just a handful of such nests to overall fly population size.

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